



# MESOZOIC SPIDERS

SPINNEN DES ERDMITTELALTERS



BEITR. ARANEOL., 9 (2015)

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# **MESOZOIC SPIDERS (ARANEAE)**

## **ANCIENT SPIDER FAUNAS AND SPIDER EVOLUTION**

PAPERS ON FOSSIL AND EXTANT ARANEAE AS WELL AS FOSSIL  
AMBLYPYGI, RICINULEI, SCORPIONES AND UROPYGI

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### **FOSSILE SPINNENFAUNEN UND DIE EVOLUTION DER SPINNEN**

ARBEITEN ÜBER FOSSILE UND HEUTIGE SPINNEN SOWIE FOSSILE  
GEISSELSPINNEN, KAPUZENSPINNEN, SKORPIONE UND GEISSELSKORPIONE

JOERG WUNDERLICH (ed.)

**The photos on the book cover show Mesozoic spiders in Burmese amber of the Mid Cretaceous:**

AT THE TOP LEFT: Male of the ancient family Psilodercidae, *Leclercera ellenbergeri* n. sp., body length 1.4 mm. Note the quite long and thin legs of this excellently preserved male!

AT THE TOP RIGHT: Female of the extinct family Lagonomegopidae, *Picturmegops signatus* n. gen. n. sp., body length 3.6 mm. Note the excellently preserved distinctive colour pattern on the prosoma and on the opisthosoma which is caused by hairs! This colouration had probably two different functions, see the family below.

IN THE MIDDLE LEFT: Female of the ancient family Archaeidae, *Burmesarchaea grimaldii* (PENNEY 2003), body length 2.8 mm. Note the special position of the chelicerae, the scutate body and the opisthosomal furrows!

IN THE MIDDLE RIGHT: Male of the extinct family Lagonomegopidae, *Lineaburmops hirsutipes* n. gen. n. sp., body length 5 mm. The peculiar extinct spider family Lagonomegopidae was very diverse in genera and in the shape and the colour as well as in other characters in the age of the dinosaurs during at least 70 million years in the Cretaceous. Note the beautiful preserved bands of white hairs on the prosoma!

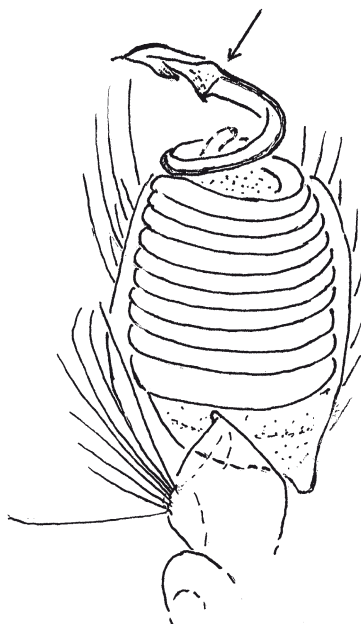
AT THE BOTTOM LEFT: Male of the family Uloboridae, *Paramiagrammopes patellidens* n. sp., body length 2.2 mm, the member of an extinct genus. All genera shown on this cover are extinct).

See also the next page: the cover photo AT THE BOTTOM RIGHT!

## The fossil spider of the year 2015

(selected by the editor and friends):

This peculiar male fossil spider, dorsal aspect, body length only 2.8 mm, lived 100 million years ago in a rain forest of Myanmar (Burma). It is first described in this volume as *Burmadictyna excavata* of the extinct Cretaceous family Sal-ticoididae, a group of orb-web weaving spiders.



What is unique in this spider species? From certain structures of the male copulatory organ we can conclude a special mating behaviour of this species which is known to be similar in some spiders of today. This behaviour concerns the most important part of the male copulatory organ, the EMBOLUS of the pedipalpus (see the drawing above) which has the main function of a penis: it transfers the sperm to the female copulatory organ.

The embolus of this fossil male has quite an unusual structure:

(a) It is coiled in 12 loops of spirals which build a long cylinder. I estimate that this genital part represents 3.5 (!) times the length of the spider's body. No one knows the reason for the evolution of such a long introductory structure of the male genital organ, and how it was used by the spider!

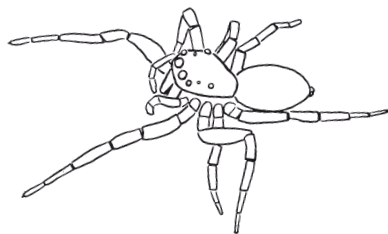
(b) The apical part of the embolus (arrow in the drawing) is strongly modified and widened, bearing barbs in a harpoon-shaped structure. It has a basal constriction, which I regard to be connected with a breaking line in this area. – What about the function of this structure?

Male spiders of several families of today – frequent orb weavers – are known to possess a very special behaviour in connection with a peculiar part of their embolus: A part of this copulatory organ breaks off and is left within the genital duct of the female after copulation. Such a „mating plug“ is considered to prevent the intromission of sperm by other males, to secure the development of offsprings only of its own. Furthermore it is a peculiar case of GENITAL SELF-MUTILATION, and the same pedipalpus is probably not usable for a further copulation. Such structures exist at the end of both emboli in all the three known fossil males of this genus; so we may conclude that none of them did have sex. The present male (photo) is the first proof of such a behaviour in fossil spiders. It demonstrates that the use of mating plugs is a very old behaviour in spiders, dating back at least 100 million years. –The spider is described p. 314-317.



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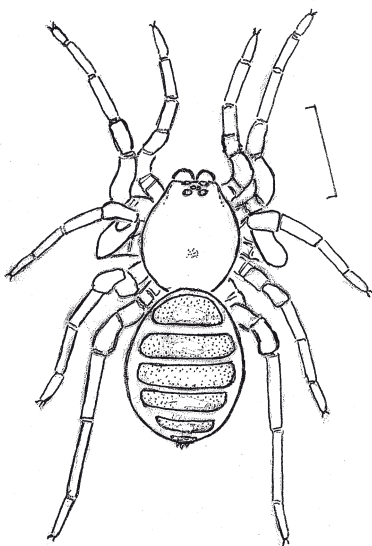
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## INTRODUCTORY REMARKS

In this volume predominantly various fossil spiders from different eras and areas – preserved mainly in Cretaceous amber from northern Myanmar (Burma, Birma) – are described or revised by the editor of this volume. A paper on an extant spider by A. TANASEVITCH and the editor, two papers by the editor, a paper on Cretaceous Amblypygi, Ricinulei and Uropygi: Telephonida by the editor and three papers on Cretaceous Scorpiones by W. LOURENÇO are also included in this volume.

The main subject treated in this volume has been chosen as the title of this book.

Further reading: See the back cover of this volume!



Reconstruction of a juvenile fossil mesothelid spider (the first fossil report of the „segmented spiders“ in amber (suborder Mesothelae, family Liphistiidae: *Cretaceothele lata* n. gen. n. sp.) in 100 million years old Burmese amber from Myanmar, body length 1.6 mm, dorsal aspect. The adult spider would probably have been more than two cms long. Note the dorsal opisthosomal plates of this ancient spider in which a distinct opisthosomal segmentation has been retained in contrast to all „advanced“ spiders. Therefore these peculiar spiders may be called „living fossils“; they are restricted to the tropics today. See the description below, p. 101-103 and the photos 10-13.

## DESCRIPTION OF AN UNUSUAL FOSSIL CRAB SPIDER (ARANEAE: THOMISIDAE S. L.: STEPHANOPINAE) IN EOCENE BALTIC AMBER

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**Abstract:** The taxa *Syphax secedens* n. sp. of the Syphaxini n. trib. (Araneae: Thomisidae s. l.: Stephanopinae) in Eocene Baltic amber are described, Syphaxini is supposed to be an old branch of this family. Few specimens of – predatory, parasitic? – insects (Hymenoptera?) are reported which are enclosed in the prosoma of the holotype of *S. secedens*.

CJW = collection of J. WUNDERLICH.

Photos: A MINOLTA camera SRT 101 (reflex camera) was used for the production of slides – KODAK professional 100 which were scanned -, a binocular microscope of LEITZ, and lighting by a twin flexible-arm illuminator with LED sources, CL-41, from OPTICA microrcopes, Italy.

Acknowledgements: For very helpful discussions I thank PETER JÄGER and PEKKA LEHTINEN, for leaving the male of *S. secedens* I am grateful to MARIUS VETA (Lithuania).

Crab Spiders (Thomisidae) in Eocene Baltic amber are rather rare, adult spiders are even extremely rare, see WUNDERLICH (2004, 2008). Probably the members of this family – at least the ancient members of the Stephanopinae (see below) – lived at the ground at that time (and therefore were only rarely captured by the fossil resin) in contrast to several advanced taxa of today – like *Heriaeus* and some *Xysticus* – which live in higher strata of the vegetation.

*Syphax* is an extinct genus of the tropical subfamily Stephanopinae; this subfamily is extinct today in Europe. Juveniles of *Syphax* are not too rare; the male is described here for the first time.

Provisional key to the thomisid genera in Baltic and Bitterfeld ambers except *Succiniraptor radiatus* (KOCH & BERENDT 1854): See WUNDERLICH (2004: 1751).

## **SYPHAXINI n. trib.**

**Type genus** (by monotypy): *Syphax* KOCH & BERENDT 1854.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (figs. 9–11): Tibial apophysis completely absent, patella with a large two-partite ventral apophysis, cymbium and bulbus small and slender, bulbus with at least three apophyses in a distal position, embolus relatively short, slightly bent, in a distal position.

Further important characters: Prosoma (figs. 2–4) narrowed anteriorly, clypeus very long, anteriorly and laterally strongly sloping vertically, basal cheliceral articles slender and fairly long, eyes: anterior laterals distinctly the largest, median eyes small, chelicerae and fangs long and slender, teeth of the fang furrow hidden, feathery hairs absent, legs (photo): Position probably (!) laterigrade, I (and most probably II) quite large, claw tufts and scopulae (figs. 6-7, photo) well developed, bristles numerous, fairly short and stout on leg I, few short and indistinct trichobothria, metatarsal trilobate membrane absent, coxa-trochanter autotomy, opisthosoma only partly preserved, covered with thin hairs, tutaculum absent.

**Ecology and behaviour:** The long legs I and II combined with the short leg IV – as well as the existence of dense claw tufts and leg scopulae, see WOLFF et al. (2013) – point to a sit-and-wait prey capturing behaviour like in other Thomisidae. The rareness of these species in the fossil resin as adult spiders – only the holotype is known – may be caused (a) by the relatively large body size of these spiders, and (b) by the ground-living habitat of these spiders. Mainly juvenile thomisid spiders are known from the Baltic amber which may have been blown by the wind into the fossil resin as ballooners, see WUNDERLICH (2004: 68-70, 1752).



**Relationships:** The indistinct leg trichobothria are apparently a typical character of the Thomisidae s. l. According to the well developed claw tufts and leg scopulae I regard Syphaxini as a member of the Stephanopinae, related to the Stephanopini. In the Borboropactini leg I is distinctly the largest, II is smaller, the femora, the tarsal trichobothria, the eyes, and the male pedipalpus are distinctly different, see WUNDERLICH (2008: 482). Derived thomisid characters like stout basal cheliceral articles and a tutaculum are absent in the Syphaxini. The absence of a pedipalpal tibial apophysis and the presence of a ventral patellar apophysis are unique within the Thomisidae.

Note: A retroventral tibial apophysis of the male pedipalpus exists also in the genus *Halodromus* MUSTER 2009 (extant, S-Europe) of the family Philodromidae, in which (e. g.) the size and the position of the eyes are different, the legs III and IV are longer compared with I and II, the bristles are long and slender, and a RTA exists.

**Distribution:** Eocene Baltic amber forest.

**Syphax** KOCH & BERENDT 1854

The gender of the name is masculine.

**Type species:** *Syphax megacephalus* KOCH & BERENDT 1854 (a single juvenile as the holotype).

Further species: *Syphax* is a „sampling genus“ of five species which are originally included, besides the type species *fuliginosus*, *gracilis*, *radiatus* and *thoracicus*. Most species are based on juveniles whose determination – even to the generic level – may be unsure; the present male is the first known male of the genus. Therefore the real number of described congeneric species is unknown. *Radiatus* (= *paradoxus* WUNDERLICH 2004) has been chosen as the generotype of *Succiniraptor* WUNDERLICH 2004 (under Borboropactidae) (\*), see WUNDERLICH (2008) (\*\*). *Fuliginosus*, based on a single specimen, has a body length of 7.4 mm, and – according to its large size – may be the single adult specimen (a female) of *Syphax* known by KOCH & BERENDT (1854).

-----  
(\* ) The family Borboropactidae WUNDERLICH 2004 – see WUNDERLICH (2004:1738-1740) and (2008: 482-483) – has not been accepted by LEHTINEN and has been downgraded to a tribe of the thomisid subfamily Stephanopinae. I am not sure if this downgrading is justified. According to the strong teeth of both margins of the fang furrow, the well developed claw tufts (existing in the Dietinae, too), and leg scopulae as well as probably the not distinct laterigrade leg position in my opinion Stephanopidae may well be a family of its own and may probably include the Borboropactinae at a subfamilial level.

(\*\*) Note that in the paper by WUNDERLICH (2008: middle part of p. 479) „the hitherto unknown female of *Syphax radiatus*“ has to be corrected to „the hitherto unknown MALE of *Syphax radiatus*“.

**Diagnosis and relationships:** See the new tribe.

**Distribution:** Eocene European amber forests (Baltic and Bitterfeld ambers).

***Syphax secedens* n. sp.** (figs. 2-11), photos 1-7

**Etymology:** From *secedens* (lat.) = apart, different, according to the relationship of the species being quite apart from all other known members of the Thomisidae.

**Material:** Male holotype in Eocene Baltic amber, F2542/BB/CJW; probably later on SMF.

**Preservation and syninclusions** (photos, figs. 1 and 5): The spider is preserved in a clear yellow piece of amber which is 3.2 cm long and was heated. The spider's legs are spread sideways. The prosoma, the right leg III and the left leg IV are preserved almost completely, the right leg II and the left leg III have been lost by autotomy beyond the coxa, several articles of the other legs are cut off and the opisthosoma is cut off through the middle. Remains of the left legs I and II apparently stuck out from the surface of the fossil resin after its embedding and their cuticula is oxidated. A longitudinal fissure through the spider's body became more indistinct after contact with benzylum benzoicum. Opisthosoma and prosoma of the spider are filled with resin. The anterior part of the opisthosoma (fig. 5) and the posterior part of the prosoma are broken off within the resin (their margins are irregular), the petiolus is lost. Because of this special kind of preservation one can look through the opisthosoma from behind at the inner part of the prosoma. Few legs (fig. 1) and opisthosomas of at least two small insects indet. (ants or other Hymenoptera?) are preserved inside (!) the prosoma of the spider. These – parasitic or predatory? – specimens will have to be studied in the future. – Few stellate hairs, tiny bubbles and a transparent tube-shaped structure are preserved in the same piece of amber.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (figs. 9-11): Patella with a divided ventral apophysis, bulbus – besides the almost straight embolus – with 3 or 4 apophyses in a distal position.

### **Description** (♂):

Measurements (in mm): Body length ca. 6.5, prosoma: Length 3.8, width 3.1; opisthosoma: Length probably ca. 3.0, width 2.8, height 2.0; leg I: Femur 3.8, patella 1.5, tibia 3.4, metatarsus ca. 2.1, tarsus ca. 1.0; femur II ca 4.0; tibia III 1.8; leg IV: Femur 2.6, patella 1.1, tibia 2.1, metatarsus 1.6, tarsus 1.0.

Colour: Prosoma and legs dark brown (legs not annulated), opisthosoma light brown. Prosoma (figs. 2-4, photos) 1.2 times longer than wide, anteriorly abruptly narrowed, cephalic part only slightly raised, hairs short, thin and indistinct, feathery hairs absent, cuticula finely scaly, 8 eyes in a wide field, posterior row distinctly recurved, lateral eyes large, on humps (especially the anteriors) and well separated from each other,

anterior laterals largest, anterior medians directed forward, fovea hidden, clypeus long and vertically sloping anteriorly and laterally, basal cheliceral articles long and slender, probably existing teeth of the fang furrow hidden by long hairs, fangs fairly long, other mouth parts partly hidden, gnathocoxae fairly long and fairly converging, I did not recognize a serrula, labium about as long as wide, sternum ca. 1.3 times longer than wide, not protruding between the coxae, coxae IV close together. – Legs (figs. 6-8, photos): Position probably (!) laterigrade, order I/II (probably I ca. = II)/IV/III, I quite long, III distinctly shortest, IV distinctly shorter than I-II, trochanters not notched, coxa-trochanter autotomy existing on two legs, hairs short, feathery hairs absent, unpaired tarsal claws absent, paired claws with ca. a dozen teeth, densely developed false claw tufts of apparently thin hairs, dense pseudoscapulae (thin hairs) exist on tarsi and metatarsi (distal half), they are more densely developed on legs I-II and distinctly divided longitudinally. Trichobothria indistinct; I found a single questionable apical trichobothrium on the metatarsi (fig. 7), its position in 0.95, but no sure one on the tarsi although few ones may exist; tibial trichobothria not studied more closely, apparently quite short/indistinct. Bristles numerous and only fairly long, quite thin on III and IV, existing on femora (almost stout on I-II), patellae, tibiae and metatarsi; leg I: Femur dorsally 2, prolaterally 5, retrolaterally 1, apically 2, tibia ventrally 5 pairs including an apical pair, dorsally 2, prolaterally 4 including an apical one, retrolaterally 3 including an apical one, metatarsus ventrally 2 pairs, laterally 1 pair, apically a garland of 5 short bristles, leg IV: Femur 6, tibia ca. 1 dozen, metatarsus prolaterally 2, ventrally 2 and apically a garland of ca. 5 short bristles. – Opisthosoma (fig. 5, photos) (the posterior half is lost) slightly depressed dorso-ventrally, hairs short, thin and scarce, feathery hairs absent. – Pedipalpus (figs. 9-11) (see also above) with stout articles, femur straight, tutaculum absent. The sclerite which is called median apophysis here may be divided. The embolus is guided by a longitudinal furrow of the cymbium.

**Relationships** ( see above, „Further species“). In *S. megacephalus* (juv. holotype) the clypeus is distinctly shorter than in *secedens*, and in *S. fuliginosus* (female) the clypeus is fairly shorter than in *secedens* which may be closely related. I do not want to exclude that the differences (the long clypeus of the large *S. secedens*) are caused by allometric growth. According a note by KOCH & BERENDT (1854: 80) regarding *gracilis* the two juvenile syntypes may be members of another genus. According to a note by KOCH & BERENDT (1854: 80) regarding *thoracicus* the chelicerae are hidden and the eyes are only partly observable.

**Distribution, ecology and behaviour:** See above.

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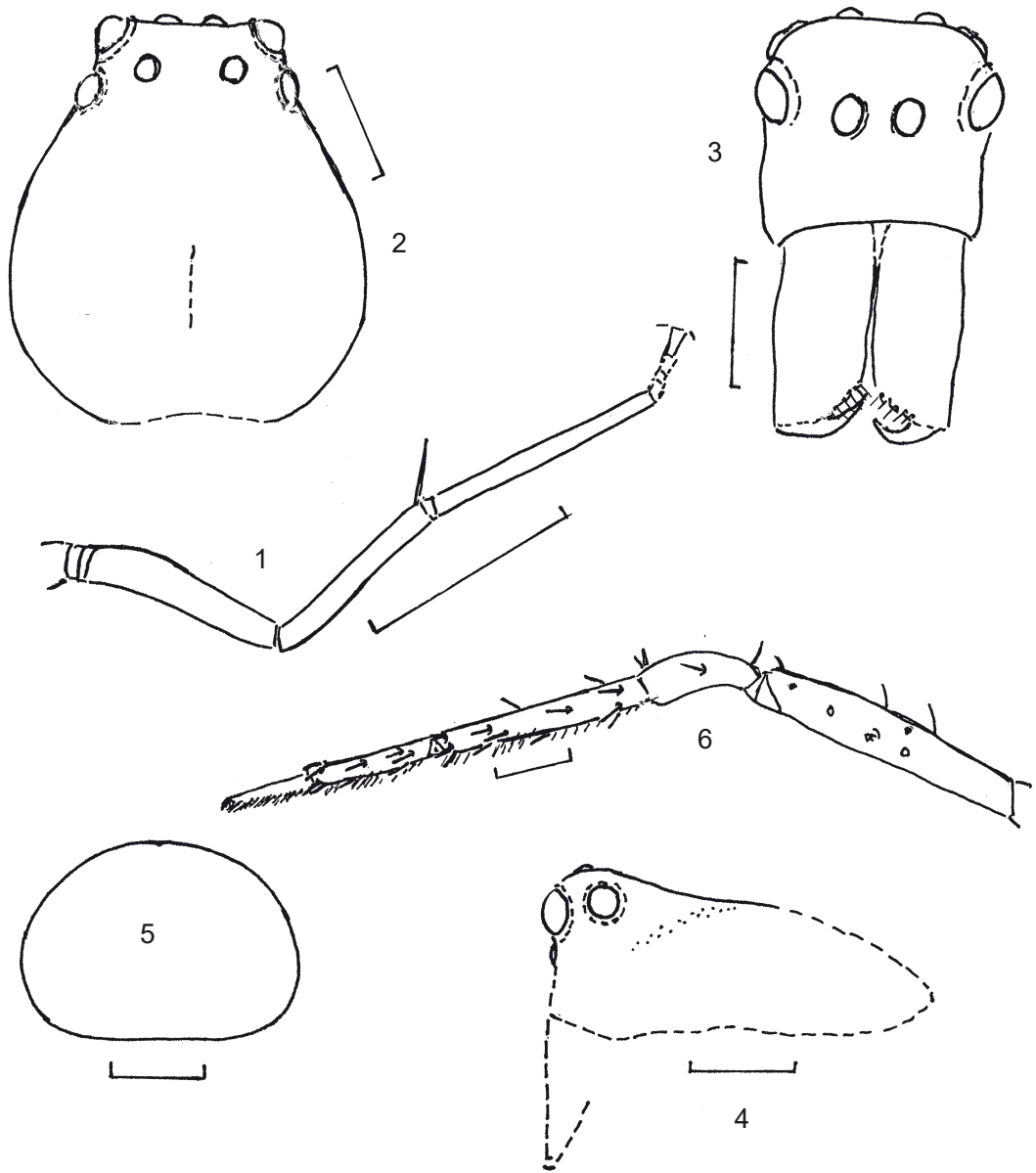


Fig. 1) Leg of an insect (Hymenoptera?) inside the prosoma of the male holotype of *Syphax secedens* n. sp. (Thomisidae), lateral aspect. The tarsus of the insect reaches the anterior part of the spiders opisthosoma. Scale bar 0.5 mm;

figs. 2-11: *Syphax secedens* n. sp. (Thomisidae), ♂;

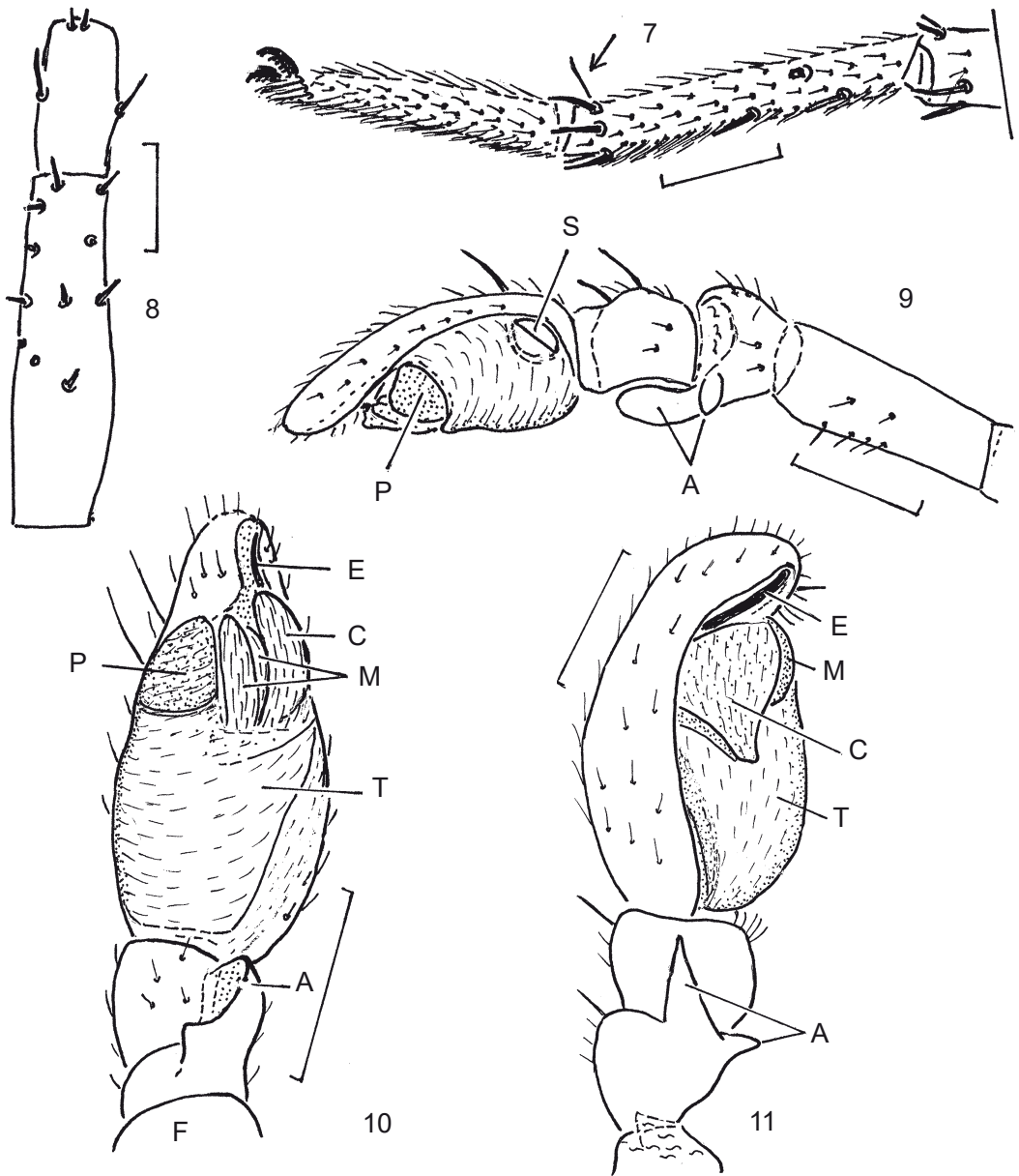
2-4) dorsal, anterior and lateral aspects of the prosoma; fig. 4) is a sketch of the hard observable prosoma;

5) outline of the opisthosoma, transverse cut through the middle, posterior aspect;

6) prolateral aspect of the right leg I. The prolateral femoral bristles are broken off.

Only few hairs are drawn;





- 7) retrolateral aspect of the left tarsus and metatarsus IV. Note the dense false claw tuft, the scopulae and the single questionable metatarsal trichobothrium (arrow); dorsal aspect of the right femur and patella;  
 9) prolateral aspect of the right pedipalpus. Only few hairs are drawn;  
 10) ventral and slightly basal aspect of the left pedipalpus;  
 11) retrolateral aspect of the right pedipalpus.

Scale bars 1.0 mm in figs. 1-6 and 8, 0.5 mm in figs. 7 and 9-11. A = divided apophysis of the patella, C = conductor, E = embolus, F = femur, M = median apophysis, P = prolateral tegular apophysis, S = questionable bipartite subtegular structure, T = tegulum.

**„FROZEN BEHAVIOUR“: THE OLDEST FOSSIL PROOFS OF SPIDER EATING SPIDERS (ARANEAE) IN 45 MILLION YEARS OLD EOCENE BALTIC AMBER AND IN 100 MILLION YEARS OLD CRETACEOUS AMBER OF MYANMAR (BURMITE)**

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**Abstract:** Araneophagy by fossil spiders is shortly discussed. Reports of spider eating spiders (Araneae) are treated: (a) in Eocene Baltic amber: For the first time a member of the extinct family Spatiatoridae – a member of the mainly spider-feeding superfamily Archaeoidea – is described capturing a female of the spider family Synotaxidae. A member of the family Archaeidae capturing a female Theridiidae and a member of the family Mimetidae in the web of two Linyphiidae have previously been reported and are shortly repeated. (b) in Cretaceous amber (Burmite) a member of the extinct family Lagonomegopidae (Archaeoidea) is described which has been captured, spun in and sucked out probably by a mygalomorph spider of the family Dipluridae. A member of the family Spatiatoridae in Burmite is also reported.

**Key words:** Araneae, araneophagy, Archaeidae, Archaeoidea, Baltic amber, behaviour, Burmite, cannibalism, Cretaceous, Dipluridae, Eocene, fossils, Lagonomegopidae, Linyphiidae, Mimetidae, Mygalomorpha, prey, Spatiatoridae, spiders, stridulating, Synotaxidae, Theridiidae.

For leaving me the female of *Spatiator* sp. I am grateful to MARIUS VETA (Lithuania).

Most extant and Eocene spiders are generalist predators of insects and other arthropods. Various prey of fossil spiders in Eocene Baltic amber has been published by WUNDERLICH (2004: 89-98, 195, photos p. 560-588). Some spiders are specialized on

particular prey, e. g. members of the family Zodariidae on ants – see CUSHING (2012), WUNDERLICH (2004) –, others are specialized on spiders, e. g. most members of the family Mimetidae and most Archaeoidea like Archaeidae, see below.

Discoveries of fossil spiders preserved together with spiders as their prey or even preying on them – and which are furthermore identifiable at least to the family level – are extremely rare. Within about several million inclusions in Eocene Baltic amber – including more than a hundred thousand spiders – I found only three examples which are treated below. Additionally shortly described is a spider's prey of a spider – probably a member of the Mygalomorpha – in Cretaceous amber from Myanmar (Burma) which has been spun in and sucked out.

## **Fossil spiders as spider predators reported in the present paper:**

### (I) Spiders in Eocene Baltic amber:

In most cases the spider's predator is unknown in the fossils but in two examples the predator has been identified to the family or even generic level in a previous paper; a third case is added below (2b, a member of the extinct family Spatiatoridae). Spiders of two superfamilies are reported below:

#### (1) Superfamily Araneoidea, family Mimetidae

See WUNDERLICH (2004: 94, 563, photo 615).

A juvenile member of the family Mimetidae, probably of the genus *Succinero* WUNDERLICH 2004, is preserved together with two females of the genus *Custodela* PETRUNKEVITCH sp. indet. (Linyphiidae) within the part of the capture web of *Custodela*. The body length of all spiders is about 1.7 mm. Web and spiders are preserved in the same layer of the amber. The mimetid spider is „sitting“ on a spider's thread. Apparently spiders and web were enclosed by the fossil resin at the moment in which the mimetid spider prepared an attack on the linyphiid spiders.

#### (2) Superfamily Archaeoidea

(2a) *Archaea* sp. indet. (Archaeidae) (fig. 2) (\*)

The *Archaea* is in close contact to the questionable Theridiidae, its obvious prey. Probably the *Archaea* is sucking out its prey through a leg but this is not sure because its mouth parts are hidden. The dorsal folds of the theridiid opisthosoma may indicate that it was really the prey of the *Archaea*.

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(\* ) See WUNDERLICH (2004: 93-94, 98, fig. 5; 567, photo 626): Report on the first sure fossil araneophagous archaeoid spider. Besides this pair two further archaeid spiders are mentioned which are preserved near three members of the family Theridiidae which should have been potential prey of the Archaeidae.

Note: The fig. 51 in the book of BACHOFEN-ECHE (1949: 55) shows a member of the genus *Archaea* with an ant near its chelicerae, but the spider is not in contact with the ant. I investigated these specimens, and in my opinion the combination of these arthropods is nothing else than an accident.

(2b) *Spatiator* sp. indet. (Spatiatoridae) (fig. 1), photos 8-9

Spatiatoridae PETRUNKEVITCH 1942: See WUNDERLICH (2004: 767-768) and (2008: 79-80).

Material: A – apparently egg-bearing – female of *Acrometa* sp. indet (Synotaxidae) captured by a juvenile member of *Spatiator* sp. indet. (Spatiatoridae) in Baltic amber, F2566/BB/CJW, collection of the author.

Measurement of the spiders (in mm): Body length *Spatiator* ca. 2.7, *Acrometa* 2.0, prosomal length *Spatiator* 1.25, *Acrometa* 0.85. Colour of the body: *Spatiator*: Prosoma dark (silvery) brown, opisthosoma light grey; *Acrometa*: Prosoma medium brown, opisthosoma light grey.

The spiders (fig. 1) are fairly well and completely preserved in a flat piece of amber. Mainly ventrally the body of both specimens is covered with a white emulsion, the left leg I of *Acrometa* is loose, autotomized, lying left of the spider. This autotomy may indicate that both spiders were captured by the fossil resin alive. *Spatiator* holds *Acrometa* partly with its anterior legs from the dorsal right side, and probably bites into the basal part of the right leg IV of its prey, but the view of this area is partly hidden. – Some spider threads are preserved in the same piece of amber.

## Discussion:

Spiders are abundant in most terrestrial ecosystems. Their biomass was high already in the Eocene, and thus it is not surprising that spiders of several families were reported as the prey of spiders, from the Eocene, too, see WUNDERLICH (2004: 93-98, photos 615-620, 626): Members of the families Synotaxidae (*Acrometa* sp. indet.), questionable Theridiidae indet., Linyphiidae (*Custodella* sp. indet.), Zoropsidae s. l. (?*Eomata-*

*chia* sp. indet.) and Salticidae (*Gorgopsina* sp. indet.). *Eomatachia* and *Gorgopsina* were spun in in threads in contrast to the remaining spiders. Reports of cannibalism in fossil spiders are rare, see WUNDERLICH (2004: 113, 565, photo 620). On specialized spider-preying spiders: See WUNDERLICH (2004: 93-99).

#### Mimetidae:

Most extant members of the family Mimetidae feed on spiders which construct capture webs, including Linyphiidae. Mimetidae do not construct a capture web of their own. Preparing their attack they may imitate a prey or mating partner of a web-building spider at the margin or within the capture web. The present inclusions in amber represent the only known fossil report of this behaviour of a mimetid spider.

#### Archaeoidea (Archaea and Spatiator):

Most extant members of the superfamily Archaeoidea (= Palpimanoidea) are spider eaters (araneophagous), except several Mecysmaucheniinae. Araneophagy is unknown from Mesozoic spiders (\*) but it is reported from Eocene Archaeidae and Spatiatoridae. Apparently archaeoid spiders feed only on members of other superfamilies. How does this work? Most Archaeoidea stridulate with the help of retrolateral cheliceral files. Such stridulating is known to be used in connection with the mating behaviour, e. g., in the family Linyphiidae, but recently LIZNAROVA et al. – Abstract Book of the 19. Internat. Congress of Arachnology, Taiwan (2013: 208) – reported a quite different additional function of stridulating in spiders: of a family of the superfamily Archaeoidea, the Palpimanidae: „We assume that stridulation is used in intraspecific communication to avoid cannibalism.“. This idea makes sense in the whole superfamily Archaeoidea whose members feed on spiders but stridulating may spare specimens of related con-familiar taxa. Palpimanidae are unknown from the Mesozoic and the Eocene.

It is remarkable that the spider eating fossil archaeoid spiders in question have certain characters in common: (1) They construct no capture web; (2) they possess cheliceral „peg teeth“ (see the paper on Mesozoic spiders in this volume) (\*); (3) they possess retrolateral cheliceral stridulatory files (except the Cretaceous Lagonomegopidae, see above and below); (4) their prey – as far as known today – are members of the superfamily Araneoidea which build capture webs, (5) the predator may be not much larger than the prey, both may even be of about the same size; (6) the predators attack their prey from the posterior dorsal side but not from the front like most Salticidae. This is probably the best position for an attack of a dangerous/poisonous potential prey, especially if the predator and the prey have about the same size (figs. 1-2).

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(\*) The existence of „peg teeth“ in Mesozoic archaeoid spiders may indicate araneophagy already in that era up to ca. 200 million years ago. The first Cretaceous and Mesozoic member of the genus *Spatiator* in Burmite is described in this volume, see the paper on Mesozoic spiders in this volume, photo 131. – Interestingly the existence of cheliceral „peg teeth“ of various spiders is apparently connected with araneophagy as well as with cheliceral stridulatory files; examples are Mimetidae (cheliceral files are rare) and most members of the superfamily Archaeoidea (probably indistinct or absent in the extinct Cretaceous family Lagonomegopidae – see below – in which such files were absent but cheliceral „peg teeth“ existed).



## (II) A spider in Cretaceous amber from Myanmar (Burma):

Araneophagy by spiders has not been reported from the Mesozoic. Most of the specialized spider-preying spiders like Mimetidae and Zodariidae – both were frequent in the Eocene and build no capture web – are unknown from the Mesozoic. Another spider-feeding family of today, the Archaeidae and related families, were frequent in the Mesozoic, e. g. in Cretaceous Burmite, but such spiders have not been reported as araneophagous up to now. Contrarily another member of the superfamily Archaeoidea, of the family Lagonomegopidae, is reported feeding on Diptera, see the paper on Mesozoic spiders in this volume.

Recently I discovered the male member of the Lagonomegopidae in Cretaceous Burmese amber which has been the prey of a spider (fig. 3, photo 113). It is the holotype of a new genus and new species, *?Paxillomegops brevipes* WUNDERLICH F2684/ BU/CJW, see the paper on Mesozoic spiders in this volume (Archaeoidea). Its body length is ca. 4 mm.

Parts of the spider are enclosed in a partly dense irregular two-dimensional larger part of a web which I regard as the capture web of a larger spider or the funnel. Sticky droplets of the web are absent. The spider is injured and crumbled, the position of the legs is unnatural, most legs are bent close to the body (photo), some articles are broken off, the opisthosoma is strongly shrunk, most probably sucked out, remains of questionable white digestive secretion are preserved on the left femur I.

Which species of spiders – and of which family? – fed on this lagonomegopid spider? Archaeoid spiders do not build capture webs, Agelenidae and related families are unknown from the Cretaceous, a capture web of a member of the superfamily Araneoidea should contain sticky droplets. The owner of the larger capture web in question should have been a larger spider. Putting together all these characters I suppose that a member of the mygalomorph spider family Dipluridae has fed on the lagonopid spider: Members of this family are well known from Burmese amber – see the paper on Mesozoic spiders in this volume –; they are larger animals, and are known to build capture webs consisting of a sheet web and a funnel-shaped retreat. Furthermore Dipluridae injure and crumble their prey with the help of their large and strongly toothed chelicerae. They do not suck out their prey through a leg like numerous araneomorph spiders, in which only a weakly or even undestroyed cover remains.

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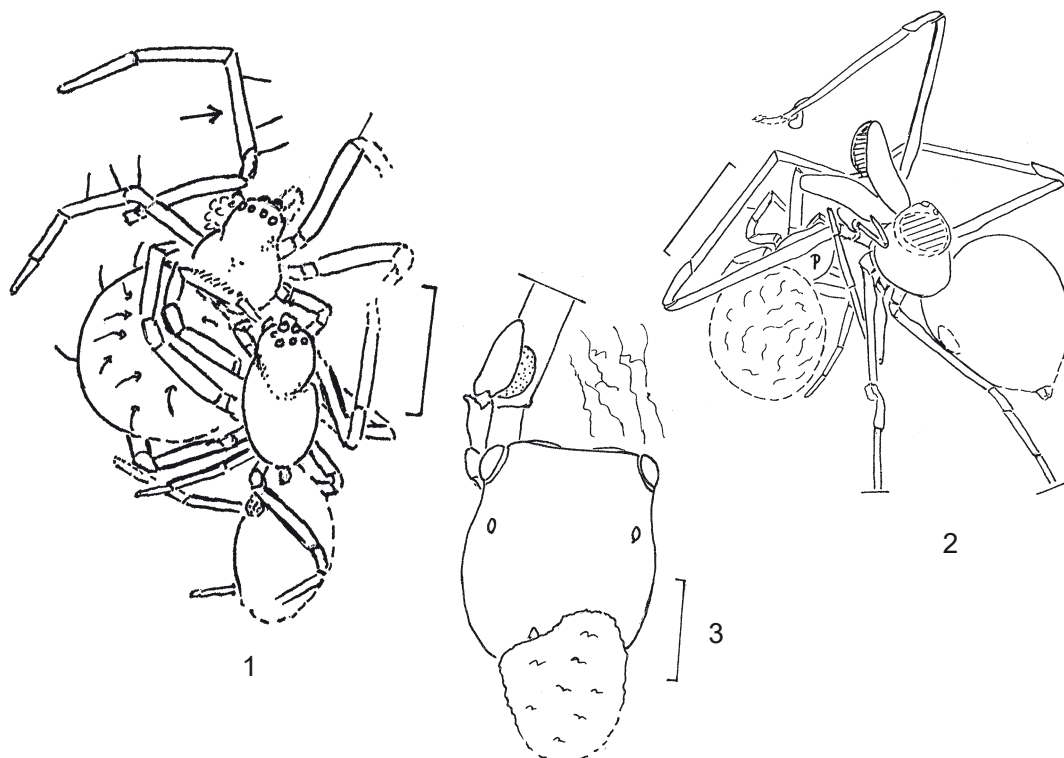


Fig. 1) „Frozen behaviour“ of two fossil spiders in Eocene Baltic amber, dorsal aspect: A female of *Acrometa* sp. indet. (family Synotaxidae) (on the left) captured by a juvenile *Spatiator* sp. indet. of the extinct archaeoid spider family Spatiatoridae. The left leg I of *Acrometa* (arrow) is loose (autotomized within the amber). Not all legs and leg articles and only few bristles of *Acrometa* are drawn. Scale bar = 1 mm.

Fig. 2) „Frozen behaviour“ of two fossil spiders in Eocene Baltic amber, dorsal aspect: A juvenile female of *Archaea* sp. indet. (Archaeidae) (on the right) holding its prey, a probably juvenile member of the family Theridiidae indet. Note the folds of the dorsal part of the theridiid's opisthosoma which may indicate this spider to be the prey of the *Archaea*. Extant Archaeidae are known to be spider eaters. The dorsal part of the „head“ of the *Archaea* is cut off; not all legs are drawn. P = prosoma of the theridiid spider. Scale bar = 1 mm.

Fig. 3) „Frozen behaviour“ of a fossil spider in Cretaceous Burmese amber (part), dorsal aspect: A male of *?Paxillomegops brevipes* WUNDERLICH (family Lagonomegopidae) in the capture web (few threads are drawn in front of the spider's prosoma), probably of a member of the mygalomorph spider family Dipluridae. Note the shrunk and sucked out opisthosoma below. Scale bar = 1 mm.

## ON THE EVOLUTION AND THE CLASSIFICATION OF SPIDERS, THE MESOZOIC SPIDER FAUNAS, AND DESCRIPTIONS OF NEW CRETACEOUS TAXA MAINLY IN AMBER FROM MYANMAR (BURMA) (ARACHNIDA: ARANEAE)

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**Abstract:** The Mesozoic spider (Araneae) faunas – mainly preserved in ambers – are listed and discussed, their evolution, fauna and biogeography are dealt with. Observations on the behaviour and the biology of Mesozoic spiders are treated, e. g. parts of capture webs, prey, an egg sac, camouflage, the first case of a mating plug and genital selfmutilation of a male in 100 million year-old Burmese amber. – The mesozoic spider fauna of mainly higher strata (preserved in amber, besides relatively few taxa in stone) has turned out to be strongly dominated by haplogyne taxa besides members of the entelegyne Deinopoidea: Uloboridae. Taxa of the ecribellate Araneoidea are extremely rare, few reports of the families Nephilidae, Zygiellidae and probably Theridiidae exist. Sure Mesozoic reports of members of the today most diverse Linyphiidae and of the RTA-clade like Salticidae or Lycosidae are missing (!). So apparently most families of spiders radiated – or even originated – only DURING A SIXTH of the 400 million years of spider evolution. – Diversity of the faunas and extinctions: See the list of the families and the annotated list. – The results of my (preliminary) studies of the Mesozoic (mainly Cretaceous) spider faunas are as follows:

- Up to 39 families are reported, the determination of 7 or 8 of these is unsure, only 9 (less than a third of the surely reported 30 families) are entelegyne.

- Almost all of these families are reported from the Cretaceous; the Juraraneidae are only known from the Jurassic, the Mongolarachnidae from the Jurassic to the Cretaceous, Spatiatoridae from the Cretaceous to the Eocene (Baltic amber). Mesothelae – probably the only spiders of the Palaeozoicum and surviving up to now – are reported first from Mid Cretaceous Burmese amber (Burmite).
- 12 (more than one third) of the surely reported families are extinct; only one of these, the Spatiatoridae, survived up to the Eocene. Besides the mygalomorph Fossilcalcaridae all the extinct families are members of the Haplogynae.
- Ca. 110 genera are reported: 1 of the Mesothelae, 11 of the Mygalomorpha, ca. 100 of the Araneomorpha: Up to 78 of the Haplogynae (incl. the Archaeoidea) and ca. 25 of the Entelegynae (= 1/4 of the Araneomorpha).
- Most genera are only known from the Cretaceous; 5 from the Triassic: *Ambiortiphagus* (?Atypidae), *Argyrarachne* (Araneomorpha indet.), *Mesaranea* (Araneoidea indet.), *Rosamygale* (?Hexathelidae) and *Triasaraneus* (Araneomorpha indet.); 5 from the Jurassic: *Eoplectreurys* (Plectreuridae), *Juraraneus* (Juraraneidae), *Jurarchaea* (Archaeidae), *Sinaranea* (fam.?) and *Tatbragaraneus* (Uloboridae): The only genus of the Entelegynae.
- Members of only very few genera – all are members of the Haplogynae – survived up to now, probably *Orchestina* (Oonopidae), *Leclercera* (Psilodercidae) and *Scytodes* (Scytodidae).
- CIBELLATE genera: (a) Araneomorpha: ca. 25 % in the Cretaceous but only ca. 10 % in the Eocene Baltic amber forest; (b) Araneoidea: > 50 % in the Cretaceous but only ca. 7 % in the Eocene (in which cribellate members of the RTA-clade dominate). A strong removal of cribellate genera exist during more than 100 million of years.
- Ca. 140 Mesozoic SPIDER SPECIES are known. No Mesozoic species survived up to now or is known to survive up to the Eocene (e.g. to the Baltic amber forest).

Erroneous, dubious and incorrect determinations and conclusions are discussed; reports of several spider (sub)families like Araneidae, Deinopidae, Linyphiidae, Mecysmaucheniinae (sub Mecysmaucheniidae) and Tetragnathidae have to be deleted from the list of Mesozoic spiders. – Considerable results of this study regard the phylogeny and evolution of spiders. Some ideas on the – mainly palaeozoic and mesozoic – early evolution of spiders including a chronocladogram, the classification of spiders and hypothetical extinct taxa as well as a list of the main innovations in the long evolution of spiders are treated. A TWICE ORIGIN OF THE CRIBELLUM is accepted. The possible existence of two „BIG BANGS OF SPIDER RADIATION“ is discussed which probably happened (1) just after the mass extinction events during the Triassic: the „Triassic explosion of the Cribellates“ (Haplogynae and Entelegynae part (a): Oecobioidea and Araneoidea including the deinopoid branch), and (2) the „Palaeocene explosion“ (after the KT-events) of members of the Entelegynae part (b), the RTA-clade. The origin and diversification of orb-weaving Araneoidea is found much older than the origin of the not orb-weaving families like Linyphiidae and Theridiidae. This find indicate that the araneoid kinds of irregular capture webs derived from the orb web but not the reverse. Results of molecular-genetic studies are not compatible with proofs of fossil taxa. – Taxonomy: Transfers: The Cretaceous taxon *Archaeomecys arcantiensis* SAUPE & SELDEN 2009 (from France) is transferred from the family Mecysmaucheniidae to the Archaeidae: Archaeinae (**n. relat.**). The genus *Filiauchenius* WUNDERLICH 2008 – including its type species *paucidentatus* – may be a member of *Lacunauchenius* WUNDERLICH 2008 (**quest. n. syn.** and **n. comb.**). The genus *Hypertheridiosoma* WUNDERLICH 2012 is transferred from

the Theridiosomatidae to the Praeterleptonetidae (**n. relat.**) which may be polyphyletic. – Certain family diagnoses (e. g. of the Oecobiidae, Spatiatoridae, Theridiosomatidae and Uloboridae) have strongly to be modified if the extinct (Mesozoic) taxa are included. – A new spider classification is proposed (p. 46): The extinct taxon (order) Uraraneida SELDEN et al. 1991 is regarded as a suborder of the order Araneae (**n. stat.**), based mainly on the existence of an opisthosomal spinning apparatus, and as sister taxon of the suborder called Araneida. Araneomorpha SMITH 1902 is regarded as sister taxon to the Mygalomorpha. As Microorders of the suborder Araneomorpha are regarded the „Basal Haplogynae“ **n. taxon** and the Cleistospermiata **n. taxon**. With some hesitation I regard the branch Hypochilomorpha MARX 1888 in a wide sense, including the nominal superfamilies Austrochiloidea and Hypochiloidea. As related branches are regarded the Entelegynae ROEWER 1961 which is restored, see fig. G, and first the Dipneumonomorphae PETRUNKEVITCH 1933 (= Apneumonomorphae PETRUNKEVITCH 1933 and Araneoclada PLATNICK 1977) (**n. syn.**). – Described for the first time are furthermore (all in Mid Cretaceous Burmite): A single family: Fossilcalcaridae (Mygalomorpha), 4 subfamilies: Longissipalpinæ and Pedipalparaneinæ of the Mongolarachnidae, Vetiatorinæ of the Spatiatoridae and Retrooecobiinæ of the Oecobiidae; 35 genera and 66 species of 17 families: Dipluridae, Epsilodercidae, Fossilcalcaridae, Hersiliidae, Lagonomegopidae, Mongolarachnidae, Oecobiidae, Pholcochyroceridae, Plumorsolidae, Praeterleptonetidae, Psilodercidae, Salticoididae, Segestriidae, Spatiatoridae, Tetrablemmidae, Theridiidae and Uloboridae. A Cretaceous member – probably Leptonetoidea or Oecobioidea or Pholcoidea – indet. in stone from Liaoning (China) is described but not named.

**Key words:** Amblypygi, Apneumonomorphae, Araneae, Araneoclada, Araneoidea, Araneomorphae, araneophagy, Austrochiloidea, biogeography, Burma, Burmite, capture web, Cretaceous, Cribellatae, cronocladogram, Deinopoidea, Dipneumonomorphae, evolution, evolution, extinctions, fossils, genital selfmutilation, Haplogynae, Hypochiloidea, Hypochilomorpha, innovations, Jurarchaeinae, Jurassic, Labidognatha, Leptonetoidea, Liphistiidae, mating plug, Mesothelae, Mesozoicum, Myanmar, Mygalomorpha, Opisthothelae, Palaeocribellata, Palaeozoicum, parasites, phylogeny, plagiognathy, plesion, plug, prey, radiation, self-mutilation, Triassic, Uraraneida.

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**Remarks:** The following material – probably important to this study – was not available as loans: Fossil spiders kept in the Mus. Nat. Hist. New York (David Grimaldi). Ron Buckley (USA) was not willing to send me previously described fossil spiders in Burmese amber from his private collection. Unfortunately loans of fossil spiders in Canadian amber stored in Canadian museums



were not allowed. The publication of spiders in Burmite, kept in the Nanjing Inst. Geol. Palaeont. in Nanjing, China, my loan in 2014, was forbidden; therefore descriptions, drawings and photos of most Araneae could not be included in this study.

Note: Originally the present paper and volume should have come out in 2014 but because of the inclusion of numerous recently discovered Cretaceous spiders and the very time-consuming work in correcting previous erroneous determinations – concerning e. g. the families Araneidae, Archaeidae, Deinopidae, Dictynidae, Linyphiidae, Lycosidae, Oonopidae, Thomisidae and Tetragnathidae – this volume was finished not before the Spring of 2015.

**Material** (see also the paragraph directly above as well as below): I got fossil spiders from several friends and dealers of several countries. The material is kept in the private collection and institution of the author (CJW), the Laboratory of Arachnology in 69493 Hirschberg, Germany. The fossil material will probably be given to the Senckenberg Museum Frankfurt a. M. in the future, like most of my previously published material. Loans of the CJW are (and will be) managed by the present author.

Remark: I got most of the material which is described in this paper raising considerable private funds.

**Techniques:** For cutting and polishing of the material a machine of the firm HAMAG was used by me like in previous studies.

Photos: A Minolta camera SRT 101 (reflex camera) was used for the production of slides – KODAK professional 100 and Fujichrome daylight Provia 100F – which were scanned, a binocular microscope of LEITZ, and lighting by a twin flexible-arm illuminator with LED sources, CL-41, from OPTICA microscopes, Italy.

A documentation of certain structures with the help of X-rays and CT will be useful in the future, e. g., for spiders preserved in muddy pieces of amber like *Fossilcalcar praeteritus* (Fossilcalcaridae), *Autotomiana hirsutipes* (Praeterleptonetidae) and several Lagonomegopidae.

Measurements of articles of legs – mainly caused by their bent position – are difficult in some fossils spiders, and may be not exact in all specimens.

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## INTRODUCTION

See p. 25 and the introductions by WUNDERLICH (2008: 532-536) and (2012:161-162).

The present work represents the last part of my trilogy on ancient spider faunas (1). It is based on investigations during 35 years altogether. The publications as books of the „Beitraege zur Araneologie“ (Beitr. Araneol.) started in 1988 with the tropical fossil spider fauna of Hispaniola, preserved in Dominican amber (Miocene, more or less 20 million years old), were continued in 2004 with the mainly subtropical fossil spider fauna of Europe, mainly preserved in Baltic amber (Eocene, about 40-45 million years old), and are finished now with the present volume in 2015 with the mainly tropical fossil spider faunas in various Mesozoic deposits which includes ca. 70-140 million years old amber deposits and some deposits of stone. The best studied Mesozoic „window to the past“ at present is the Cretaceous amber fauna of Myanmar (Burma) preserved in about 100 million years old Burmite (2), (3). The Mesozoic arachnid taxa represent important messages of the central part of the evolution of spiders.

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- (1) Published in the Beitr. Araneol.,  
vol. 2 (1988) on spiders in Miocene Dominican amber,  
vol. 3 A and B (2004) (which was completed with the diverse family Theridiidae in  
vol. 5 (2008) on Eocene spiders in Baltic amber),  
and finally the present vol. 9 (2014) on Mesozoic (mainly Cretaceous) spiders  
(which completes previous short studies (2004, 2008, 2011 and 2012)).
  - (2) Besides Cretaceous spiders in ambers some remarks on various older Mesozoic  
spider taxa are added in this volume which are preserved in stone. Much more still  
undescribed Mesozoic spider taxa exist in stone of Liaoning in China, according  
to P. SELDEN (in litt.) and in stone of Santana (Brazil). The spider fauna in Creta-  
ceous Ethiopian amber has to be studied in the future.
  - (3) The present investigations of spiders would have been impossible without the  
phenomenal work by EUGENE SIMON on extant spider taxa, published more  
than one century ago, important ideas and revisions mainly of extant spiders by  
LEHTINEN (1967) and the pioneer works on fossil spiders in Eocene Baltic amber  
by KOCH & BERENDT (1854) and PETRUNKEVITCH (e. g. 1942, 1958). P. SELDEN  
documented excellently numerous spider taxa which are preserved in stone.

Findings about fossil spiders in amber and stone may allow to bring the numerous  
branchings of the tricky evolution of this order into a chronological sequence, see the  
superfamily Araneoidea. The existence of Cretaceous fossils – as well as the absence  
of peculiar advanced families like the Salticidae – may allow conclusions regarding the  
work and the speed of the spider evolution, see WOOD et al. (2013).

It was striking when I discovered that two of the most diverse spider families of today  
– the Wolf Spiders (Lycosidae) and the Jumping Spiders (Salticidae) – are missing

from the Eocene (the Lycosidae) resp. from the Mesozoic (Cretaceous) (both families), and that all determinations of these families from these epochs were misidentifications. Mainly the actual discovery of undescribed fossil taxa of the Mesothelae: Liphistiidae in BURMESE AMBER (Burmite) – being 100 million years old – as well as the exciting discovery of peculiar members of the extinct and very old – palaeozoic – Uraraneida SELDEN & SHEAR 2008 (preserved in stone) give (and gave me) hints to some new ideas about the early evolution of spiders within the Palaeozoic and Mesozoic periods, the first half of spider evolution, which took a span of almost 400 million years altogether.

Main aims of this paper (see also WUNDERLICH (2012: 161)): Names, diagnoses and relationships of higher taxa of spiders (Araneae) as well as parts of the evolution, and the classification of spiders are treated; the biogeography and the faunas of Mesozoic spiders are also dealt with including a discussion on dubious or erroneously determined taxa. Various fossil spiders from different eras and areas – mainly in Cretaceous amber from northern Myanmar (Burma) – are described or revised, a list including some remarks and the biography of the taxa is given.

A detailed overview over the Mesozoic fauna – including descriptions of numerous known and new taxa – of one of the most diverse orders of arthropods: the spiders (Araneae) – is given for the first time. (A comprehensive investigation of fossil spiders in Miocene Dominican amber: See WUNDERLICH (1988), a detailed investigation of fossil spiders in Eocene European (Baltic, Bitterfeld and Ukrainian) ambers: See WUNDERLICH (2004, 2008).

Known/available/studied material. Up to 10 to 15 years ago only very few spider taxa in Cretaceous ambers were known. During the last decade more and more material has been found (and partly published in taxonomical studies), mainly in amber from Northern Myanmar (Burma), Burmite, few from Jordan, the Zarqa river basin. I saw – or know from various publications – about one thousand Mesozoic – mainly Cretaceous – specimens, among them more than one hundred adult males. Males – in which the copulatory structures should be at least fairly well observable – are quite important to clarify their relationships.

The number of present workers on fossil spiders – spiders which are preserved mainly in Cretaceous and Tertiary ambers – is extremely low, besides the present author they are mainly J. DUNLOP and P.A. SELDEN (on various arachnid orders which mainly are preserved in stone), D. PENNY (few taxa in amber) and H. M. WOOD (mainly Archaeoidae). Especially explicit araneologists – they may be specialists of diverse families or a single one only – are needed for studies in the future. Unfortunately most araneologists are not interested in studying fossil spiders. Such studies need a lot of experience, patience, time, and special techniques but they offer an exciting view on the altering/ changing of characters, behaviour, diversity and biogeography of spiders during the evolution of hundreds of millions of years, see WOOD et al. (2013).

Selected important new publications – mainly books – on Mesozoic and Palaeozoic – including Cretaceous – spiders: DUNLOP & PENNEY (2012), PENNEY & SELDEN (2011), PENNEY (ed.) (2010) (including Cretaceous amber deposits), WOOD et al. (2013) and WUNDERLICH (2008, 2011, 2012). – More than 60 years ago PETRUNKEVITCH (1953) and (1955: 128-152) (contents P44 under „Order Araneida CLERCK 1757“) published on fossil Arachnida incl. Araneae.

Amber from Myanmar (= Burma, Birma) is usually called Burmite, but the oldest name seems to be Birmit, based on the term introduced by HELM (1894), see the internet: WIKIPEDIA. – Deposits of Burmese amber are mainly known from North Myanmar (Burma), the Kachin State, e. g. close to the Hukawag valley – see ROSS et al. in PENNEY (ed.) (2010: 208-235) – from various mines, including the present material, but there are other less known areas and lagerstaetten.

Note on the frequent pear-shaped bubbles („droplets“) at the surface of Burmite pieces; see no. 2 in the paper by WUNDERLICH (2012: 161). Such „bubbles“ or „droplets“ may be the result of boring bivalves, see CRUICKSHANK & KO KO (2003) which found such bivalve shells embedded near the surface of pieces of Burmite and reported Burmite-bearing sediments „deposited in a nearshore marine environment.“. Such „droplets“ are also known in Spanish amber, see PENALVER & DELCLOS in PENNEY (ed.) (2010: 239) and below, for example near the holotype of *Praeterleptoneta maior* n. sp. (Praeterleptonetidae). Such „droplets“ are typical for numerous pieces of Burmite but they are absent in Palaeogene ambers (e. g. Baltic and Dominican amber) and in copal (e. g. from Myanmar, see few lines below).

Comparison of Burmite and Baltic amber (Succinit): See WUNDERLICH (2012: 161).

The producers of the Cretaceous resins, their climates and environment: See WUNDERLICH (2008: 534). Araucarian pines – similar to the extant genus *Agathis* or Taxodiaceae – are supposed to be the (main) producers of the amber. See PENNEY (ed.) (2010).

The age of the Cretaceous resins (in million years), see PENNEY (ed.) (2010), WUNDERLICH (2008: 534): Canadian and New Jersey ambers almost 80, most Spanish amber, Siberian amber from Taimyr ca. 80-105, Ethiopian amber probably 95 (this age is actually questioned by certain authors; it may be even younger than Cretaceous), Burmite about 100 (95-105), amber from Jordan and Lebanon 125-140 (almost Jurassic!).

Remark on COPAL from Myanmar (Burma): On a recent trip to Myanmar I got a piece of copal from Northern Myanmar, sold by a dealer in Myitza, allegedly collected at the same locality as true amber but near the surface of the ground. Its age and the existence of organic inclusions are unknown. This dark material smears during cutting and polishing, the smell is quite different from amber during polishing, and the frequent typical grey pear-shaped bubbles at the surface of true amber – see above – are absent.

The preservation of Cretaceous inclusions is quite variable, from excellent in clear yellow/greenish amber (see the photos), to grey, red-orange and dark brown, frequently more or less to strongly deformed (mainly deformed by pressure, probably by natural heating, too) in muddy resin which includes numerous tiny brown bubbles, see the photos and WUNDERLICH (2008: 534) or mechanically injured by inclinations of prosoma and/or opisthosoma. The different preservation of structures is demonstrated by the different proportions of the tibia of the male pedipalpus of *Parvosegestria obscura* n. gen. n. sp. (Segestriidae) of a well preserved and a deformed specimen. Seemingly the tibial proportions of these specimens contradict a conspecificity of these males but other characters – mainly the structures of the pedipalpus – indicate the conspecificity. – The numerous layers – I found more than 20 layers within 1 cm of a piece of amber – indicate a quite thinly liquid, see *Burmesiola daviesi* n. sp. (Hersiliidae). Arthropod inclusions in Cretaceous ambers are not seldom more or less decomposed, see the photos. But

basically the three-dimensionally preserved organic inclusions in fossil resins offer tremendous possibilities for various palaeontological conclusions. Fine structures such as spinules of spinnerets, sense organs, copulatory structures, and even cells are recognizable, as well as remains of sticky droplets, see WUNDERLICH (2008: Photos p. 801), structural colours (photo 106) or poison and blood, see WUNDERLICH (2004: 27, figs. p. 29: in Palaeogene Baltic amber). The colour of the spider's body is frequently not (well) preserved in deformed spiders which may additionally be covered with an emulsion, but in some specimens like *Picturmegops* (the archaeoid family Lagonomegopidae, photo 114) it is excellently.

Conclusions on the evolution and on family diagnoses: See below, e. g. Archaeoidea, Praeterleptonetidae, Uloboridae and Oecobiidae. Peculiar/exciting fossils may teach us about the evolution of advanced new characters „STEP BY STEP“. – Family diagnoses MAY BE QUITE DIFFERENT IF EXTINCT TAXA ARE INCLUDED or they are regarded in a strict or wide sense. The characters of newly discovered fossils may enlarge the knowledge and change dramatically the diagnoses of higher taxa like families, the family Spatiatoridae (Archaeoidea) is an example. (Even the diagnoses of arachnid orders may be different, see the paper on Cretaceous Ricinulei in this volume).

Remark on the species-concept in palaeontology: The concept of biospecies is usually not applicable in fossils (coupling pairs are exceptions). Therefore some of the paratypes may be not conspecific with the accompanying holotypes although differences of the holotypes are weak or not observed. An example is *Burmosolus nonplumosus* n. gen. n. sp. (Plumorsolidae). See also WUNDERLICH (2008: 42-43).

The habitats: Most Mesozoic taxa are preserved in ambers and have therefore been dwellers of higher strata of the vegetation. See the paragraph „Lebensformtypen“ and „Lebensweisetypen“ (life styles) in the paragraph on phylogenetics.

The frequency of spiders in Burmite may be about 3 % or some more of all animal inclusions (my provisional estimation). (It is reported as 4-5 % in Eocene Baltic amber). The frequency of Acari is more than three times higher to my experience.

The body size of adult spiders in Burmite varies from only ca. 1 mm (Oonopidae, Tetrammidae, Burmascutidae as well as certain Archaeidae, Uloboridae and Theridiosomatidae) up to ca. 7 mm (male Dipluridae and Uloboridae) and even 8 mm (the largest female Lagonomegopidae with a leg span of few cm). Jurassic members of *Mongolarachne* may have been ca. 16 mm long. The body size of most adult spiders lies between 1.5 and 3 mm. See WUNDERLICH (2008: 535). The body size of extant spiders – the average and the extremes – may be larger than their Cretaceous relatives, see e. g. the families Segestriidae, Spatiatoridae and Uloboridae.

Conclusions regarding certain pattern/structures/behaviour of the fossils: See WUNDERLICH 2008: 535-536 and below: Archaeoidea/Lagonomegopidae: E. g. cheliceral „peg teeth“ and retrolateral cheliceral files may allow indirect conclusions on the kind of prey and on the mating behaviour, see the chapter on phylogenetics. Regarding the behaviour I may add the existence of bristles of a „preening hairs/comb“ on metatarsi III-IV which exist e. g. in the superfamily Archaeoidea (= Palpimanoidea) and some Hersiliidae (fig. 329); this structure is absent in spiders which build capture webs. The



extreme rareness of leg autotomy in Cretaceous spiders (but see the genus *Autotomi-ana*) in contrast to Eocene or extant spiders may be caused by the absence of members of the RTA-clade and higher families of the Araneoidea s. str. in the Cretaceous in which leg autotomy is frequent and exists between different articles. – „Clasping spines“ on the male leg I (II) are used during the copulation and known e. g. from some Mygalomorpha (fig. 17, photo), Plectreuridae and Segestriidae: Most Ariadninae. Their existence in the family Hersiliidae and the whole superfamily Oecobioidea (fig. 331) is reported here for the first time; it may be a quite remarkable „regain“ in this taxon. The – in the geological sense – oldest breakable tip of the embolus (figs. 350-352) is reported from *Burmadiectyna excavata* (Deinopoidea: Salticoididae); it indicates the existence of a „mating plug“ already in the Mid Cretaceous. The – in the geological sense – oldest clutches of eggs are reported with a female of the superfamily Leptonetoidea, probably of the extinct family Praeterleptonetidae, see fig. A-B p. 43–45. and the photo 91. A questionable cocoon (egg sac) in Burmite is preserved in the same piece of amber as remains of an Oecobiidae indet., F2377/BU/CJW. Remains of the cover of an egg sac are preserved with the holotype of *Pholcochyrocer guttulaeque* WUNDERLICH 2008: 594, photo 84. – The preservation of structural colour of hairs (probably a kind of camouflage or/and connected with the mating behaviour): See the family Lagonomegopidae (photos 106, 114) and WUNDERLICH (2008: 782 f).. Almost all cribellate spiders use capture webs; so we may assume that the Mesozoic members of (e. g.) the families Mongolarachnidae, Pholcochyroceridae and Uloboridae were capture web dwellers. Numerous parts of webs, partly apparently cribellate, are preserved with members of the family Uloboridae, see below (e. g. with the holotype of *Paramiagrammopes longicylpeus* n. p.) as well as the chapters on this family in the papers by WUNDERLICH (2008, 2011 and 2012). The part of a questionable capture web is preserved quite near the male holotype of *Pedipalparaneus seldeni* n. gen. n. sp. (Pholcochyroceridae: Mongolarachnidae). The webs needs a closer study. A large part of a capture web including sticky droplets is preserved with the holotype of *Cymbiolagonops cymbiocalcar* (Lagonomegopidae), photo 101, a not capture web building spider. – In Cretaceous members of the family Segestriidae the third pair of legs was already directed anteriorly like in confamiliar spiders of today. This leg position may indicate their tube-living behaviour like in extant relatives although such tubes are still unknown in Cretaceous spiders. Peculiar structures allow conclusion on the relationships of spiders, e. g., the pattern of the opisthosoma in a spider of the infraorder Mesothelae (figs. 5, 7, photos 10-11): Existence of tergites as well as number, position and structure of the spinnerets. The peculiar (almost unique) structure of the calamistrum in certain Uloboridae or the structures of the male pedipalpus in the Praeterleptonetidae allow conclusions on the phylogeny and the palaeodistribution of spiders (see, e. g., the families Lagonomegopidae, Praeterleptonetidae and Uloboridae). The detection of the minimum age of taxa and characters as well as of the transformation of characters (see the Archaeoidea, fig. D) or on the (chrono-)biogeography (see e. g. the superfamily Archaeoidea) or on the existence of (palaeo)relict taxa.

Erroneous determinations which caused numerous wrong conclusions – e. g. concerning cladograms – have to take into account, see the chapter II.

Prey: See WUNDERLICH (2008: 536) and the paper of „Frozen behaviour“ in this volume. Here I add some material in Burmite:

(1) In a 3.3 cm long piece of Burmite – F2473/BU/CJW – a large part of a capture web

including sticky droplets are several Diptera, 2 Coleoptera and other insects preserved, partly in contact with the threads. At least some of these animals were apparently prey of a spider.

(2) Two Diptera: Nematocera are preserved with the male holotype of *Cretotheridion inopinatum* n. gen. n. sp. (Theridiidae), photo 175, see below;

(3) Two Diptera: Nematocera are preserved with a juvenile of *Archaelagonops* sp. indet. (Lagonomegopidae), see below.

(4) A male lagonomegopid spider as the possible prey of a member of the mygalomorph family Dipluridae, see below: Archaeoidea: Lagonomegopidae, photo 113.

(5) In a part of a spider's questionable capture web, F2011/BU/CJW, a Diptera: Nematocera is preserved which may have been the prey of a spider.

(6) The existence of taxa of the superfamily Archaeoidea – mainly of members of the family Archaeidae and a specimen of the genus *Spatiator* PETRUNKEVITCH 1942 (Spatiatoridae, see below) in Burmite – indicate the indirect proof of ARANEOPHAGY already in the Mid Cretaceous, see the paper on „Frozen Behaviour“ in this volume.

Remark: Insects as possible prey exist furthermore near the following spiders: *Parvos-egestia pintgu* n. sp. (Segestriidae), *Spinipalpus vetus* n. sp. (Pholcochyroceridae) and *Spinipalpitibia maior* n. sp. (Praeterleptonetidae), see below.

Parasites (ectoparasites and egg parasites): (1) Parasitic larvae of Acari like Erythraeiidae are occasionally to be found near Cretaceous spiders, see below, e. g. the holotype of *Leclercera ellenbergeri* n. sp. (Psilodercidae). (2) A questionable Mantispidae larva (photo 28) is preserved near a juvenile mygalomorph spider, probably an Atypidae, see below. (3) A probably egg-parasitic Hymenoptera of the family Mymarommatidae (J. JANZEN det.), F2628/BU/CJW, is preserved on the opisthosoma of a female Lagonomegopidae indet., see below.

Syninclusions of different spider families: A piece of Burmite – F2673/BU/CJW – contains members of three spider families (they are strongly deformed by natural pressure and heating): A juv. Hersiliidae indet., a juv. Lagonomegopidae indet. and an ?ad. female of the family Tetrablemmidae. – A female Araneae indet. – F2762/BU/ CJW – is preserved in a piece of Burmite together with 10 orders of arthropods. – Three Araneae: *Burmorchestina* sp. (Oonopidae), *Eomysmauchenius* sp. (Archaeidae) and *Burlagonomegops* sp. (Lagonomegopidae) are preserved in a larger piece of Burmite, F2272/BU/CJW, see WUNDERLICH (2012: 167-168).

# I. PHYLOGENETICS

## PARALIPOMENA

What made SPIDER EVOLUTION work? The long evolution within the old order Araneae is – besides environmental catastrophes like the KT-events – not only a matter of *INNOVATIONS* (\*), *TRANSFORMATIONS* and *MODIFICATIONS* like the development of a burrowing behaviour, of true spinnerets and their translocation ventrally as well as to the end of the opisthosoma, the development of piriform silk glands, the transformation of orthognathy via plagiognathy to labidognathy and nippers-shaped fangs, modifications of the triads of the eye field, development of a gnathocoxal serrula and peculiar sense organs as well as their specializations like the optical apparatus of Deinopidae, Lagonomegopidae and Salticidae, a cribellum, high performance silk fibers and capture webs of various types – especially an orb web –, sticky droplets, brood-care behaviour, an entelegyne stage, a male-female copulatory locking system (e. g. in the RTA-clade) and a fast sequence of generations, but also a matter of **LOSSES** and „SIMPLIFICATIONS“ like the loss of the opisthosomal segmentation, reduction of the number of lungs, heart ostia, receptacula seminis (to a single pair) and parts of the brain (centralization, increase of efficiency), losses of the cribellum, an unpaired tarsal claw (connected with hunting behaviour), and the moulting of adults. Such „large functional steps“ may have caused a faster evolution, distinctive diversifications and faunal changes e. g. of/by the RTA-clade after the KT-events.

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(\*) In my opinion life – the organic evolution/adaptation – is unalterably characterized by such innovations – in contrast to anorganic processes. Regarding the enormous importance of innovations within the evolution of spiders (as well as of other organisms): See above. I call these processes – they are more than simple „developments“ and include the inherent possibility of changes from quantity to quality like the origin of sensibility and other kinds of INWARDNESS – provisionally „EVOLVOLUTION“, and I do not want to exclude that it represents a further (fifth) „dimension“ beyond the fourth dimension of the „space-time continuum“. – Evolvement may be an adequate term to explain the sequence of different stages of being, of (anorganic? and) organic evolvement (in which innovations like chemosynthesis, sexuality and inwardness exist) – probably including stars, galaxies and probably the whole universe –, of their „development“, characterized by an unfolding of possibilities, and limited a priori by degrees of scope (variability). See the terms „MORPHOGENESIS“ and „KONSTRUKTIONSTYPEN“ (see the organic evolvement) in the sense of GRASSHOFF (2014). Such concepts are ignored or neglected by most recent authors.

A CLADOGRAM of fossil taxa reflects the reality in only a quite limited way. Because of many characters there must in fact exist much more branchings in the evolution of spiders within a time span of 400 million years than we can imagine and demonstrate by a cladogram. Conclusions are only provisional, and – in practice – not every newly discovered branch and level needs a name of its own!

Remarkably just the most diverse branch of extant spiders (of the order Araneae) – the Dipneumonomorpha which include the Entelegynae, see figs. A, C below – is called “Microorder“. This SINGLE derived branch represents a low level but includes a huge amount of diversity (probably 100 000 described and undescribed extant species), and diversified quite late, after the end of the Cretaceous; that means only during the last 6 hours of the 24 hours of a day (!), similar to other advanced high taxa like Gramineae, orchids, and the advanced part of the boney fishes, singing birds, as well as placental mammals. Obviously various reasons caused the differing speed of the evolution.

The extinct Devonian genus *Attercopus* (Uraraneida) was „placed as sister-taxon to all living spiders“ by SELDEN et al. (1991), the extinct genus *Permarachne* (Uraraneida, too) was showing „clear evidence of belonging to the Mesothelae“ by ESKOV & SELDEN (2005: 111); DUNLOP & SELDEN (2009) regarded Uraraneida as the sister taxon to Araneae and other orders, and PENNEY & SELDEN (2011: 72) placed Uraraneida (again) as sister taxon to all spiders. So certain results of cladists are apparently rather short-lived.

JW

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„To discover how the extinct species have from time to time been replaced by new ones down to the very latest geological period, is the most difficult, and at the same time the most interesting problem in the natural history of the earth.“

A. R. WALLACE (1855)

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Mal' Dir ein Kladogramm,  
und sei ein großes Licht,  
und mal' Dir noch ein zweites dann –  
geh'n tun sie beide nicht!  
Denn für dieses Leben ist der Mensch nicht schlau genug,  
und sein Ordnungsstreben führt zum Selbstbetrug!

JW, in Anlehnung an BERTHOLD BRECHT

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## **ON THE EARLY EVOLUTION AND THE CLASSIFICATION OF HIGH SPIDER TAXA**

See also below, the infraorder Mesothelae and the Microorder Hypochilomorpha as well as the Archaeoidea (= Palpimanoidea) and various families like Archaeidae, Lagonomegopidae, Pholcochyroceridae, Praeterleptonetidae, Oecobiidae, Salticoididae, Theridiosomatidae and Uloboridae.

Some aspects of phylogenetic and faunistic are overlapping; therefore see also the chapter on faunistic as well as above (Paralipomena).

At the beginning of my present work I asked myself a question which appears quite simple/trivial at first sight: What is a spider? What are the undoubtedly diagnostic/ apomorphic characters of – extant AND extinct – spiders?

The sure detection of the sister group of spiders, e. g. probably Amblypygi or Uraraneida – and the discovery/investigation of well preserved Palaeozoic like Uraraneida, and Early Mesozoic fossils – appear most important to answer these questions, and for finding out the basal branchings of the Araneae, Araneida, Mygalomorpha and Araneomorpha.

Historical review (Araneae): See, e. g., FOELIX (1996: 4-5), LEHTINEN (1967: 277-280), PLATNICK (1977: 4-8), WUNDERLICH (2011: 570) and the following paragraphs. See also above, the paragraph „Selected important new publications (books) on Mesozoic and Palaeozoic – including Cretaceous – spiders.

The sister taxon of the Araneae. Probably most of the recent araneologists regard the Amblypygi as the sister order of the Araneae – this supposition may be correct, see fig. B – but there is no general agreement among araneologists, see WEYGOLDT (2000: 9). Synapomorphies and Sympleiomorphies of Amblypygi and Araneae according to my opinion: See fig. B. DUNLOP & SELDEN (2009: Fig. 1) placed Uraraneida as sister taxon to Araneae + Haptopoda + Amblypygi + Thelyphonida + Schizomida but only two years later PENNEY & SELDEN (2011: 72) considered this taxon as nearest to the Araneae as did I in the same year (2011: 570). I agree with the sister grouping by PENNEY & SELDEN (2011) basically, but I disagree in their judgement of the level of the Uraraneida and the branchings of higher taxa, see figs. A-C. – Prior to the discovery of the Uraraneida the taxon Mesothelae was regarded as the most „primitive“ (ancient) high taxon of the Araneae, see the cladogram given by POCOCK (1892) in PLATNICK & GERTSCH (1976: fig. 1).

Diagnoses/apomorphies and relationships of the Araneae and Araneida: See fig. B. Both are mainly characterized by – poison and spinning – GLANDS.

Selected taxa, levels and names (see the figs. A-C, **G**, and the Uraraneida below): Araneae is used/diagnosed here for/as a taxon in which basically opisthosomal spinning glands exist (as an apomorphic character), and a flagellum (telson) still existed (as a plesiomorphic character). In my opinion Uraraneida originated (as sister branch) from a hypothetical extinct branch, see fig. A. Opisthothelae POCK 1892 is used here – besides a hypothetical extinct taxon, see fig. A – as a branch in which the anterior median spinnerets are a retention, and from which Mygalomorpha POCK 1892 (under Mygalomorphae) (1) and Araneomorpha SMITH 1902 originated not as „true“ sister taxa in a strict sense (2). – Araneomorpha is used for a – probably basically – cribellate clade which is almost identical with „Araneomorphae“ sensu PENNEY & SELDEN (2011). – I furthermore propose the use of the name Hypochilomorpha MARX 1888 in a wide sense – in the sense prior to FORSTER et al. (1987), e. g., PETRUNKEVITCH (1933), FORSTER (1955) and GERTSCH (1958) – for a branch which represents the sister group to the Dipneumonomorpha PETRUNKEVITCH 1933. PETRUNKEVITCH (1933) introduced the newly ranked suborder Hypochilomorpha, only including the family Hypochilidae MARX 1888, the single known family of this suborder at that time (3). Furthermore PETRUNKEVITCH (1933) created the new taxa Dipneumonomorphae and Apneumonomorphae – both as suborders – for spider taxa which are more derived than the Hypochilidae MARX 1888. Apneumonomorpha has turned out as a triphyletic taxon which includes three families of three different superfamilies: (a) Caponiidae: „Haplogynae“: (?) Dysderoidea, (b) Telemidae: „Haplogynae“: Leptonetoidea (see WUNDERLICH (2012)), and (c) Symphytognathidae (s. l.): Entelegynae: Araneoidea. The artificial mixture of these taxa was based by PETRUNKEVITCH mainly on the absence of lungs. Today it is generally accepted that the absence of lungs are convergent losses caused mainly by dwarfism, and the three taxa in question are not strogly related to each other. They actually are members of the Dipneumonomorpha sensu PETRUNKEVITCH 1933, and Apneumonomorpha therefore is a synonym of Dipneumonomorpha. The taxon Araneoclada PLATNICK 1977: p. 19, fig. 31 is exactly identical with Dipneumonomorpha PETRUNKEVITCH 1933 (see figs. 3 and 30 in PLATNICK (1977)). Therefore Araneoclada has to be regarded as junior synonym of Dipneumonomorpha (**n. syn.**). Araneoclada was ranked as a „Hypopicoorder“ by PLATNICK (1977), and a „Gigapicoorder“ by FORSTER et al. (1987). Dipneumonomorpha is ranked as „Microorder“ in the first part of the present paper (but see the proposed new classification of spiders and fig. G!), and diagnosed as follows (see fig. B): Labidognath (fig. 4) a single pair of lungs, endocephalic venom glands, three pairs of heart ostia, leg (coxa-trochanter?) autotomy. Further – plesiomorphic – characters: See the Araneomorpha in fig. B. Included are all derived spider taxa which are more advanced than the Hypochilomorpha in the wide sense of this paper (= Neocribellata CAPORIACCO 1939 except Austrochiloidea), see fig. B. The derived Labidognatha BERLAND 1932 – the taxon was not treated by PLATNICK (1977) – includes the Hypochilidae and therefore is not identical with or an older synonym of the Dipneumonomorpha but synonymous with the Araneomorpha. Hypochilomorpha is almost identical with the traditional „Palaeocribellatae“ (Hypochiloidea s. str.) but I include Austrochiloidea, see fig. B and the discussion below. – Dipneumonomorpha in the sense of this part of the present paper (as sister group to the Hypochilomorpha) is almost identical with the traditional „Neocribellatae“ sensu FORSTER et al. (1987) but Austrochiloidea is excluded (with little reservation); but see the new Microorder „Basal Haplogynae“ below, fig. G!. – Dipneumonomorpha is a well diagnosed taxon WITHOUT REGARDING THE EXACT RELATIONSHIPS OF THE AUSTROCHILOIDEA (included within the Hypochilomorpha or not), and the names Palaeocribellata and Neocribellata are



regarded as superfluous by me. The relationships of the Austrochiloidea are not quite sure in my opinion; it may be strongly related to (or to be included in) the Hypochilomorpha or the most basal branch of the Dipneumonomorpha (unlikely in my opinion); it is regarded as a member of the Neocribellatae, and sister to the Archaeoidea (sic!) by GRISWOLD et al. (2005). Mainly because of their plagiognathy, and basically the existence of two pairs of lungs (4) I suppose close relationships of the Austrochiloidea to the Hypochilidae. Endocephalic venom glands and other characters exist in the Austrochiloidea as derived characters in contrast to the Hypochiloidea; they may have evolved convergently to the Dipneumonomorpha, but see fig. G!. The separate evolution of members of these two nominate superfamilies DURING 250 MILLION YEARS may well have caused their various differences which are summarized by PETRUNKEVITCH (1933), repeated and completed by PLATNICK (1977).

Remark: In my opinion the inflationary creation of names for branches – especially of relatively low levels – is not justified, and the creation of new names for every (sister group) branching is probably not useful nor justified. So – besides Uraraneida and Araneida (fig. A) – also Mesothelae and Opisthothelae may alternatively be ranked as suborders, and the branches Mygalomorpha, Araneomorpha, Hypochilomorpha and Dipneumonomorpha may all be ranked as infraorders. But see fig. G!

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(1) I prefer the spelling Araneomorpha, Dipneumonomorpha, Mygalomorpha, ... (not Araneomorphae, ...) following LEHTINEN (1967).

(2) The branchings of the cladograms (A, B) are strongly simplified; „blind“ ending (extinct) branches must exist frequently but are rarely shown, see the branchings at the „Araneae in the wide sense“ and the „Opisthothelae“ as well as the discussion below.

(3) The family Thaididae (= Austrochilidae ZAPFE 1955) was still unknown to PETRUNKEVITCH (1933). It may be included in the Hypochiloidea (this paper) or not, see below in this paragraph and the Hypochilomorpha further below.

(4) Austrochiloidea includes the families Thaididae and Gradungulidae. In *Austrochilus* and *Thaïda* of the Thaididae the posterior pair of lungs has been lost.

Uraraneida – type genus *Attercopus* SHEAR et al. 1987 – is called „order“ e. g. by DUNLOP & PENNEY (2012: 16). Two taxa are included in the Uraraneidae: (a) *Attercopus fimbriunguis* SHEAR et al. 1987 (unplaced at the family level, see SELDEN et al. (2008), placed by SELDEN et al. (1991) as basally to the Mesothelae), Devonian, and (b) *Permarachne novokshonovi* ESKOV & SELDEN 2005 (family Permarachnidae ESKOV & SELDEN 2005, Permian; placed originally with „clear evidence“ in the Mesothelae by these authors).

These fossils are preserved in stone and were first described in a plesion. A plesion is a taxon that does apparently not fit in any particularly higher taxon (and which may not yet have been named). The term is especially used for genera which appear distinctive but are still poorly known.

Remark: SELDEN et al. (1991: 272) noted regarding the tarsus of *Attercopus*: „The proximal joint bears two articulations which correspond to the articulations on the metatarsus.“. According to SELDEN (E-mail in 2012) this does not mean that the articles are divided (really articulated).



Diagnosis of the order Uraraneida according to DUNLOP & PENNEY (2012: 107):

„Uraraneids can be characterized by having silk-producing spigots arranged in two rows along the presumed posterior edge of its sclerotized ventral abdominal plates; and not borne on spinnerets as in spiders. Retention of a posterior flagellum <present paper, fig. 1> also differentiates them from spiders.“

If one ignores all the plesiomorphic characters suggested by me (fig. B) – e. g., the orthognathous position of their chelicerae (fig. 1) – only „the SLENDER SHAPE of the flagellum“, and probably the absence/loss of leg trichobothria remain as a (weak) diagnostic characters (fig. B); see THE LIST OF STILL UNKNOWN CHARACTERS of the Uraraneida below (we are waiting for additional and better preserved fossils\*):

- position of the eyes (existence of triads\*\*?),
- existence of leg trichobothria (absence? No proof up to now),
- existence of a postcerebral pump,
- presence/absence of a pedipalpal metatarsus,
- shape and copulatory function of the pedipalpus of adult males,
- existence of a sperm web,
- existence of burrowing behaviour (supposed by me) and a trap door,
- existence of an egg sac/cocoon (because of the lateral position of the spigots unlikely to me),
- the function of the flagellum,
- the kind of leg autotomy (absent?),
- the function of the silk (originally for covering the burrow?).

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\* probably poison glands exist in the Uraraneida; ducts in their fangs may have been overlooked; they are quite indistinct e.g. in the Mesothelae, and have been overlooked in this taxon, e. g., by HAUPT!

\*\* The existence of eye triads may well be an ancient character in arachnids, see KRAUS & KRAUS (1993, fig. 4). This character was ignored in the investigations by most authors. The position of the triads (besides a pair of anterior median eyes) has apparently been modified numerous times in quite different ways, apparently retaining and reversed in certain taxa.

Relationships: If the uraraneid pattern – existence of opisthosomal spinning glands, hairless fangs, cheliceral glands (according to SELDEN et al (1991: 245)), not articulated tarsi and metatarsi, and the existence of a tarsal organ (detected in *Attercopus*) (fig. B) – they all are unique within the orders of the Arachnida; the characters of the legs (articles coxa, trochanter, femur, patella, tibia, metatarsus and tarsus, ALL UNSEGMENTED) are exactly like in (other) Araneae (!) – are accepted as apomorphic characters of the Araneae, it would be logical to include the Uraraneida as a suborder of the Araneae (fig. B). If Uraraneida is considered as an order of its own, the probable sister taxon of the order Araneae – Amblypygi – would change to the sister order of Araneae + Uraraneida but not simply of the Araneae.

Notes on selected characters:

(See WUNDERLICH (2011: 571-572)).

The FLAGELLUM (TELSON) (fig. 1) of both known taxa of the Uraraneida – apparently a plesiomorphic character of the Araneae – is its most conspicuous structure besides the opisthosomal spigots, see fig. B. In my opinion the flagellum is probably lost in the Araneida convergently to the Amblypygi (remaining is a tubercle in this order), see fig. B.

EYES. TRIADS: See above: (\*\*). The existence of eye triads in several Haplogynae like Pholcidae as „plesiomorphic remains“ (or reversals?) may be best understood by the cladogram in fig. B. – NARROW EYE FIELD AND EYE TUBERCLE: The ground-living life style may be an ancient behaviour of spiders – latest in (the ancestor of) the Araneida, in which the telson was lost -, and enemies like dangerous millipeds may have caused a burrowing behaviour early in the evolution of these animals. The reduction of the size of eyes – and a narrow eye field on a tubercle – may be connected with a subterranean life style. Similar eyes may have been retained in the Filistatidae which are not free-living hunters but live hidden in tubular retreats.

POSITION AND STRUCTURES OF THE CHELICERAE. PLAGIOGNATHY (with the position of the fangs as in figs. 3 and 7) evolved from orthognathy (fig. 2) probably three times: (a) in (the ancestor of) the Mesothelae (which bear protruding horizontal basal cheliceral articles, fig. 7), (b) in certain Mygalomorpha (e. g. in Antrodietidae and Migidae, which bear protruding basal cheliceral articles similar to fig. 3), and (c) in (the ancestor of) the Hypochilomorpha (in the present wide sense) which bear vertical basal cheliceral articles; position of the fangs as in fig. 3).

Remarks: (1) Plagiognathy was not treated by FORSTER et al. (1987). (2) The converging position of the tips of the fangs is influenced by the widely spaced bases of the fangs which work against each other. See HOMANN (1985) and KRAUS & KRAUS (1993). (3) According to KRAUS & KRAUS plagiognathy is a plesiomorphic character, and orthognathy in Amblypygi may be different from orthognathy in spiders. These authors did not yet know the clearly orthognathous cheliceral position in the Permian genus *Permarachne* of the Uraraneida, see ESKOV & SELDEN (2005: Fig. 5). (4) The modified labidognathous position of the chelicerae of Dysderidae like *Dysdera* has been called „semi-orthognathous“ by KRAUS & KRAUS; in these spiders „the first postembryonic stages were nearly labidognathous“.

ORIGINS OF THE CRIBELLUM: See below, e. g. the supplement on the superfamily Archaeoidea as well as the Hypochilomorpha below and fig. G, p. 287.

TARSAL AND METATARSAL TRICHOBOTHRIA: Their loss by the (ancestor of the) Araneomorpha may be REVERSED at least three times: in the (ancestor of the) RTA-clade, in the lagonomegopid branch (Lagonomegopidae and Micropalpimanidae) of the Archaeoidea, and in the Caponiidae (Dysderoidea); see the supplement on the superfamily Archaeoidea below. – Their existence (a proof is wanting) or absence (it may be a loss) in the Uraraneida is unsure.

LEG AUTOTOMY: The kind of leg autotomy is unknown in the Uraraneida. In the Araneae (Araneida) exist various kinds (in certain taxa autotomy is absent, e. g., in the araneoid families Tetragnathidae and Mimetidae). Most frequent is a break between coxa and trochanter, and therefore I suppose a tendency for the coxa-trochanter autotomy in the Araneae in which numerous losses and reversals exist. According to PETRUNKEVITCH (1933: 347) leg autotomy is absent (lost? See fig. G!) in the family

Hypochilidae, and to my knowledge in all members of the Hypochilomorpha. Is leg autotomy an apomorphic character of the huge and diverse branch Dipneumonomorpha (lost and transformed numerous times)?

Remark: I prefer the term „autotomy“ – but not „autospasy“ in the more narrow sense – following (e. g.) FOELIX. The term autotomy cannot be wrong in this respect because it is used a wider sense.

### **The relationships and the level of the MESOTHELAE POCOCK 1892**

(photos 10-11, figs. 5-9)

If the taxon Uraraneida is included in the order Araneae (in a wide sense) – see WUNDERLICH (2011: 567f) and above, see figs. A-B – Mesothelae is regarded on the level of an infraorder; if Uraraneida is excluded, Mesothelae should be regarded as a suborder of the Araneae sensu stricto (as used traditionally).

Mesothelae is the most ancient and oldest (Carboniferous) high taxon of the Araneae which members still exist today as relicts, in the single family Liphistiidae. It probably is the only taxon of „true“ spiders of the Palaeozoicum.

Spiders of this infraorder may be called „Segmented spiders“ because of their segmentation in two respects, (a) of their segmented opisthosoma (fig. 5, photos 10-11), (b) of their segmented/articulated lateral spinnerets (fig. 7, photo 13).

**Selected characteristic features of the Mesothelae** (see below, e. g. the diagnostic characters as well as fig. B): In this infraorder plesiomorphic characters of the branch Araneida in the sense of the present paper outlive, e. g.,

(a) an articulation/segmentation of the opisthosoma (several transverse dorsal plates, tergites, fig. 5), (b) two pairs of lungs/lung covers (fig. 7), (c) four pairs of ventral opisthosomal spinnerets which (d) possess an anterior position (fig. 7).

### **Supposed main diagnostic (mainly apomorphic) characters of the Mesothelae: Liphistiidae:**

- Plagiognathy (fig. 7; fangs also as in fig. 3) (\*);
- four pairs of opisthosomal spinnerets situated in an anterior position (fig. 7) (\*\*);
- articulated/multisegmented lateral spinnerets (fig. 7),
- a posteriorly elongated sternum (fig. 9) (except in quite young spiders), which is prominent and deeply declined at the margin (fig. 7),
- a quite wide labium (fig. 7),

- a ventral outgrowth of the pedicel behind the sternal extension (fig. 9),
- longitudinal retrobasal invaginated coxae IV (fig. 9),
- spurs (specialized sensory hairs) on tibia I-III of juveniles and adult females, see HAUPT (2003: 23: fig. 16C-D, 90),
- modified trichobothrial bases; see HAUPT (2003: 18-22),
- a male pedipalpus with a large retrobasal paracymbium which bears spines,
- probably two plates/scuta (sternites) covering the two pairs of lungs.  
(teeth on the margins of the cheliceral furrow: See below, „further important characters“: remark (1)).

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 (\*) according to my hypothesis plagiognathly convergently evolved in certain Mygalomorpha (e.g., Actinopodidae, Migidae) and in Araneomorpha like Hypochilidae, see WUNDERLICH (2012: 572f, 589) and below. The converging position of the tips of the fangs is caused by the widely spaced bases of the fangs which work against each other. See HOMANN (1985) and KRAUS & KRAUS (1993).

(\*\*) A single median spinneret only exists in certain *Heptathele*.

Remark: In certain papers the Mesothelae were reported as having no poison glands, based on erroneous observations by HAUPT (2003: 6), but such glands exist – see FOELIX (2011: 50-52)  
 – although ducts and openings in the fangs are quite indistinct.

**Further important characters:** Ecribellate, unpaired tarsal claw and tarsal organ existing, male pedipalpus used for sperm transfer, existence of epiandrous glands, receptacular cluster, living in tubular burrows which are closed by a trap door, larger spiders, body length usually 1-4 cms, fovea a deep pit, legs stout, bearing strong bristles in adults, long living spiders (up to 20 years at least in females).

Remarks: (1) In the extinct Carboniferous plesion genus *Palaeothele* SELDEN 2000 – which is related to the Liphistiidae – teeth exist on BOTH margins of the cheliceral furrow (like in the Mgalomorpha), in contrast to extant members of the Mesothelae (Liphistiidae), in which only the anterior margin bears teeth. In the present fossil the posterior margin is hidden; teeth may exist or not. – (2) Clavate trichobothria exist in the genus *Liphistius* in contrast to other extant or known fossil genera of the Mesothelae.

**Relationships of the Mesothelae:** In its sister group – Opisthothelae (= Mygalomorpha + Araneomorpha, see fig. B) – a distinct opisthosomal segmentation is lost (most often the opisthosoma is soft, but a dorsal scutum exists not seldom, and remains of a segmentation may exist, e. g., in the mygalomorph Antrodiaetidae as well as in the more advanced Hypochilidae), the spinnerets are translocated to the end of the opisthosoma (few superficial „reversals“ exist in the Araneomorpha, e. g. in the family Prodidomidae, the number of the spinnerets articles is reduced, only four heart ostia exist, the poison glands are larger, the poison duct is larger, too, and translocated more distally, a dragline exists).

**Ecology and behaviour:** Most extant species are restricted to forests. The spiders live in tubular burrows which are closed by a trap door which possesses radial signal lines similar to certain Mygalomorphae like Ctenizidae; this apparently is an ancient pattern.

There is no indication that the life style of the fossils was different to extant spiders, the Burmese amber was produced by trees of a rain forest, see above.

**Distribution:** Known only from the Northern Hemisphere up to now (fossils of the Northern Hemisphere a much better known than fossils of the Southern Hemisphere!). Today exclusively South East Asia. – Fossil: Europe and North America (Carboniferous); South East Asia (first report): Burma/Myanmar (Cretaceous) (see below: *Cretaceothele* n. gen.).

**Diversity of extant and fossil higher taxa:** The only extant family of the Mesothelae is Liphistiidae (= Heptathelidae) of South East Asia; it includes few genera in about 100 species. The known fossils – three extinct families (named „Mesothelines“ by DUNLOP et al. in the World Spider Catalog by PLATNICK (2012)) as well as an extinct genus: A so-called „plesion taxon“ (see above) – are known from the Carboniferous of North America and Europe. On both continents members of the Mesothelae are extinct since an unknown period. – The present fossil in 100 million years old amber from Myanmar (Burma) (photos 10-13, figs. 5-7) bridges the huge gap in time between the 300 million years old Carboniferous fossils and today's taxa; furthermore it is the first fossil report from Asia. A similar case has recently reported in the arachnid order Ricinulei from Burmese amber, see WUNDERLICH (2011: 233-244) and this volume. Mesothelae is the only „true“ high spider taxon – see SELDEN et al. (2013) – which has been reported already from the Palaeozoic.

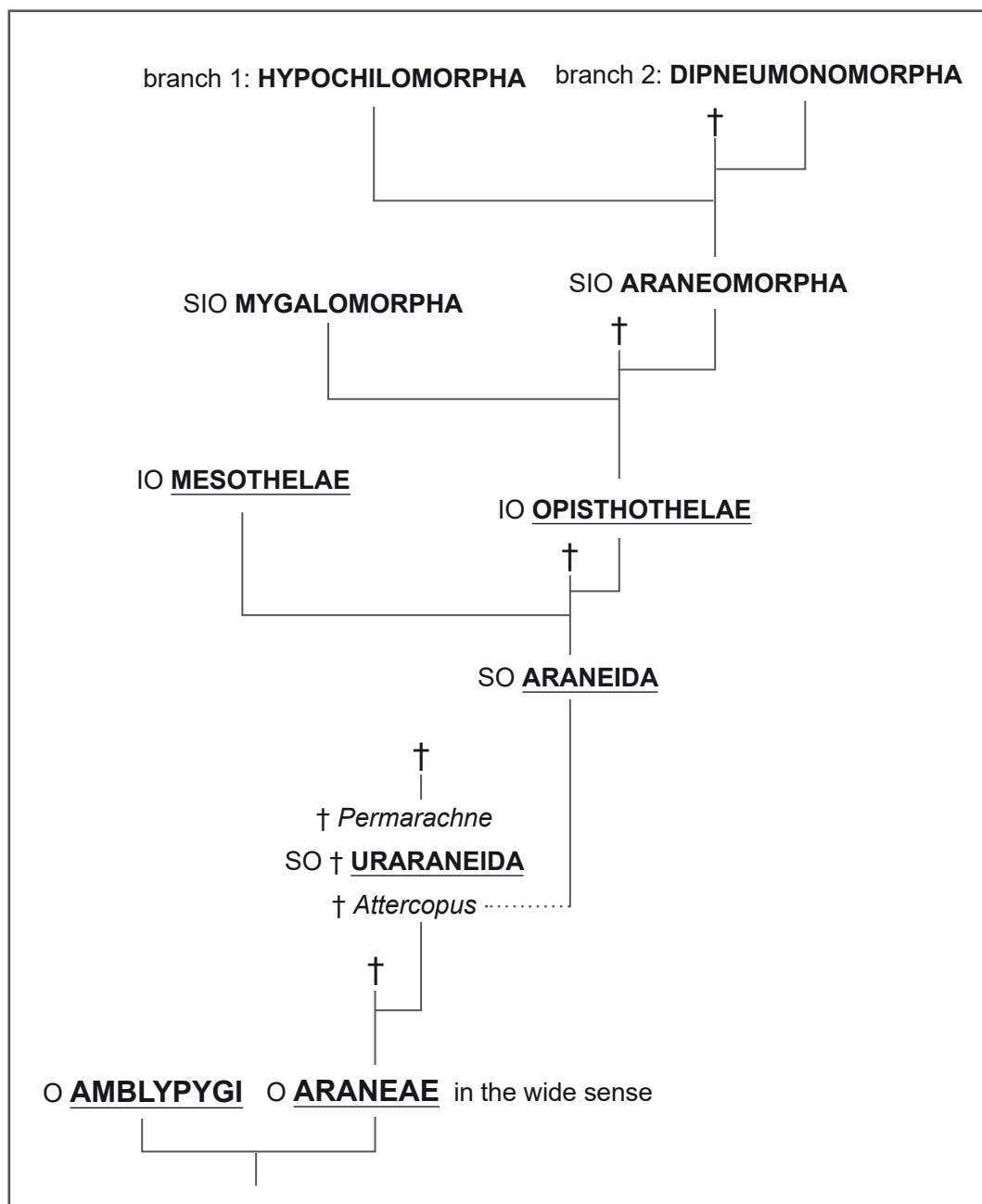


Fig. A. Strongly simplified hypothetical cladogram of the highest branches of the Araneae – and its possible sister taxon Amblypygi – during the first 200 million years of their evolution. More advanced branchings (lines) lead to the right direction. Four hypothetical extinct „blind ending lines“ are added in this figure. – Eras of branchings: Uraraneida/Araneida: Devonian, Mesothelae/Opisthothelae: Carboniferous, Mygalomorpha/ Araneomorpha: Probably Early Triassic. Abbreviations of the provisional levels: O = order, SO = suborder, IO = infraorder, SIO = subinfraorder. See fig. G p. 287.

## HYPOCHILOMORPHA

plagiognathy (figs. 3, 7), more posterior position of the posterior pair of lungs (further characters: See below: Hypochililoidea)

## DIPNEUMONOMORPHA

(remaining taxa like Filistatoidea, Haplogynae“ and „Entelegynae“)  
labidognathy (fig. 4), replacement of the posterior pair of lungs by tracheae, endocephalic venom glands, leg. autotomy, only 3 pairs of heart ostia

## MYGALOMORPHA

loss of the anterior median spinnerets, plagiognathy, labial and gnathocoxal cuspules, sternal sigillae, small eyes with tendency to a narrow eye field on a tubercle

## ARANEOMORPHA

replacement of the anterior median spinnerets by a cribellum, loss of tarsal trichobothria, vertical position of the basal chelical articles, long legs?, no moulting as adults, tendencies to evolve a capture web in higher strata and cheliceral stridulatory files, loss of digging behaviour

## MESOTHELAE

(extant: Liphistiidae; extinct: e.g. *Palaeothele*, a questionable liphistiid Carboniferous liphistiid genus)  
plagiognathy and multisegmented lateral spinnerets (fig. 7), deeply sloping sternum, and modified coxa IV (fig. 9), ventral outgrowth of the pedicel (fig. 9), small eyes in a narrow field on a tubercle (figs. 5-6); (further characters: See below)

## OPISTHOTHELAE

displacement of the spinnerets to the end of the opisthosoma, loss of clear opisthosomal segmentation, only 4 pairs of heart ostia, dragline



+ URARANEIDA

(Devonian to Permian; genera *Attercopus* & *Permarachne*)  
slender shape of the flagellum,  
loss of leg trichobothria?

ARANEIDA

loss of the telson/flagellum, translocation of the lateral opisthosomal spigots to 4 pairs of TRUE spinnerets in a VENTRAL position, connected to the disposition for building trap doors, digging behaviour, egg sacs and capture webs, venom glands, wide labium and sternum (figs. 7, 9), male pedipalpus functioning for sperm transfer?, egg sac?

AMBLYPYGI

loss of the telson (a postanal tubercle remains), pedipalpi functioning as capturing basket and bears a „cleaning brush“, strongly flattened body, autotomy between reduced patella and tibia, leg trichobothria: on patellae II-I V in fossils or on tibiae in extants

ARANEAE

opisthosomal spinning glands and simple spigots ventrally near the lateral margins (used for subterranean tubes?), tarsal organ, cheliceral glands, hairless fangs, stout legs without articulated tarsi and metatarsi, disposition for a coxa-trochanter autotomy, male pedipalpus functioning for sperm transfer? (see Araneomorpha), venom glands??, 5 pairs of heart ostia?

Synapomorphies: Postocerebral sucking pump (stomach), pedicel, orthognathy which includes protruding basal cheliceral articles similar to fig. 2, (slender) labium, probably loss of the pedipalpal metatarsus, and evolution of a peculiar anal tubercle.

Symplesiomorphies: Opisthosomal segmentation (see figs. 1, 5), two pairs of lungs, telson, eye triads, plagula ventralis, leg articulations (at least the tarsi), very long leg I, narrow sternum, leg trichobothria (?), 6 pairs of heart ostia, moulting as adults.

Fig. B. Hypothetic cladogram of the highest branches of the Araneae and its possible sister taxon Amblypygi, based on selected important characters. Compare figs. A, C and G p. 287.

## **Proposed new classification of the Araneae (s. l.):**

**Remark:** New ranks are proposed except the Araneae which are regarded in a wide sense here, including the Uraraneida as a suborder. See the discussion above and the **fig. G** p. 287.

Order Araneae CLERCK 1757 (s. l.)

Suborder Uraraneida SELDEN et al. 1991

Suborder Araneida CLERCK 1757

Infraorder Mesothelae POCOCK 1892 (1)

Infraorder Opisthothelae POCOCK 1892

Subinfraorder Mygalomorpha POCOCK 1892

Subinfraorder Araneomorpha SMITH 1902 (2)

Microorder Basal Haplogynae **n. taxon** (3)

Microorder Cleistospermiata **n. taxon**

branch 1: Hypochilomorpha MARX 1888 s. l. (4)

branch 2: Dipneumonomorpha PETRUNKEVITCH 1933 (5)

subbranch a: Leptonetoidea (6)

subbranch b: Archaeoidea

subbranch c: Entelegynae ROEWER 1961 (7)

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(1) Today exists only the family Liphistiidae THORELL 1869).

(2) ~ Labidognatha BERLAND 1932.

(3) Probably monophyletic. Including Filistatoidea and Synspermiata (= Dysderoidea s. l. + Pholcoidea).

(4) Including the superfamilies Austrochiloidea ZAPFE 1955, and Hypochiloidea MARX 1888.

(5) = Araneoclada PLATNICK 1977, Apneumonomorphae PETRUNKEVITCH 1933 and the "LAE-clade".

(6) Including cribellate and ecribellate, extant and extinct families, see below.

(7) This most derived and most diverse taxon includes the Eresidae, the huge RTA-Clade (\*), the superfamilies Oecobiodea and the today very diverse Araneoidea s.l. (= „Orbiculariae“).

Notes: (1) These provisionally branches do not reflect the system of the Araneomorpha; **see fig. G** below, in which Eresidae and Nicodamidae are not treated.

(2) This branch is not identical with the Araneoclada PLATNICK 1977, Apneumonomorphae PETRUNKEVITCH 1933 or Dipneumonomorpha PETRUNKEVITCH 1933, see above.

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(\*) It includes the diverse Trionycha (e. g. Agelenidae and Lycosidae) as well as the most derived and most diverse „Dionycha“ like Gnaphosidae, Thomisidae and Salticidae.

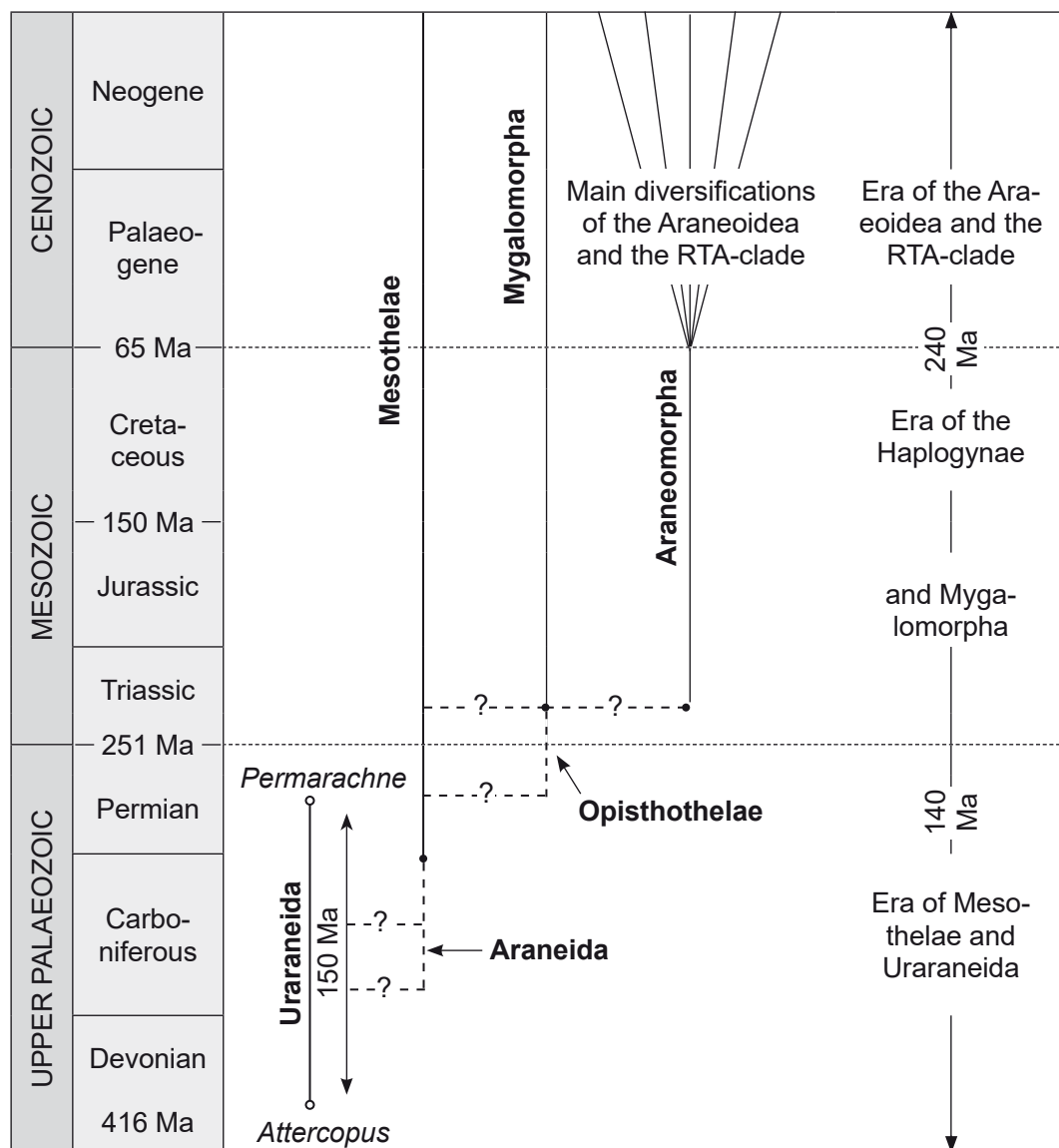
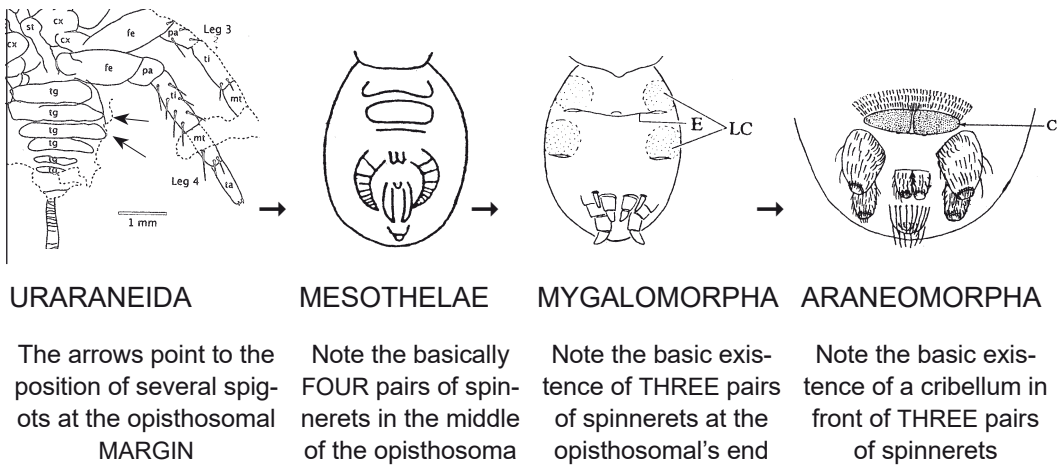


Fig. C. Hypothetic chronocladogram (\*) of the highest branches of spiders (Araneae). Ma = million years. Oldest proofs: † = Taxa of the Uraraneida, ◐ = Mesothelae, ● = Mygalomorpha, \* = Araneomorpha (Hypochilomorpha † Dipneumonomorpha). Remarks: (1) The main eras of spiders basal RADIATIONS may be Permian and Triassic. (2) The main era of enormous DIVERSIFICATIONS happened in the Palaeogene as demonstrated by the final lines of the huge/diverse branch Araneomorpha, which includes almost 90 % of all extant spider taxa within the subbranch Dipneumonomorpha (including, e. g., the „Haplogynae“, the superfamily Araneoidea and the RTA-clade). (3) The oldest known genera of this clade are *Argyrahne* and *Triassaraneus* of the Triassic which are almost as old as the oldest Mygalomorpha. These genera may be related to the Hypochilomorpha (but a cribellum has not been reported) or to certain „Haplogynae“ like the Leptonetoidea. (\*) The term „chronocladogram“: See WUNDERLICH (2004: 836, 1765f).

# Discussion

Araneae is a very diverse and – in the geological sense – old order, thus the real number of branchings during its evolution of 400 million years must be much higher than shown in figs. B and D which are strongly simplified if one would focus more closely. Doubtlessly further branches will be known in the future after the discovery of more fossil/extinct Palaeozoic and Mesozoic taxa. The level, the number and the designations/terms of the branches of higher taxa of the Araneae are by far not definitive; see the different theoretical aspects shown by WILLMANN (1985; 115, 130, figs. 27, 32) which concerns species and also taxa of higher levels. Various branchings – like the loss of the telson or the evolution of true spinnerets as well as their translocation at the origin of the Araneida – surely occurred not simultaneously but in several branchings STEP BY STEP, and numerous „blind lines“ of extinct taxa must have existed. Four of such extinct lines – hypothetical „sister taxa“ – are shown in fig. A; see also fig. C. After the discovery of a further extinct taxon a new sister taxon may „appear“, a previous sister taxon may have to be deleted, and new names for newly defined clades may be proposed. The numerous characters of the branch Araneomorpha (see fig. B) surely did also not evolve simultaneously, therefore – examined more closely and consequently – Mygalomorpha and Araneomorpha are NOT EXACTLY sister taxa although they are treated as sister taxa. The existence of plagiognathy (rsp. the transformation of the basal cheliceral articles from a horizontal to a vertical position) – as steps to the labiognathy of the Dipneumonomorpha – may have happened before the replacement of the anterior spinnerets by a cribellum. If so, plagiognathy would not be an apomorphic character of the Hypochilomorpha but probably of an earlier – unknown – branch of the Araneomorpha.

The translocation of the position and the number of spigots (in the Uraraneida) and spinnerets reflects the evolution of the highest taxa of spiders; see the order of the drawings from the left to the right below, ventral aspects of the opisthosoma:



# ON THE MESOZOIC AND PALEOGENE EVOLUTION OF SPIDERS

and remarks on their ecology

Eocene: See WUNDERLICH (2004: 258-270) on evolutionary „trends“, „missing links“ and co-evolution; Cretaceous: (2008: 541-582) and (2012: 161-168) on palaeobiogeography, biodiversity, extinctions, co-evolution and „missing links“. See also above as well as the partly overlapping chapter on the spider faunas below, the paragraphs on the superfamily Archaeoidea and on the relationships of the haplogyne superfamilies below.

Can the (in the geological sense) oldest proof, the sequence of high (suprageneric) fossil spider taxa as well as peculiar faunal „gaps“ – see below: the chapter of the Mesozoic spider faunas – during hundreds of millions of years of spider evolution teach us something about their phylogeny? I think: IT CAN, and the fossils will probably tell us more than recent alleged results or „molecular clocks“ (\*). Some examples:

(1) If the finds are correct which are based on fossils we can conclude that cribellate Entelegynae (Deinopoidea, Eresoidea and Oecobioidea) are much older than entelegyne members of the „true“ RTA-clade (see fig. G!), their origin differs by more than 100 million years (!), see below, and the entelegyne stage evolved separately in both clades (\*\*). Based on the known fossils this conclusion appears to be plausible (\*\*\*). The possible existence of two „BIG BANGS OF SPIDER RADIATION“ is discussed which probably happened (1) just after the mass extinction events during the Triassic: the „Triassic explosion of the Cribellates“: Haplogynae and Entelegynae part (a), the Araneoidea s. l. (incl. the Deinopoidea), the Eresoidea and the Oecobioidea, and (2) the „Plaeocene explosion“ (after the KT-events) of members of the Entelegynae part (b), of the RTA-clade, see below.

(2) Most authors regard the Araneoidea s. str. ORB WEB as very old and the irregular webs of this superfamily as derived but according to few authors – like LEHTINEN (2013: 92) – the irregular capture web of the Araneoidea is older than the orb web which should be derived: „The predecessors of the orb web spinners in Araneoidea are the spinners of sheet web (Linyphioidea) and of three-dimensional webs (Theridioidea), ...“. Several Mid or even Early Cretaceous fossils of members of orb-weaving Araneoidea – Nephilidae, Theridiosomatidae and Zygellidae – are clearly older than members of irregular capture web builders like Cyatholipidae, Linyphiidae, Nesticidae and Synotaxidae (Theridiidae – a single Mid Cretaceous specimen has been found – may be an exception, see below). The fossil proofs strongly contradict LEHTINEN's hypothesis.

(3) OLDEST PROOFS of high taxa and FAUNAL GAPS of fossils are of an enormous significance regarding the reconstruction of spiders phylogeny, see the paragraph on the Mesozoic spider fauna below, especially the absence of members of the RTA-clade and the linyphioid branch of the Araneoidea in the Mesozoicum. The family Lycosidae and the

subfamily Erigoninae of the Linyphiidae – they are among the most frequent and cosmopolitically distributed high spider taxa today – are absent not only in the Mesozoicum but they still were absent in the Eocene (the European ambers of the Eocene) and only found in the Miocene in Dominican amber ca. 20 million years ago. – The (in the geological sense) oldest „true“ spiders are the segmented Mesothelae (fig. 5, photos 10-13); they are probably the only spiders of the Palaeozoicum and survived up to now as relicts in the tropics. In this paper the family is first reported from Mid Cretaceous Burmese amber (Burmite) bridging the oldest (Carboniferous) proofs and the reports of today.

#### **(4) Results of MOLECULARGENETIC STUDIES.**

**(a)** Recently HORMIGA (2014) – based on moleculargenetic studies – doubted the monophyly of the Araneoidea s. l. (= „Orbiculariae“) and even strong relationships of the two main branches: The ecribellate Araneoidea s. str. and the cribellate Deinopioidea s. str., and he also doubted the monophyly of the orb web in contrast to most recent authors and in contrast to the proof of both groups of „orbiculariae“ which are well documented already from the Triassic. If the splitting of these groups happened already more than 200 million years ago their quite different genes are NOT AT ALL a surprise, and it has to be considered that the extant taxa (and their genes) are not at all identical with taxa which are extinct since a long time. I think that single-founded conclusions basically have to be regarded with hesitation.

**(b)** According to MORADMAND et al. (2014) the family Sparassidae should be the „most basal group within the RTA-clade“, 186 million years old, although not a single sure Mesozoic proof (during the almost 200 million years of this period) of this family or even of the whole RTA-clade exists (!), see below. This appears to me as a really „funny story“ in the fabulous world of molecular genetic. – Did Cretaceous members of this clade exist on the Southern Hemisphere in which Cretaceous/Mesozoic fossil spiders are only weakly studied? Various (extant) members of the RTA-clade are well known as ballooners – as well as Eocene fossil spiders, see WUNDERLICH (2004) – and they surely would not be restricted to the Southern Hemisphere for millions of years after their origin.

**(c)** According to DIMITROV et al. (2012) „The first pholcids appeared and diversified in the early Mesozoic about 207 Ma ago (185-228) Ma <,> before the breakup of the supercontinent Pangaea.“. I don't know a single Mesozoic member of the family Pholcidae among about 1000 mesozoic spider specimens.

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(\* According to HORMIGA & GRISWOLD (2014: 503) „So far, fossils have contributed little to resolve phylogenetic relationships.“ See also WUNDERLICH (1986: 96) (Three decades ago!). But see the important papers by ESKOV & ZONSHTEIN (1990) on mygalomorph spiders and the paper by WOOD et al. (2013)!

(\*\*) According to LEHTINEN (2013: 91) the cribellum (or a similar structure) evolved also twice in spiders: „Filistatidae ... has no true cribellum, just an independently evolved structure homologous to anterior median spinnerets of Liphistiomorpha, ...“. Note: the ancient Filistatidae possesses a divided cribellum in contrast to the more derived Hypochilomorpha. The more derived „Divided Cribellum Clade“ is (also) characterized by a divided cribellum, see fig. G and ESKOV & ZONSHTEIN (1990).

According to LEHTINEN (2013: 31) „There are two main lines of evolution in Araneomorph spiders. Araneoidea, Archaeoidea, and Nicodamidae have scaly surface of appendages while these surfaces in the other main group with real haplogynes and remaining entelegyne families are of „fingerprint type“. I can not confirm this statement. As I pointed out previously (1986: 108) the fingerprint type of the epicuticula exists in cribellate spiders – probably connected with the function of cribellate threads – but the scaly type exists in ecribellate spiders. Both types may even occur within the same family, the Nicodamidae: the scaly type exists in the ecribellate genus *Nicodamus* and the fingerprint type in the cribellate genus *Megadictyna*, see WUNDERLICH (1986: 214, figs. 209 and 210) (!).

(\*\*\*) The reflecting tapetum of the „secondary eyes“ of these two huge spider branches differs also more or less: The GRATED TAPETUM type is common in most hunting spiders of the RTA-clade, the CANOE-SHAPED tapetum exists in most Araneoidea (but also in some families of the RTA-clade!). See FOELIX (2011: 105).

#### The differing spider taxa and faunas in different epochs may be hints to the spider evolution:

(1) the CHANGES OF THE COMPOSITION OF HIGHER (ARANEOMORPH) SPIDER TAXA AND THE SPIDER FAUNAS from the Upper Triassic to the Upper Cretaceous (that means during about 140 million years) appear to my present knowledge much less pronounced than the most dramatical change from the Upper Cretaceous to the Late Palaeocene or Early Eocene (a time span of only about 20 million years) (!). See also the chapter on the faunistic below.

Within only 20 million years or less probably about three quarters of the about 120 extant spider families radiated – or even originated –: A „Palaeocene explosion“ after the K-T events which is well documented. The reasons for this FAST EVOLUTION – the radiation of the ecribellate Entelegynae, of all (?) families of the RTA-clade (and of most families of the Araneoidea s. str. as well), which I call the „BIG BANG NUMBER TWO OF SPIDER RADIATION“ (see also above and below, no. 6) – are enigmatic and most probably not monocausal.

Note on two insect orders in a letter by MICHAEL ENGEL in IV 2014: „Although termites and ants are known from the Cretaceous, the bulk of their diversity appeared in the Eocene and afterwards. For example, the family Termitidae comprises 70 % of all termite species and this family first appeared in the Eocene. The most diverse subfamilies of ants did the same“.

(2) The GAPS OF THE MESOZOIC SPIDER TAXA AND FAUNAS; THE ABSENCE OF THE MOST DERIVED SPIDERS (\*) of all (!) members of the very diverse Dionycha (e. g. Salticidae) (\*), even of the whole RTA-clade (e. g. Lycosidae and Salticidae) as well as most members of very diverse families of the Araneoidea s.str. like the Linyphiidae and Theridiidae are striking and surprising. Except Lycosidae these taxa were very diverse in Eocene European (e. g. the Baltic) ambers around 45 million years ago (!).



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(\* ) Most Mesozoic taxa are preserved in amber, and the amber mainly includes dwellers of higher strata of the vegetation and not spiders of the soil like many extant members of the RTA-clade. No sure member of the RTA-clade has been discovered in stone of deposits of Liaoning in China. See also fig. G below.

(3) In 2008 – see WUNDERLICH (2008: 547, fig. 3; see also fig. 4) – I concluded that the Mesozoic may have been dominated by haplogyne spider families, “THE AGE OF THE HAPLOGYNAE” (with regard to the Araneomorpha), and this conclusion is fully confirmed by the present investigation: I now know more than half of the surely reported spider families of the Araneomorpha from the classical Haplogynae (16) of this epoch but only 7 of the Entelegynae. DUNLOP & PENNEY (2012: 123) – apparently not familiar with these families, and ignoring my results (2008, 2011, 2012) – doubted this composition of the ancient fauna. It may be not a fault to look occasionally at the results of different authors. – Comparison on the generic level: See below: “Faunistic”, change.

(4) It is conspicuous that the radiation of the taxa of the RTA-clade and most Araneoidea s. str. near or after the end of the Cretaceous happened „simultaneously“ with the extinction of several diverse Mesozoic spider families of the Haplogynae like the Lagonomegopidae – see WUNDERLICH (2011: fig. p. 543) – the Mongolarachnidae and the Praeterleptonetidae.

(5) The oldest proofs of the Entelegynae are Triassic to Cretaceous reports of orb-weavers of the superfamily Araneoidea s. l.: (a) of the cribellate deinopoid Uloboridae and Salticoidae and (b) of the ecribellate araneoid Nephilidae, Theridiosomatidae, probably Theridiidae, and Zyggiellidae. The diversification and even probably the origin of not orb-weaving Araneoidea – irregular capture web dwellers like Cyatholipidae, Linyphiidae, Nesticidae, Synotaxidae and Theridiidae – is surely much younger.

(6) According to (still too less!?) fossil documents as well as conclusions which mainly regard the structures of the capture web – an early „BIG BANG NUMBER ONE OF SPIDER RADIATION“, a „Triassic explosion“ of cribellate spiders *INCLUDING THE ENTELEGYNE DEINOPOIDEA* – probably happened after a mass extinction in the Early Mesozoic, in the Upper Triassic 210 million years ago (\*) (or already in the Lower Triassic 250 million years ago?), (a) after the origin of the cribellum, the high performance of silk fibers (and the use of capture webs in higher strata of the vegetation) by the ancestor of the Hypochilomorpha, and (b) in connection with several „fast“ (convergent) losses of the cribellum (\*\*). Strong radiations occurred probably during only about 20 million years. „A bit later“ – probably already in the Jurassic – the Oecobioidea radiated, see the chronocladogram published by WUNDERLICH (2004: 836); and apparently in the Triassic the cribellate Araneoidea s. l. radiated (see above, no. 1), the orb web originated (in a vertical position?) – apparently PUSHED BY THE DIVERSIFICATION OF FLYING INSECTS. Remarkably both distinctive radiations (nos. 1 and 2) happened apparently soon after an event of mass extinction: 65 *rsp.* probably 210 million years ago. In my opinion both events and radiations happened not accidentally. DID GLOBAL CATASTROPHES PUSH STRONGLY THE EVOLUTION OF SPIDERS? See also above: Paralipomena and chapter I. According to the known fossils the (entelegyne) Araneoidea s. l. radiated twice: (a) The CRIBELLATE deinopoid branch within the Big Bang no. one (together with the classical

Haplogynae) as well as (b) within the Big Bang no. two: The ECRIBELLATE araneoid branch, mainly those families which had changed their capture web from the orb to an irregular web, e. g. the Linyphiidae and the Theridiidae (together with members of the RTA-clade).

Remarks: (1) „Probably“ and „apparently“ means that we still need more proofs by fossil taxa to be quite sure, mainly from the Jurassic and Triassic. (2) According to several authors the praecambrian EDIACARA-fauna radiated also in only about 20 million years or even less, like the following „Cambrian explosion“.

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(\*) See WOOD et al. (2013: fig. 3 p. 273).

(\*\*) According to my knowledge the percentage of cribellate genera declined dramatically from the Cretaceous (ca. 25 %) to the Eocene (ca. 10 %); see the chapter on faunistics below and WUNDERLICH (2008: 546) on the Araneoidea s. l.. Apparently the spinning apparatus of the ecribellate spiders evolved further on during 200 million years.

#### The enigmatic root and the fast radiation/diversification of taxa of the RTA-clade.

The Palaeocene represents a huge gap of the fossil documentation (Lagerstätten); unfortunately this is exactly the period in which I expect the main radiation of the RTA-clade which is by far the most diverse group of spiders today and was likewise diverse already in the Eocene, see WUNDERLICH (2004).

The RTA-clade is probably a monophyletic taxon. The origin of the entelegyne RTA-clade(s) is one of the most tricky problems of spider evolution; its root is still enigmatic, and hopefully fossils will solve this secret, probably with the help of excellently preserved spiders in Burmese and other Cretaceous ambers in which even internal female genital (vulval) structures may be preserved. – It is conspicuous that no sure fossil proof of a member of the RTA-clade exists from a period older than the end of the Cretaceous. Contrarily certain moleculargenetical studies – e. g. of the family Sparassidae, see above – point to a Cretaceous or even Jurassic origin of the RTA-clade.

I do not want to exclude that – besides the enigmatic family Eresidae – an extinct Late Cretaceous species related to or within the lagonomegopid branch of the Archaeoidea (photos 92-117) – a still unknown species which had an unspecialized eye position, see the Micropalpimanidae – lead to „the“ RTA-clade which perhaps started an explosive radiation around 65 million years ago and was diversifying mainly during the Palaeocene. The very diverse extinct family Lagonomegopidae is known in amber from the beginning to the end of the Cretaceous during almost 80 million years, see below and WUNDERLICH (2008: 543, fig. 2). Although in members of the family Lagonomegopidae the real genital stage is unknown, its complicated structures of the bulb are similar to an entelegyne structure. Probably the „lagonomegopid branch“ was entelegyne and the remaining Archaeoidea are secondarily haplogyne, see this branch and fig. G p. 287.

Several important characters of the lagonomegopid branch – e. g. the trichobothriotaxy (the existence of several tarsal and more than a single metatarsal trichobothrium as well), the existence of leg scopulae, the existence of a retrolateral tibial apophysis of the male pedipalpus, the larger cymbium which encloses main parts of the bulb, and the complicated structures of the bulb including several sclerites – are typical characters of „the“ RTA-clade and point to their relationships. A similar case may be the origin of

the birds as a still hidden (not definitely identified) branch of the dinosaurs (one of several related branches).

Does a member of (a relative of) the Lagonomegopidae represent the root of one branch of higher – entelegyne – spiders, of the RTA-clade? The existence of pro-marginal cheliceral „peg teeth“ of the Lagonomegopidae may contradict their predicted relationships but these modified bristles may have been replaced by true teeth during the evolution (they have been lost e. g. in the Stenochilidae!). These suggestions are new and appear likely to me but they may be wrong, and the lagonomegopid structures in question may be nothing else than structures which developed convergently to characters of the RTA-clade, comparable with certain structures of extinct fossils of reptiles which are similar to characters of mammals!

In a molecular study MORADMAND et al. (2014) recently consider the family Sparasidae „as most basal group within the RTA-clade.“. RAMIREZ (2014) regards the genus *Liocranoides* KEYSERLING 1881 (Tengellidae?) as sister of the dionychan lineage. I doubt that the most basal or the sister group of the Dionycha or of the RTA-clade will be found within extant taxa but one better investigate fossil taxa. Based on molecular studies HORMIGA (2014) recently doubted the monophyly of the „Orbiculariae“; Cretaceous fossils may be helpful to rectify or falsify this opinion.

Do ingenious ideas exist regarding the late development of the TRA-clade?

PENNEY et al. (2003) „provide the first evidence that spiders suffered no decline at the family level during these <Cretaceous – Tertiary> mass extinction events.“ and „it is unlikely that we will discover many, if any, more strictly fossil spider families in the Cretaceous.“ I know 10 strictly Cretaceous spider families (see the lists) – a similar situation (extinct Cretaceous families) exists to my knowledge in several insect orders like Diptera and Hymenoptera -, and clearly a huge decline of – haplogyne – spider families (connected with a rise of entelegyne taxa) exists after the end of the Cretaceous.

What was (what happened) different after the Cretaceous-Palaeogene event 65 million years ago which e. g. caused (besides other events) the extinction of the dinosaurs? Has this event to do with the extinction of haplogyne spider families and/or the radiation of members of the RTA-clade? (The ancestor of araneomorph spiders is generally considered to have been a cribellate capture web dweller; besides the superfamily Araneoidea the RTA-clade is most derived within the araneomorphs).

In Mid Cretaceous amber from Myanmar (Burma) I know numerous capture web-dwelling spiders as well as sit-and-wait-predators. But WHERE WERE THE VAGILE HUNTERS of araneomorph (\*) spiders?

In this respect evolution, ecology, behaviour and biogeography are strongly connected.

ECOLOGY: In general/basically we may distinguish between several „Lebensformtypen“ resp. „Lebensweisetypen“ („life styles“ may be an adequate term in English), see BALOGH (1958:77-82) and STORCH et al. (2001: 46). Regarding the prey capturing of spiders we may distinguish three main types of „Lebensweisetypen“ (besides peculiar kinds like those of Deinopidae or „Bola Spiders“):

- (1) sessile „capture web dwellers“ which are frequent in higher strata of the vegetation and also frequently preserved in ambers, e. g. cribellate spiders of the extinct families Mongolarachnidae and Pholcochyroceridae (photos 65-73) as well as cribellate and ecribellate members of the superfamilies Leptonetoidea and Araneoidea s. l. (photos 155-175).

- (2) more or less sessile „sit-and-wait predators“ which build no capture web:
  - (a) waiting for prey on various substrates. In ambers: certain Hersiliidae (Oecobioidae) on the bark of trees and members of the superfamily Archaeoidea (photos 92-139) like Archaeidae and probably Lagonomegopidae (on twigs?);
  - (b) spiders waiting for prey hidden in tubes or cracks: Frequent in ambers are e. g. members of the family Segestriidae (photos 24-35);
  - (c) spiders waiting for prey under a tent like extant members of the Oecobiidae and probably extinct Oecobiidae: spiders of *Zamília* (photos 145-148) during the Cretaceous (and of the related genus *Mizalia* in the Eocene as well);
- (3) „vagile hunters“:
  - (a) Prowling hunters like members of the family Scytodidae and apparently certain extant Salticidae (most members use prey capturing by jumping);
  - (b) vagile hunters (a jumping behaviour is frequent): mainly members of the huge branch of the entelegyne RTA-clade, the Dionycha, which are – still? – not reported from the Mesozoic (!).

Taxa of the types (1) and (2) are frequent and diverse in Mesozoic and Eocene ambers as well as today. Several „sit-and-wait predators“ (like members of the Archaeidae and of the Lagonomegopidae, see these families below) were probably nocturnal. – Araneomorph taxa of the type (3b) are NOT reported from the Mesozoic (\*) but – the members of the RTA-clade – were very frequent and diverse in Eocene amber forests as well as today, e. g. families like Gnaphosidae, Salticidae and Zodariidae of the Dionycha. The first step to their evolution was probably the loss of the cribellum (probably it was lost already previously) as an initial ignition. These spiders are frequently FAST RUNNERS of the soil, frequently evolved a JUMPING BEHAVIOUR and HIDING/ MOULTING SACS. In numerous families the unpaired tarsal claw has been lost, a – e. g. coxa-trochanter – leg autotomy, tarsal and metatarsal trichobothria exist; leg scopulae evolved frequently. These are spiders of a peculiar life style „Lebensweisetyt“. Their habitus is similar to certain members of the extant family Lagonomegopidae in Burmite. Did the entelegyne Sparassidae replace the extinct haplogyne Lagonomegopidae at the beginning of the Paleogene?

According to certain authors about 50 % of all species became extinct at the end of the Cretaceous. This „mass extinction event“ extinguished (e. g.) all dinosaur taxa except the birds, but the effect on spiders is not well known (see above), and the reasons for the late – apparently post-Cretaceous – radiation/diversification of the RTA-clade still remains a secret. Did such diversification happen outside from forests in steppe and grassland from which fossil resin is absent or quite rare? Did the Palaeocene/Eocene development of grassland favour the development of the special lifestyle of „vagile hunters“, see above (3)? And has it been connected with the strong diversification of (socially living) ants? See WUNDERLICH (2008: 550).

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(\*) Vagile hunters of the type (3b) are also TINY HAPLOGYNE araneomorph spiders (in contrast to the LARGER ENTELEGYNE hunters of the RTA-clade): the Orchestiniinae of the family Oonopidae. This ancient family still exists; it is reported from the whole Cretaceous (*Burmorchestina* in Burmite) but it should be much older. – Mygalomorph spiders are not included in this discussion. (Dipluridae, photos 15f, existed in the Burmese amber forest, Theraphosidae – it is regarded as a „young“/derived taxon – is unknown from the whole Mesozoic).

Note concerning an insect order: VRSANSKY (2002) published the evidence „that the order Mantodea as specialized carnivores originated from the new family Liberiblattinidae of the Jurassic cockroaches (Blattaria),...“. Other families – related to the Mantodea – originated from the same branch as the Mantodea. Another branch originated millions of years earlier from the same extinct family Liberiblattinidae, and lead to the extant family Umenocoleidae which is known since the Early Cretaceous.

The restricted view on extant taxa solely, and the importance of fossil taxa:

The families TETRABLEMIDAE (see below) and PHOLCIDAE may be regarded as sister taxa if only extant families are taken in consideration but their various important differing characters must have been caused by various particular steps during the long evolution of these families and their relatives; therefore a „true“ sister taxon of the Tetrablemmidae should well be found within Mesozoic extinct spiders in the future. Furthermore the apparent absence of the Pholcidae in the Mesozoic – the oldest proof comes from Eocene Baltic amber – may indicate a much lower age of the Pholcidae compared with the Tetrablemmidae.

See the family Oecobiidae and the superfamilies Archaeoidea and Araneoidea s.l.: The deinopoid branch.

Probably entelegyne families like NEPHILIDAE and THERIDIOSOMATIDAE – as well as related families like Theridiidae, Linyphiidae and Synotaxidae, too – displaced the haplogyne PRAETERLEPTONETIDAE (\*) during the Lower Cretaceous and/or Early Palaeogene, see WUNDERLICH (2004). – Why did this happen? As in other members of the superfamily Araneoidea in these families the capture web bear sticky droplets on capturing threads in contrast to members of the ancient Praeterleptonetidae (\*\*). Probably this „innovative“ evolutionary advantage was the (main) reason for the success of the Theridiosomatidae and the extinction of their ancient haplogyne competitors, e. g. the Praeterleptonetidae. – The replacement of the orb web by irregular capture webs after the end of the Cretaceous – e. g. by Linyphiidae, Synotaxidae and Theridiidae – may have been an important „innovation“, a method which probably „opened the door“ to an easy capturing of ant workers, which represent a quite high biomass in the Paleogene but not earlier.

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(\*) as well as the Mongolarachnidae and other families, members of the Pholcoidea. SELDEN et al. (2013) described the extinct family Mongolarachnidae from the Jurassic – see Cretaceous taxa of this family below -, and pointed to a probably greater diversity of the „orbicularian stem“ group during the Jurassic. At least some of the ancient taxa like *Zhizhu* are more likely haplogyne in my opinion, see below: Deinopoidea and Mongolarachnidae.

(\*\*) Also the haplogyne Pholcidae evolved capture threads which bear sticky droplets (like in the Araneoides s. str.), members of this family are unknown from the Mesozoic but existed already in the Eocene – see WUNDERLICH (2004) – and are very diverse today. See WUNDERLICH (2008: 553).

„Long-living“ genera: See WUNDERLICH (2012: 167). In this list the genus *Ariadna* most probably has to eliminate. See the chapter on faunistics.

Dwarfism and gigantism: See below, e. g. the families Segestriidae, Theridiosomatidae, Uloboridae and Zygiellidae. Usually we find larger species in confamiliar extant and Eocene families than in Mesozoic relatives but – as an exception – the oldest member of the Uloboridae is quite large.

An incomplete possible CHRONOcladogram of certain suprageneric taxa of the family OECOBIIDAE – it covers 200 million years – has been published by WUNDERLICH (2004: Fig. p. 836) in connection with the oecobiid characters (p. 835). The Mid Cretaceous dubious new subfamily Retrooecobiinae in Burmite (its relationships are unsure) has to be added to this chronocladogram. – See also WOOD et al. (2013).

## II. ERRONEOUS AND DUBIOUS DETERMINATIONS OF MESOZOIC SPIDERS AND INCORRECT CONCLUSIONS

See „unsure relationships“ of certain taxa in the lists below.

Errors, facts and fakes in the sense of ALDOUS HUXLEY („confirmation bias“):  
*Facts do not stop to exist just because they are ignored.*

*Errors themselves are not the biggest problem but the missing acceptance and missing corrections are.*

*Palaeontologists have to work like criminalists: their conclusions are often based on circumstantial evidences and have to question and prove again and again.*

JW

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The list of unsure or erroneous determinations of fossil spiders is long, see WUNDERLICH (2008: 539-540) and (2012: 540-542). Several authors – mainly no araneologists and even no biologists – caused a chaotic/horrible situation in this matter. Errors may be caused by insufficiently observable/hidden structures or by artefacts, by the presence of only juvenile spiders of a taxon, by misinterpretations of structures resp. restricted knowledge of spider taxonomy, by mistaken kinds of fossil resins or fakes (\*). Certain errors are also caused by the fact that the diagnoses of some spider families – see e. g. Mongolarachnidae, Oecobiidae and Uloboridae below – have to be strongly modified if extinct (Mesozoic) taxa are included. Furthermore convergently evolved



body shapes as well as various structures like bristles, spines and trichobothria may complicate a correct determination – e. g. by the present author -, see below, the families Praeterleptonetidae (extinct) compared with Theridiosomatidae and Tetrablemmidae compared with Oonopidae: Gamasomorphinae.

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(\*) I will discuss here the unqualified conclusions in a paper by POINAR & BUCKLEY (2012). These authors described new taxa – the spider genus *Geratonephila* (an adult male and a juvenile of the family Nephilidae) and the wasp genus *Cascoscelio* of the family Platygasteridae –, the alleged social behaviour of the spiders, and the wasp as an alleged potential prey of the spiders. The piece of amber was said to be Mid Cretaceous amber of Burma but apparently the kind of this amber was not studied more closely, and I doubt that it is true Burmese amber: Neither a member of the Nephilidae nor of the Platygasteridae have been reported from Burmese amber up to now; among hundreds of spider inclusions in Burmite I have never found a member of the genus *Nephila*. I agree with the comment by PENNEY (2012): No evidence exists of social behaviour of the spider species, and no evidence that both spider specimens are conspecific. No apomorphic character is provided for the genus *Geratonephila* and the structures of the male pedipalpus are exactly as in the extant genus *Nephila* LEACH 1815 (#) which is frequent in Miocene Dominican amber. In my opinion *Geratonephila* is nothing else than a junior synonym of *Nephila* (**n. syn.**). The shape of the embolus of *Nephila tenuis* WUNDERLICH 1986 (figs. 156-157 p. 195) is variable and depends strongly on its aspect and the kind of deformation by the preservation. Therefore I regard the type species of *Geratonephila* – *burmanica* – as a questionable junior synonym of *Nephila tenuis* WUNDERLICH 1986 of Dominican amber (**quest. n. syn.**). – Because of the numerous errors – which may mislead investigators in the future – this paper is an example of papers which should never appear.

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(#) The pedipalpal position of the holotype in fig. 3 is unclear, it may be more ventrally than laterally.

Another alleged member of the family Nephilidae: *Nephila jurassica* SELDEN et al. 2011 has been described from the Jurassic of China, based on an adult female. SELDEN et al. (2013) transferred the species to the genus *Mongolarachne* of the ancient family Mongolarachnidae, see below. This erroneous assignment led WOOD et al. (2013: 267) to wrong conclusions on the phylogeny of huge branches, the Araneoidea and the RTA-clade.

Completely wrong conclusions on the phylogeny of spiders and on fossil spider faunas are based on uncountable erroneous light-minded determinations. They caused (and cause) optically nice but foolish „cladograms“ including so-called „ghost lines“ and will mislead students of biology, palaeontology and phylogeny in the future for many years; see e. g. PENNEY & SELDEN (2011: 72-73) and PENNEY (2013: 300-301). In these books members like the families Lycosidae and Pisauridae are erroneously reported from the Cretaceous. Relevant corrections by the present author were and are ignored. The alleged existing members of sister groups in the Cretaceous, e. g. of the families Dictynidae (a member of the „divided cribellum clade“) or Philodromidae, Pisauridae and Thomisidae (members of the RTA-clade) may provide „ghost lines“ which had better be called „lines of phantasy“. Reports of both huge clades are (still) unknown from the whole Mesozoic, see below.



In my opinion the conclusion on the simultaneous existence of the sister taxon of a fossil taxon is not justified. Such conclusions are based on an unreflected simple, formal and unbiological kind of thinking. The oldest (fossil) proof of a taxon is not necessarily identical with the origin of its sister taxon.

PENNEY et al. (2003) „provide the first evidence that spiders suffered no decline at the family level during these <Cretaceous – Tertiary> mass extinction events.“ and „it is unlikely that we will discover many, if any, more strictly fossil spider families in the Cretaceous.“ I know 10 strictly Cretaceous spider families (see the list) – a similar situation exists in certain insect orders like Diptera and Hymenoptera -, and clearly a huge decline of – haplogyne – families exists after the end of the Cretaceous.

In the following I will give an example of wrong conclusions which are based on errors of determination as well as of misunderstandings of the relationships of higher spider taxa: In 2008 I concluded that the Mesozoic may have been dominated by haplogyne spider families, and this conclusion is fully confirmed by the present study, see above and below. DUNLOP & PENNEY (2012: 123) doubted this composition of the ancient fauna. One reason: These authors regarded the haplogyne spider superfamily Archaeoidea (under Palpimanoidea) – it includes e. g. Archaeidae, Lagonomegopidae (their members are quite frequent in the Mesozoic) as well as Micropalpimanidae (\*), Huttoniidae (most probably a wrong determination) (\*\*) and Spatiatoridae (\*\*\*) – erroneously still as an entelegyne taxon (in contrast to the results by HUBER (2004)), and included erroneously numerous entelegyne families (like Corinnidae, Deinopidae, Dictynidae, Linyphiidae, Philodromidae, Pisauridae, Sparassidae, Tetragnathidae and Thomisidae) in the Mesozoic spider fauna. On the other hand numerous published haplogyne taxa which were frequent in the Mesozoic – see WUNDERLICH (2008, 2011) and the chapter on the Mesozoic spider fauna below – were ignored by these authors; their existence in the Mesozoic does apparently not fit in the conclusions of these authors.

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(\* ) Remarkably the family Micropalpimanidae (see below) was declared as „not valid“ by PENNEY & SELDEN (2011: 60) although it was never synonymized or downgraded; see also DUNLOP & PENNEY (2012: 123-124): „... synonymize the extinct families Spatiatoridae and Micropalpimanidae with Huttoniidae IN THE NEAR FUTURE.“ (Several years later I see that certain palaeontologists use thinking probably in million of years like the age of the fossils...).

(\*\*) In my opinion the family Huttoniidae – only juvenile fossils are known – has to be removed from the list of Mesozoic spiders, see below: The superfamily Archaeoidea.

(\*\*\*) Mesozoic members of the Spatiatoridae are reported for the first time in this paper.

In the following I list several FURTHER EXAMPLES OF ERRONEOUS OR DUBIOUS DETERMINATIONS, and I will start with errors of my own (see also allaged Cretaceous DICTYNIDAE below):

Previously – before the knowledge of better preserved material – I (2011, 2012) regarded erroneously certain TETRABLEMMIDAE as members of the OONOPIDAE: Gamasomorphinae. With hesitation I regarded certain SALTICOIDIDAE as DICTYNIDAE, see below, following the erroneous determination by PENNEY. Furthermore – after the study

of much more and better preserved material – I hopefully can provide now more correct diagnoses of the Leptonetoidea and its taxa. Also with hesitation I light-minded overtook an erroneous determination by PENNEY of the family DEINOPIDAE in Burmite, see below. *Hypotheridiosoma* WUNDERLICH 2012 was erroneously regarded by me as a member of the family THERIDIOSOMATIDAE of the superfamily Araneoidea but it is now – after the study of well preserved new material – regarded as a probable member of the extinct family PRAETERLEPTONETIDAE (superfamily Leptonetoidea) but see below! Few years ago I regarded the Zarqaraneini WUNDERLICH 2008 (preserved in Jordanien amber) with hesitation as a member of the Araneoidea: Protheridiidae but now I transfer it – also with some hesitation: the existence/absence of a triad of their posterior spinnerets has still to study with the help of a MicroCT (in prep.) – to the superfamily Leptonetoidea: Praeterleptonetidae. The family Protheridiidae has to be removed from the list of the Mesozoic spider fauna.

*Orchestina rabagensis* SAUPE et al. 2012, described in the family Oonopidae, may be the member of a different family, see below (Oonopidae).

SAUPE & SELDEN (2009) reported the first fossil (Cretaceous) member of the family Mecysmaucheniidae which I consider as a subfamily of the Archaeidae (the level may be a matter of opinion), and I transfer the genus *Archaeomecys* to the Archaeidae s. l., see below.

The peculiar Jurassic family Juraraneidae ESKOV 1984 – the only known species of this family is *Juraraneus rasnitsyni* ESKOV 1984, based on a single male which probably is subadult, see SELDEN (2013) -, preserved in stone, was placed by ESKOV and also by SELDEN (2012) in the superfamily Araneoidea. SELDEN reported metatarsal calamistra in this taxon which were not judged as calamistra by ESKOV. Although allegedly cribellate and although the eyes, details of the spinning apparatus – including a cribellum – and the pedipalpus – e. g., the sure existence of a paracymbium – are unknown in the single specimen, SELDEN (2012: 319) placed it, e. g., based on its shape (\*) „ancestral to the Araneidae“, but in fig. 7 it is placed at the base WITHIN the family Araneidae. If this position of *Juraraneus* was correct, a loss of the cribellum must have happened (a) once within the branch of the Araneidae and (b) three times separately within the Araneoidea. Furthermore the diagnosis of the Araneoidea (s. str.) has to be modified strongly from basically ecribellate to cribellate.

Is *Juraraneus* really a cribellate taxon? In my opinion (a) the position of the alleged/questional cribellum – see fig. 2 in SELDEN (2012) – is too far from the spinnerets compared to all known extant and fossil cribellate spiders. (b) The DORSAL position of the calamistrum in the sense of SELDEN is quite different from the RETRODORSAL position of all known (extant) cribellate spiders. (c) The alleged calamistrum of the right metatarsus IV is twice the length of the left one. (d) In a Cretaceous spider from Liaoning (China), F2454/LI/CJW, a questional member of the family Araneidae, which may lack a cribellum, shows a structure quite similar to the structure considered as a calamistrum by SELDEN. (e) The fine structure of hairs of the alleged calamistrum have not been documented by SELDEN by a photo or a drawing. Therefore I doubt the interpretations by SELDEN, regard the „calamistra“ sensu SELDEN as POSSIBLE artefacts (remains of bristles??), and the genus *Juraraneus* as PROBABLY ecribellate.

Because of its characters – e. g. the absence of feathery hairs, a wide cymbium and the complicated structures of the bulbus – see SELDEN (2012) (\*\*) – as well as the rosette-shaped position of the spinnerets. In contrast to most (but not all!) Araneidae the leg

bristles of *Juraraneus* are slender. The taxon may be not far from the root of the Araneoidea s. str., the ecribellate (?) branch of the Araneoidea s. l. (= „Orbiculariae“), BUT IT WELL MAY BE A MEMBER OF THE HAPLOGYNAE, e. g. of or near the diverse superfamily Leptonetoidea, the families Pholcochyroceridae and Mongolarachnidae.

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(\*) A wide opisthosoma and stout legs exist also in certain Uloboridae, e.g., in *Hyptiotes*.

(\*\*) According to SELDEN (2002: 319) „*Juraraneus* is not a deinopoid because it lacks ... the femoral trichobothria of this superfamily.“ In contrast to this statement – and well-known – femoral trichobothria occur only in (most members of) the family Uloboridae in this superfamily, and are completely absent in the family Deinopidae.

The family Mongolarachnidae has been regarded by SELDEN et al. (2013) as related to the „cribellate orbicularians“ but in my opinion it is a member of a more ancient taxon of the Leptonetoidea, see below.

*Palaeomicromenetus* PENNEY 2003 has been described under Deinopidae but is now – with little hesitation – regarded as a member of the family Salticoidae, see below. Therefore the family Deinopidae has to be removed from the list of Mesozoic spiders.

The Jurassic *Seppo koponensis* SELDEN & DUNLOP 2014 – based on a probably adult female in calcit – has been regarded as a member of the superfamily Archaeoidea (under Palpimanoidea) and not assigned to family level. The authors of this taxon founded their determination mainly on the existence of socket „peg teeth“ (which really are modified bristles) but their tip apparently is not blunt as usually in peg teeth. Furthermore the existence of numerous leg bristles (they are absent or extremely rare in the remaining fossil and in extant taxa of the Archaeoidea!), and a well developed pedipalpal claw (it is absent or strongly reduced in the Archaeoidea) may argue against relationships to the Archaeoidea but probably more for relationships to the Araneoidea/Deinopidea which usually/frequently possess short legs III and large to powerfull legs I as well as large basal cheliceral articles like the present fossil. The transport of a dweller of higher strata of the vegetation – like Araneoidea – on a tree or its branch to a marine deposit appears likely to me. Sure mesozoic ground-living Archaeoidea are unknown to me but dweller of higher strata of the vegetation were frequent, see below. I do not want to exclude that the enigmatic fossil in question may be strongly related to the families Araneidae or Zygiellidae.

*Macryphantes* SELDEN (1990) (= *Palaeouloborus* n. syn.), described under Tetragnathidae, is here regarded as a genus of the family Uloboridae, see below. Tetragnathidae has to be removed from the list of the Mesozoic spider fauna.

CHANG (2004) described four dubious Cretaceous members under *Araneus* (Araneidae) in stone from Liaoning (China), apparently without any knowledge of spiders. Even a family assignment is impossible. No sure Mesozoic proof of the family Araneidae exists (!), see below (the family Araneidae).

Cretaceous members of the family Linyphiidae are based on erroneous determinations, see below. I do not want to exclude that the single male of a linyphiid taxon in alleged Cretaceous Ethiopien amber (this amber is probably younger, post-Cretaceous) (a tax-

on not named or described in detail up to now). To my present knowledge the family Linyphiidae has to be removed from the list of Mesozoic spiders.

Cretaceous Dictynidae: With hesitation I regarded some spiders in Burmite as members of the family Dictynidae, e. g. a female of *Burmadictyna* WUNDERLICH 2008. After the discovery of new material – adult males – in Burmite *Burmadictyna* turned out as a member of the extinct family SALTICOIDIDAE WUNDERLICH 2008, photos 155-159, see below. Two juvenile spiders in Cretaceous amber from New Jersey were published under Dictynidae gen & sp. indet. by PENNEY (2002: 717-220). According to the undivided cribellum (fig. C) and the relatively short calamistrum (fig. B) these spiders are not members of the family Dictynidae which possesses basically a divided cribellum and a long calamistrum. I do not want to exclude that these spiders are members of the family Salticoididae, probably of an unnamed taxon. – In 2008: 649-651 I described five specimens (juveniles and probably adult females) under QUESTIONABLE Dictynidae indet. (Sp. 5 has most probably 8 eyes but not 6 as published.). I now regard most of these specimens as members of the family Uloboridae but surely not of the Dictynidae; the cribellum of sp. 4 is undivided in contrast to the Dictynidae. Therefore the family Dictynidae has to be removed from the list of Cretaceous and Mesozoic spider families.

The type species of *Archaemecys* – *A. arcantiensis* SAUPE & SELDEN 2009 – was previously published as „Arachnida Salticidae“ (!) by NERAUDEAU et al. (2002: fig. 6.8), quite a different superfamily of spiders. Another Cretaceous specimen was published by KADDUMI (2005: 47, fig. 52) from Jordanian amber erroneously as a „salticid Spider“. Members of the Salticidae are unknown from the Cretaceous. Such erroneous reports may be distributed worldwide via Internet. If the identification of the family Salticidae (and related families) in the Cretaceous are correct this would be the first Cretaceous reports of the huge branches Dionycha and probably of the whole RTA-clade. The consequence of these wrong determinations are COMPLETELY INCORRECT CLADOGRAMS of higher spider taxa – see the books by DUNLOP, PENNEY and SELDEN which have strongly to be revised!

To my experience – concerning fossil spiders in Burmite – the families Eusparassidae, (= Sparassidae), Myrmecidae (= Corinnidae), Oonopidae, Pisauridae (see below), Tetragnathidae and Thomisidae (specimens = Lagonomegopidae?) (almost the complete number of families of this list, with the exception of the Theridiidae, see below) which were reported by RASNISYN & ROSS (2000: 24) from the Burmese amber collection at the Natural History Museum London have to remove from this kind of amber (and of the list of Mesozoic spiders as well) based on my present knowledge. Probably the determination of all of these spiders was based on juveniles which determination – even to the family level – frequently is quite unsure.

Basically I consider all reports of Cretaceous/Mesozoic members of the „divided cribellum clade“ (e. g. Dictynidae) and of the RTA-clade like Lycosidae, Pisauridae and Salticidae – as based on erroneous determinations.

Remark on the superfamily Archaeoidea (= Palpimanoidea): FORSTER & PLATNICK (1984) mixed in their superfamily entelegyne (e. g. Mimetidae) and haplogyne (e. g. Archaeidae and Palpimanidae) families and regarded it as a member of the branch Entelegynae. The superfamily is based on the haplogyne (!) family Archaeidae; see e. g. HUBER (2004), and this error was never clearly corrected. This wrong assignment caused a lot of errors continuing up to now for a quarter of a century (!), see the list of fossil spi-

ders in the World Spider Catalog by PLATNICK, and the paper by HORMIGA & GRISWOLD (2014)! See below, the fig. G including notes on secondary haplogyne Archaeoidea.

Remark on EOCENE Thomisidae indet.: SELDEN & WANG (2014) regarded three specimens as members of the family Thomisidae (incertae sedis), in which the eyes are unknown and the existence of an unpaired tarsal claw appears not sure to me (absent the the authors). According to the relatively long leg IV, the absence of strong paired ventral tibial and metatarsi I-II bristles in a position CLOSE to the leg articles as well as the prominent bulbi and the unknown (absent?) pedipalpal tibial apophyses I regard these specimens as members of the family Araneidae but not of the Thomisidae.

SELDEN et al. (2015, in press, J. Syst. Palaeontology) described two species of the new cribellate genus *Zhizhu* in stone from the Middle Jurassic of China (in Liaoning the spiders were very frequent, eudominant!), and regarded it as a member of the Deinopoidea. In my opinion the relationships of this genus are quite unseure. The thickened articles of the male pedipalpus and the (sclerotized?) epigyne are similar to the superfamily Oecobioidea but the depressed and concave metatarsus IV is similar to the family Uloboridae – a „first step“ to the Uloboridae? On the other hand I do not want to exclude relationships to the extinct cribellate family Mongolarachnidae, see above. *Zhizhu* has been regarded by SELDEN as a member of the Entelegyne by its „complex male pedipalpus“ but the bulbus structures of numerous Haplogynae are quite complex, see DEELEMEN-REINHOLD (1995) and this paper! In my opinion *Zhizhu* is more likely a member of the Haplogynae, see below: the family Mongolarachnidae.

The unsatisfactory molecurar genetical findings regarding araneomorph spiders – compared with the fossil proof; see above the chapter on the Mesozoic and Palaeogene evolution of spiders – can probably be explained by the long period of araneomorph spider evolution – during 200 or even 250 million years – compared with the short (a time span of probably only 10 or 20 million years) and explosive early radiation of basal araneomorph spiders more than 200 million years ago, in which probably a quite higher rate of mutations occured and which cannot documented any more in a sure way.

### III. THE MESOZOIC SPIDER FAUNAS AND REMARKS ON THE BIOGEOGRAPHY

The fast and enormous progress in the knowledge of the Mesozoic spider fauna is best demonstrated by the new finds in the extinct family Lagonomegopidae, see below, the superfamily Archaeoidea. The first lagonomegopid member has been described from Siberian amber only two decades ago – see ESKOV & WUNDERLICH (1995) –, and now

(2015) we know 14 genera from 7 kinds of Cretaceous ambers of this family. It has turned out that the ancient Lagonomegopidae was one of the most diverse families of spiders in that era preserved in Cretaceous ambers besides the Archaeidae, Praeterleptonetidae and Segestriidae.

While only members of the Mesothelae (see fig. 5, photos 10-13) are reported from the Palaeozoic – see SELDEN et al. (2013) – between 32 to 40 families of Mesozoic (Triassic, Jurassic, Cretaceous) spiders are listed/described in this paper.

Up to now more than 1200 fossil spider species from all periods have been described; about 35 times more extant spiders have been described.

### **ANNOTATED LIST of the spider (Araneae: Araneida) taxa known from the Mesozoic, their age/era, deposit, sex, stage, and distribution:**

(Uraraneida: See above)

See the list of fossil taxa by DUNLOP in PLATNICK's Catalog of the Araneae (internet), and PENNY & SELDEN (2011: 56-62). Few corrections as well as certain opinions of the present author are stated here:

- (a) Mecysmaucheniidae (superfamily Archaeoidea = Palpimanoidea) is regarded as a subfamily of the Archaeidae;
- (b) Archaeoidea (= Palpimanoidea) is regarded as a member of the Haplogynae but not of the Entelegynae, see HUBER (2004);
- (c) Psilodercinae DEELEMAN-REINHOLD 1995 of the Ochyroceratidae has been upgraded to family rank by WUNDERLICH 2008;
- (d) Eopsilodercidae WUNDERLICH 2008 is again regarded as a family of its own.
- (e) The family Mongolarachnidae SELDEN et al. 2013 is not regarded to be related to the Uloboridae but more likely to the haplogyne superfamily Leptonetoidea and the extinct family Pholcochyroceridae;
- (f) Zygiellidae (superfamily Araneoidea) is regarded as a family of its own but not as a subfamily of the Araneidae.

Additionally new combs., new stats., and some citations are noted. Not all of the taxa indet. are listed in this list.

Most known taxa are preserved in Cretaceous ambers; certain fossils – most often members of the Mygalomorpha – are preserved not in amber but in stone, calcite, ... = **S.** \* = type species. Burmite = Cretaceous amber from N-Myanmar (Burma).



**I. MESOTHELAE**..... Carboniferous – extant

Family **LIPHISTIIDAE** THORELL 1869 ..... ?Cretaceous – extant

*Cretaceothele* n. gen. Juv. Burmite ..... Cretaceous

– \**Cretaceothele lata* n. sp. Juv. Burmite..... Cretaceous

**II. OPISTHOTHELAE** ..... Triassic – extant

**(1) MYGALOMORPHA**..... Triassic – extant

*Mygalomorpha* indet. 1 and 2: This paper. Burmite..... Cretaceous

Family **ANTRODIAETIDAE** GERTSCH 1940 ..... Cretaceous – extant

*Cretacattyma* ESKOV & ZONSHTEIN 1990. ♀. **S**..... Cretaceous

– \**Cretacattyma raveni* ESKOV & ZONSHTEIN 1990. ♀. **S**..... Cretaceous

Superfamily **ATYPOIDEA**..... ?Triassic – extant

**FAMILY** unknown:

*Friaularachne* DALLA VECCHIA & SELDEN 2013. ♂. **S**..... Triassic

– \**Friaularachne rigoi* DALLA VECCHIA & SELDEN 2013. ♂. **S**..... Triassic

Note: Described „as a possible member of the mygalomorph superfamily Atypoidea.“.

?Family **ATYPIDAE** THORELL 1870 ..... ?Triassic – extant

*Ambiortiphagus* ESKOV & ZONSHTEIN 1990. ♀. **S**. Mongolia ..... Cretaceous

– \**Ambiortiphagus ponomarenko* ESKOV & ZONSHTEIN 1990. ♀. **S**..... Cretaceous

Note: Described in the new subfamily Ambiortiphaginae which may be a family of its own.

Family **DIPLURIDAE** SIMON 1889..... Cretaceous – extant

*Cretadiplura* SELDEN in SELDEN et al. 2006. ♂♀. **S**. Brazil..... Cretaceous



– \**Cretadiplura caera* SELDEN in SELDEN et al. 2006. ♂♀. **S.** Brazil ..... Cretaceous  
*Dinodiplura* SELDEN in SELDEN et al. 2006. ♂♀. **S.** Brazil ..... Cretaceous  
– \**Dinodiplura ambulacra* SELDEN in SELDEN et al. 2006. ♂♀. **S.** Brazil ... Cretaceous  
*Phyxioschemoides* **n. gen.** ♂. Burmite ..... Cretaceous  
– \**Phyxioschemoides collembola* **n. sp.** ♂. Burmite ..... Cretaceous  
Genera indet.: WUNDERLICH (2012) and below. Juv. Burmite ..... Cretaceous

Family **FOSSILCALCARIDAE** **n. fam.** ♂. Burmite ..... Cretaceous

*Fossilcalcar* **n. gen.** ♂. Burmite ..... Cretaceous  
– \**Fossilcalcar praeteritus* **n. sp.** ♂. Burmite ..... Cretaceous

?Family **HEXATHELIDAE** SIMON 1892 ..... ?Triassic – extant

*Rosamygale* SELDEN & GALL 1992. Juv. or ♀. **S.** France ..... Triassic  
– \**Rosamygale grauvogeli* SELDEN & GALL 1992. Juv. or ♀. **S.** France ..... Triassic  
Note: The single known Mesozoic taxon of this family has been only „with some reservation“ referred to the Hexathelidae by SELDEN & GALL (1992).

Family **MECICOBOTHRIIDAE** HOLMBERG 1882 ..... Cretaceous – extant

*Cretohexura* ESKOV & ZONSHTEIN 1990. ♂. **S.** Transbaikalia. .... Cretaceous  
– \**Cretohexura coylei* ESKOV & ZONSTEIN 1990. ♂. **S.** ..... Cretaceous  
*Cretomegahexura* ESKOV & ZONSHTEIN 1990. **S.** Mongolia ..... Cretaceous  
– \**Cretomegahexura platnicki* ESKOV & ZONSHTEIN 1990. Subad. ♂. **S.** .... Cretaceous

?Family **NEMESIIDAE** SIMON 1892 ..... ?Cretaceous – extant

*Cretamygale* SELDEN 2002. Juv. or ♀. Isle of Wight ..... Cretaceous  
– \**Cretamygale chasei* SELDEN 2002. Juv. or ♀. Isle of Wight ..... Cretaceous  
Note: The single known Mesozoic taxon of this family has been only tentatively referred to the family Nemesiidae by SELDEN (2002).

**(2) ARANEOMORPHA** ..... Triassic – extant

ARANEOMORPHA with unsure relationships:

*Argyrarachne* SELDEN in SELDEN et al. 1999. Juv. **S.** USA: Virginia ..... Triassic  
– \**Argyrarachne solitus* SELDEN in SELDEN et al. 1999. Juv. **S.** USA: Virginia. Triassic

*Triassaraneus* SELDEN in SELDEN et al. 1999. Juv. **S.** Africa..... Triassic  
 – \**Triassaraneus andersonorum* SELDEN in SELDEN et al. 1999. Juv. **S.** ..... Triassic  
 See SELDEN et al. (2009)

< **(2A) HYPOCHILOMORPHA**..... extant >  
No fossil report!

**(2B) DIPNEUMONOMORPHA (= ARANEOCLADA)**  
 (See also above, Araneomorpha with unsure relationships)

## **(2Ba) HAPLOGYNAE**

Unsure relationships:

Family **JURARANEIDAE** ESKOV 1984. ?Subad. ♂. **S.**.....Jurassic

*Juraraneus* ESKOV 1984 ..... Jurassic  
 – \**Juraraneus rasnitsyni* ESKOV 1984. ?Subad. ♂. **S.** Transbaikalia.....Jurassic

Superfamily DYSDEROIDEA.....Jurassic-extant

Family **PLECTREURIDAE** SIMON 1893. Eurasia .....Jurassic – extant

*Eoplectreurys* SELDEN & HUANG 2010. ♂♀. **S.** China ..... Jurassic  
 – \**Eoplectreurys gertschi* SELDEN & HUANG 2010. ♂ ♀. **S.** China ..... Jurassic

*Montsecarachne* SELDEN 2014. ♂. **S.** Spain..... Cretaceous  
 – \**Montsecarachne amicus* SELDEN 2014. ♂. **S.** Spain ..... Cretaceous

Family **SEGESTRIIDAE** SIMON 1893 ..... Cretaceous – extant

– ?Segestriidae indet.: ESKOV & WUNDERLICH (1995: 99). Juv. Siberia ... Cretaceous  
 – ?Segestriidae indet.: WUNDERLICH 2008. Juv. Burmite ..... Cretaceous

*Denticulsegestia* n. gen. ♂. Burmite ..... Cretaceous  
 – \**Denticulsegestia rugosa* n. sp. ♂.Burmite.....Cretaceous

- Jordariadna* **n. gen.** ♂. Jordan ..... Cretaceous  
 – \**Jordariadna* (= ?*Ariadna*) *amissiocoli* (WUNDERLICH 2008) (**n. comb.**) . Cretaceous
- Jordansegestria* **n. gen.** ♂. Jordan ..... Cretaceous  
 – \**Jordansegestria detruneo* **n. sp.** ♂. Jordan ..... Cretaceous
- Lebansegestria* WUNDERLICH 2008. ♂. Lebanon ..... Cretaceous  
 – \**Lebansegestria azari* WUNDERLICH 2008. ♂. Lebanon ..... Cretaceous
- Microsegestria* WUNDERLICH & MILKI 2004. ♂. Leban. .... Cretaceous  
 – \**Microsegestria poinari* WUNDERLICH & MILKI 2004. ♂. Lebanon ..... Cretaceous
- Myansegestria* **n. gen.** ♂. Burmite ..... Cretaceous  
 – *Myansegestria caederens* **n. sp.** ♂. Burmite ..... Cretaceous  
 – \**Myansegestria engin* **n. sp.** ♂. Burmite ..... Cretaceous
- Palaeosegestria* PENNEY 2004. ♂. New Jersey ..... Cretaceous  
 – \**Palaeosegestria lutzii* PENNEY 2004. ♂. New Jersey ..... Cretaceous
- Parvosegestria* **n. gen.** ♂. Burmite ..... Cretaceous  
 – *Parvosegestria longitibialis* **n. sp.** ♂. Burmite ..... Cretaceous  
 – \**Parvosegestria obscura* **n. sp.** ♂. Burmite ..... Cretaceous  
 – *Parvosegestria pintgu* **n. sp.** ♂. Burmite...  
 – *Parvosegestria triplex* **n. sp.** ♂. Burmite ..... Cretaceous
- Segestria* LATREILLE 1804 ..... ?Cretaceous – extant  
 – ?*Segestria* sp. indet.: PENNEY 2002. Juv. New Jersey ..... ?Cretaceous
- Family **PLUMORSOLIDAE** WUNDERLICH 2008. Juv. / ad. ♀. Burmese  
 and Lebanese amber ..... Cretaceous
- ?Plumorsolidae indet.: WUNDERLICH 2008. Juv. or ad. ♀. Burmite ..... Cretaceous
- Burmorsolus* **n. gen.** ?ad. ♀. Burmite ..... Cretaceous  
 – \**Burmorsolus crassus* **n. sp.** ?ad. ♀. Burmite ..... Cretaceous  
 – *Burmorsolus nonplumosus* **n. sp.** ?ad. ♀. Burmite ..... Cretaceous  
 – *Burmorsolus* sp. indet. (n.). ?ad. ♀. Burmite ..... Cretaceous
- \**Plumorsolus* WUNDERLICH 2008. ?Juv.♀. Lebanon ..... Cretaceous  
 – \**Plumorsolus gondwanensis* WUNDERLICH 2008. ?Juv.♀. Lebanon ..... Cretaceous
- Family **OONOPIDAE** SIMON 1890 ..... Cretaceous – extant
- Oonopidae indet.: PENNEY 2002. New Jersey. Juv. or ♀ ..... Cretaceous  
 Remark: Probably not a member of the family Oonopidae, see below.

<i>Burmorchestina</i> WUNDERLICH 2008. ♂ ♀. Burmite .....	Cretaceous
– * <i>Burmorchestina pulcher</i> WUNDERLICH 2008. ♂ ♀. Burmite.....	Cretaceous
<i>Canadaorchestina</i> WUNDERLICH 2008. ♂. Canadian amber .....	Cretaceous
– * <i>Canadaorchestina albertensis</i> (PENNEY 2006). ♂. Canadian amber.....	Cretaceous
<i>Orchestina</i> SIMON 1882.....	Cretaceous – extant
– <i>Orchestina gappi</i> SAUPE et al. 2012. ♂. France.....	Cretaceous
– <i>Orchestina rabagensis</i> SAUPE et al. 2012. ♂. Spain.....	Cretaceous
Remark: In my opinion probably not an <i>Orchestina</i> , see below.	
– <i>Orchestina</i> sp. indet. 1 & 2: In SAUPE et al. 2012. ♀. Spain .....	Cretaceous
– <i>Orchestina</i> sp. indet.: In SORIANO et al. 2010. ♀. Spain.....	Cretaceous
Remark: This species was redescribed as <i>O. sp. 1</i> by SAUPE et al (2012).	

**Superfamily PHOLCOIDEA**.....Cretaceous-extant

<Family PHOLCIDAE C. L. KOCH 1851 No Mesozoic proof!>

#### **Uncertain relationships of the Pholcoidea:**

<i>Furcembolus</i> WUNDERLICH 2008. ♂. Burmite .....	Cretaceous
– * <i>andersoni</i> WUNDERLICH 2008. ♂. Burmite .....	Cretaceous
Remark: Furcembolusini WUNDERLICH 2008: 582 (under Epsilodercidae).	

?*Pholcoidea* indet. (?Mongolarachnidae). ♂. **S.** Liaoning, China.....Cretaceous

*Pholcoidea* indet. Family uncertain. ?ad. ♀. Burmite.....Cretaceous

<Family OCHYRO CERATIDAE FAGE 1912: See Psilodercidae below>  
No Mesozoic proof!

Family **EOPSILODERCIDAE** WUNDERLICH 2008. Burmite ..... Cretaceous  
See WUNDERLICH (2012: 177) and *Furcembolus* directly above..

– ?Epsilodercidae sp. indet. 1-3: WUNDERLICH (2008). Burmite ..... Cretaceous

<i>Epsilodermes</i> WUNDERLICH 2008. ♂♀. Burmite.....	Cretaceous
– <i>Epsilodermes filiformis</i> (WUNDERLICH 2012)	
(under ? <i>Psilodermes f.</i> ). ♂. Burmite .....	Cretaceous
– * <i>Epsilodermes loxosceloides</i> WUNDERLICH 2008. ♂. Burmite .....	Cretaceous
– <i>Epsilodermes serenitas n. sp.</i> ♂. Burmite .....	Cretaceous
– <i>Epsilodermes</i> sp. indet. ♀ (nov.). Burmite.....	Cretaceous
– <i>Epsilodermes</i> sp. indet. ♂ (nov.). Burmite.....	Cretaceous

Family **PSILODERCIDAE** DEELEMEN-REINHOLD 1995..... Cretaceous – extant

See the remark above and below regarding the rank of this taxon.

?*Psiloderces filiformis* WUNDERLICH 2012: See above, Eopsilodercidae.

*Leclercera* DEELEMEN-REINHOLD 1995..... Cretaceous – extant

– *Leclercera ellenbergeri* n. sp. ♂. Burmite..... Cretaceous

– *Leclercera longissipes* WUNDERLICH 2012. ♂. Burmite..... Cretaceous

– *Leclercera sexaculeata* n. sp. ♂. Burmite..... Cretaceous

– *Leclercera spicula* WUNDERLICH 2012. ♂. Burmite..... Cretaceous

– *Leclercera* sp. indet. ♂ ♀ (nov.). Burmite..... Cretaceous

*Propterpsiloderces* n. gen. ♂. Burmite..... Cretaceous

– \**Propterpsiloderces longisetae* n. sp. ♂. Burmite..... Cretaceous

Family **SCYTODIDAE** BLACKWALL 1864 ..... ?Cretaceous – extant

*Scytodes* LATREILLE 1804 ..... ?Cretaceous – extant

– ?*Scytodes hani* WUNDERLICH 2012. ?Ad. ♀. Jordanian amber..... Cretaceous

Family **TETRABLEMMIDAE** O. PICKARD-CAMBRIDGE 1873 . Cretaceous – extant

Tetrablemmidae indet.: WUNDERLICH 2012. ♂. Burmite..... Cretaceous

*Bicornoculus* n. gen. ♂. Burmite..... Cretaceous

– \**Bicornoculus levis* n. sp. ♂. Burmite..... Cretaceous

– ?*Bicornoculus* sp. ?ad. ♂. Burmite..... Cretaceous

*Eogamasomorpha* WUNDERLICH 2008. ♂. Burmite..... Cretaceous

– \**Eogamasomorpha nubila* WUNDERLICH 2008. ♂. Burmite..... Cretaceous

– ?*Eogamasomorpha clara* n. sp. ♂. Burmite..... Cretaceous

*Eoscapphiella* WUNDERLICH 2011. ♂. Burmite..... Cretaceous

– \**Eoscapphiella ohlhoffi* WUNDERLICH 2011. ♂. Burmite..... Cretaceous

*Praeterpaculla* n. gen. ♂. Burmite..... Cretaceous

– *Praeterpaculla armatura* n. sp. ♂. Burmite..... Cretaceous

– *Praeterpaculla biacuta* n. sp. ♂. Burmite..... Cretaceous

– *Praeterpaculla dissolata* n. sp. ♂. Burmite..... Cretaceous

– *Praeterpaculla equester* n. sp. ♂. Burmite..... Cretaceous

– \**Praeterpaculla tuberosa* n. sp. ♂. Burmite..... Cretaceous

*Saetosoma* WUNDERLICH 2012. ♂. Burmite..... Cretaceous

– \**Saetosoma filiembolus* WUNDERLICH 2012. ♂. Burmite..... Cretaceous

*Uniscutosoma* n. gen. ♂. Burmite..... Cretaceous

– \**Uniscutosoma aberrans* n. sp. ♂. Burmite..... Cretaceous

Tetrablemmidae indet. ♂♀ (nov). Burmite..... Cretaceous

**Superfamily LEPTONETOIDEA** ..... Jurassic/Cretaceous – extant  
 TELEMIDAE: see the family key number 27.

Family **LEPTONETIDAE** SIMON 1890..... Cretaceous – extant

*Palaeoleptoneta* WUNDERLICH 2012. ♂. Burmite ..... Cretaceous  
 – \**Palaeoleptoneta calcar* WUNDERLICH 2012. ♂. Burmite..... Cretaceous

Family **PRAETERLEPTONETIDAE** WUNDERLICH 2008 ..... Cretaceous  
 Remark: This is probably not a monophyletic family.

*Autotomiana* n. gen. ?♀, ♂. Burmite ..... Cretaceous  
 – \**Autotomiana hirsutipes* n. sp. ♂. Burmite ..... Cretaceous  
 – ?*Autotomiana* sp. 1, 2. ?juv. ♀. Burmite..... Cretaceous

*Biapophyses* n. gen. ♂. Burmite..... Cretaceous  
 – \**Biapophyses beate* n. sp. ♂. Burmite ..... Cretaceous

*Crassitibia* n. gen. ♂. Burmite ..... Cretaceous  
 – \**Crassitibia longispina* n. sp. ♂. Burmite..... Cretaceous  
 – *Crassitibia tenuimana* n. sp. ♂. Burmite ..... Cretaceous

*Curvitibia* n. gen. ♂. Burmite ..... Cretaceous  
 – \**Curvitibia curima* n. sp. .... Cretaceous

*Groehnianus* n. gen. ♂. Burmite ..... Cretaceous  
 – \**Groehnianus burmensis* n. sp. ♂. Burmite..... Cretaceous

*Hypotheridiosoma* WUNDERLICH 2012. ♂. Burmite..... Cretaceous  
 – *Hypotheridiosoma falcata* n. sp. ♂. Burmite..... Cretaceous  
 - \**Hypotheridiosoma paracymbium* WUNDERLICH 2012. ♂. Burmite ..... Cretaceous

*Palaeohygropoda* PENNEY 2004. ♂. Burmite..... Cretaceous  
 – \**Palaeohygropoda myanmarensis* PENNEY 2004. ♂. Burmite..... Cretaceous

*Parvispina* n. gen. ♂. Burmite ..... Cretaceous  
 - \**Parvispina tibialis* (WUNDERLICH 2011)  
 (from *Praeterleptoneta*). ♂. Burmite ..... Cretaceous

\**Praeterleptoneta* WUNDERLICH 2008. ♂. Burmite ..... Cretaceous  
 – \**Praeterleptoneta spinipes* WUNDERLICH 2008. ♂. Burmite..... Cretaceous

*Spinipalpitibia* n. gen. ♂. Burmite ..... Cretaceous  
 – \**Spinipalpitibia maior* n. sp. ♂. Burmite..... Cretaceous

*Zarqaraneus* WUNDERLICH 2008. ♂. Burmite ..... Cretaceous  
 – \**Zarqaraneus hudei* WUNDERLICH 2008. ♂. Burmite ..... Cretaceous  
 ?*Praeterleptonetidae* indet., ♀ with egg sacs. Burmite ..... Cretaceous

Family **PHOLCOCHYROCIDAE** WUNDERLICH 2008. ♂. Burmite. Cretaceous  
 (elevated from tribus to family rank by WUNDERLICH in 2012)

\**Pholcochyrocer* WUNDERLICH 2008. ♂. Burmite ..... Cretaceous  
 – ?*Pholcochyrocer baculum* WUNDERLICH 2012. ♂. Burmite ..... Cretaceous  
 – \**Pholcochyrocer guttulaequae* WUNDERLICH 2008. ♂. Burmite ..... Cretaceous  
 – *Pholcochyrocer pecten* WUNDERLICH 2012. ♂. Burmite ..... Cretaceous

*Spinicreber* n. gen. ♂. Burmite ..... Cretaceous  
 – \**Spinicreber antiquus* n. sp. ♂. Burmite ..... Cretaceous

*Spinipalpus* n. gen. ♂. Burmite ..... Cretaceous  
 – \**Spinipalpus vetus* n. sp. ♂. Burmite ..... Cretaceous

Family **MONGOLARACHNIDAE** SELDEN et al. 2013. ♂♀. **S.** Mongolia .....  
 ..... Jurassic – Cretaceous

\**Mongolarachne* SELDEN et al. 2013 (Mongolarachninae). ♂♀. **S.** Mongolia... Jurassic  
 – \**Mongolarachne jurassica* SELDEN et al. 2011 (= *Nephila j.*). ♂♀. **S.**  
 Mongolia ..... Jurassic

Note: Originally the taxon has erroneously been described as a member of the family Nephilidae.

*Longissipalpus* n. gen. (Longissipalpinae). ♂. Burmite ..... Cretaceous  
 – *Longissipalpus magnus* n. sp. ♂. Burmite ..... Cretaceous  
 – *Longissipalpus maior* n. sp. ♂. Burmite ..... Cretaceous  
 – \**Longissipalpus minor* n. sp. ♂. Burmite ..... Cretaceous

*Pedipalparaneus* n. gen. (Pedipalparaneinae). ♂. Burmite ..... Cretaceous  
 – \**Pedipalparaneus seldeni* n. sp. ♂. Burmite ..... Cretaceous

Note: See also above, the dubious genus *Zhizhu* SELDEN 2015 (♂♀ in Jurassic stone from China).

Superfamily **ARCHAEOIDEA** (= PALPIMANOIDEA) ..... Jurassic – extant

Unsure family:

*Sinaranea* SELDEN et al. 2008. **S.** ?Ad. ♂, ?Juv. China ..... Jurassic  
 – \**Sinaranea metaxyostraca* SELDEN et al. 2008. **S.** ?Ad. ♂, ?Juv. China ..... Jurassic



Seppo SELDEN & DUNLOP 2014. **S.** ?Ad. ♀. Germany ..... Jurassic  
 – \**Seppo koponeni* SELDEN & DUNLOP 2014. **S.** ?Ad. ♀. Germany ..... Jurassic  
 See Araneoidea s. str.

Family **ARCHAEIDAE** C. L. KOCH & BERENDT 1854 ..... Jurassic – extant  
 (Incl. Mecysmaucheninae SIMON 1895).

Archaeomecys SAUPE & SELDEN 2009 (under Mecysmauchenidae) ..... Cretaceous  
 – \**Archaeomecys arcantiensis* SAUPE & SELDEN 2009. Juv. France ..... Cretaceous

Archaeinae indet. (nov.). ♂. Burmite ..... Cretaceous

Burmesarchaea WUNDERLICH 2008. ♂♀. Burmite ..... Cretaceous  
 – \**Burmesarchaea grimaldii* (PENNEY 2003) (under *Afrarchaea*) ..... Cretaceous

Eomysmauchenius WUNDERLICH 2008. ♀. Burmite ..... Cretaceous  
 – \**Eomysmauchenius septentrionalis* WUNDERLICH 2008 ..... Cretaceous

Filiauchenius WUNDERLICH 2008. Probably synonym of *Lacunauchenius* ... Cretaceous  
 – \**Filiauchenius paucidentatus* WUNDERLICH 2008. ♀. Burmite ..... Cretaceous

Jurarchaea ESKOV 1987. ♀. **S.** Kazakhstan ..... Jurassic  
 – \**Jurarchaea zherikhini* ESKOV 1987. ♀. **S.** Kazakhstan ..... Jurassic

Lacunauchenius WUNDERLICH 2008. See *Filiauchenius*. ♂♀. Burmite ..... Cretaceous  
 – \**Lacunauchenius speciosus* WUNDERLICH 2008. ♂. Burmite ..... Cretaceous  
 – *Lacunauchenius longissipes* **n. sp.** ♂. Burmite ..... Cretaceous  
 – *Lacunauchenius pilosus* **n. sp.** ♂. Burmite ..... Cretaceous  
 – *Lacunauchenius* sp. indet. ♀. Burmite ..... Cretaceous

Patarchaea SELDEN, HUANG & REN 2008. **S.** ♂♀ ..... Jurassic  
 – \**Patarchaea muralis* SELDEN, HUANG & REN 2008. **S.** ♂♀ ..... Jurassic

Planarchaea **n. gen.** ?Ad. ♀. Burmite ..... Cretaceous  
 – \**Planarchaea kopp* **n. sp.** ?Ad. ♀. Burmite ..... Cretaceous

Family **HUTTONIIDAE** SIMON 1893 ..... ?Cretaceous – extant

Unnamed taxon in PENNEY & SELDEN (2008). Juv. New Jersey  
 and Canadian ambers ..... ?Cretaceous  
 See below: **Questionable** fossil Huttoniidae

Family **LAGONOMEGOPIDAE** ESKOV & WUNDERLICH 1995 ..... Cretaceous  
 (= Grandoculidae PENNEY 2011)

Archaelagonops WUNDERLICH 2012d, ♂♀, Burmite (type area) and Spain. See below:  
*Soplaogonomegops unzuei*. ♀: See below, *Archaelagonops* sp. indet;

– <i>Archaelagonops alavensis</i> (PENNEY 2006) (under <i>Burlagonomegops</i> , <b>n. comb.</b> ).	
juv., Spain: Alava .....	Cretaceous
– <i>Archaelagonops propinquus</i> <b>n. sp.</b> , ♂, Burmite .....	Cretaceous
– * <i>Archaelagonops salticoides</i> WUNDERLICH 2012d. ♂, Burmite .....	Cretaceous
– <i>Archaelagonops scorsum</i> <b>n. sp.</b> , ♂, Burmite .....	Cretaceous
<i>Burlagonomegops</i> PENNEY 2005b. Juv. Burmite .....	Cretaceous
– * <i>Burlagonomegops eskovi</i> PENNEY 2005b. Juv. Burmite .....	Cretaceous
( <i>B. alavensis</i> : See <i>Archaelagonops</i> ).	
<i>Cymbiolagonops</i> <b>n. gen.</b> , ♂, Burmite .....	Cretaceous
– * <i>Cymbiolagonops cambiocalcar</i> <b>n. sp.</b> , ♂, Burmite .....	Cretaceous
<i>Grandoculus</i> PENNEY 2004b. ?Ad. ♀, Canadian amber .....	Cretaceous
– * <i>Grandoculus chemahawinensis</i> PENNEY 2004b. ?Ad. ♀, Burmite .....	Cretaceous
<i>Lagonoburmops</i> WUNDERLICH 2012d. Juv. ♀, Burmite .....	Cretaceous
– * <i>Lagonomegops plumosus</i> WUNDERLICH 2012d. Juv., ♀, Burmite .....	Cretaceous
* <i>Lagonomegops</i> ESKOV & WUNDERLICH 1995, type genus of the family, juvenile,	
Siberia (type area); probably Myanmar (Burma) and USA (det. questionable).	
– ? <i>Lagonomegops americanus</i> PENNEY 2005b. Juv. USA: New Jersey ...	Cretaceous
– * <i>Lagonomegops sukatchevae</i> ESKOV & WUNDERLICH 1995. Juv. Siberia:	
Taimyr amber .....	Cretaceous
– ? <i>Lagonomegops tuber</i> <b>n. sp.</b> Juv. Burmite .....	Cretaceous
<i>Lineaburmops</i> <b>n. gen.</b> , ♂, Burmite .....	Cretaceous
– * <i>Lineaburmops beigeli</i> <b>n. sp.</b> , ♂, Burmite .....	Cretaceous
– <i>Lineaburmops hirsutipes</i> <b>n. sp.</b> , ♂, Burmite .....	Cretaceous
<i>Myanlagonops</i> WUNDERLICH 2012d. ♂, Burmite .....	Cretaceous
– * <i>Myanlagonops gracilipes</i> WUNDERLICH 2012. ♂, Burmite .....	Cretaceous
<i>Parviburmops</i> <b>n. gen.</b> , ♂, Burmite .....	Cretaceous
– * <i>Parviburmops brevipalpus</i> <b>n. sp.</b> , ♂, Burmite .....	Cretaceous
<i>Paxillomegops</i> <b>n. gen.</b> , ♂, Burmite .....	Cretaceous
– ? <i>Paxillomegops brevipes</i> <b>n. sp.</b> , ♂, Burmite .....	Cretaceous
– * <i>Paxillomegops longipes</i> <b>n. sp.</b> , ♂, Burmite .....	Cretaceous
<i>Picturmegops</i> <b>n. gen.</b> , ♀, Burmite .....	Cretaceous
– * <i>Picturmegops signatus</i> <b>n. sp.</b> , ♀, Burmite .....	Cretaceous
<i>Soplaogonomegops</i> FUENTE et al. 2013. Juv. Spain. Probably synonym of	
<i>Archaelagonops</i> ( <b>quest. n. syn.</b> ) .....	Cretaceous
– * <i>Soplaogonomegops unzuei</i> FUENTE et al. 2013. Juv. Spain: Cantabria.	Cretaceous
<i>Spinomegops</i> FUENTE et al. 2013. Juv. Spain .....	Cretaceous
– * <i>Spinomegops arcanus</i> FUENTE et al. 2013. Juv. Spain: Alava .....	Cretaceous

– *Spinomegops aragonensis* FUENTE et al. 2013 Juv. Spain: Aragon ..... Cretaceous

*Zarqagonomegops* KADDUMI 2007. Juv. Jordanian amber ..... Cretaceous

– \**Zarqagonomegops wunderlichi* KADDUMI 2007. Juv. See WUNDERLICH (2008: 615), Jordanian amber ..... Cretaceous

Lagonomegopidae indet.: Div. in Burmite (nov.) ..... Cretaceous

Family **MICROPALPIMANIDAE** WUNDERLICH 2008. ♂♀. Burmite ..... Cretaceous

*Micropalpimanus* WUNDERLICH 2008. ♂♀. Burmite ..... Cretaceous

– \**Micropalpimanus poinari* WUNDERLICH 2008. ♂♀. Burmite ..... Cretaceous

*Micropalpimanus* sp. indet: WUNDERLICH 2012. ♂♀. Burmite ..... Cretaceous

Family **SPATIATORIDAE** PETRUNKEVITCH 1958. ♂♀. Burmite; Eocene Baltic amber ..... Cretaceous – Eocene

\**Spatiator* PETRUNKEVITCH 1942. ♂♀. Burmite, Baltic amber ..... Cretaceous-Eocene

– *Spatiator putescens* n. sp. ♂. Burmite ..... Cretaceous

*Vetiator* n. gen. ♂. Burmite ..... Cretaceous

– \**Vetiator gracilipes* n. sp. ♂. Burmite ..... Cretaceous

## (2Bb) ENTELEGYNAE

**Superfamily uncertain** (really a member of the Entelegynae?):

Family **BURMASCUTIDAE** WUNDERLICH 2008. ♂♀. Burmite ..... Cretaceous

*Burmascutum* WUNDERLICH 2008. ♂♀. Burmite ..... Cretaceous

– \**Burmascutum aenigma* WUNDERLICH 2008. ♂♀. Burmite ..... Cretaceous

**Superfamily OECOBIOIDEA** ..... Cretaceous – extant

?*Oecobioidea* indet.: WUNDERLICH (2008: 566, 623, figs. 90-93). ♂. Jordanian amber ..... Cretaceous

Family **OECOBIIDAE** BLACKWALL 1862..... Cretaceous – extant

*Lebanoecobius* WUNDERLICH 2004. ♂. Lebanese amber..... Cretaceous

– \**Lebanoecobius schleei* WUNDERLICH 2004. ♂. Lebanese amber ..... Cretaceous

*Oecobius* LUCAS 1848 ..... ?Cretaceous – extant

– ?*Oecobius* sp. indet. in PENNEY (2002). ♀. New Jersey amber ..... Cretaceous

Remark: In my opinion not a member of *Oecobius* but probably a member of the subfamily Mizaliinae.

*Zamilia* WUNDERLICH 2008. ♂♀. Burmite (see also directly above)..... Cretaceous

– *Zamilia aculeopectens* n. sp. ♂. Burmite..... Cretaceous

– \**Zamilia antecessor* WUNDERLICH 2008. ♂♀. Burmite..... Cretaceous

– ?*Zamilia quattuormammillae* n. sp. ♂. Burmite..... Cretaceous

– *Zamilia* sp. indet. ♂. Burmite..... Cretaceous

– Oecobiidae indet. ♂. Burmite..... Cretaceous

*Retrooecobius* n. gen. ♂♀. Burmite..... Cretaceous

– \**Retrooecobius chomskyi* n. sp. ♂. Burmite..... Cretaceous

– *Retrooecobius convexus* n. sp. ♀. Burmite..... Cretaceous

Family **HERSILIIDAE** THORELL 1870 ..... Cretaceous – extant

*Burmesiola* WUNDERLICH 2011..... Cretaceous

– \**Burmesiola cretacea* WUNDERLICH 2011..... Cretaceous

– *Burmesiola daviesi* n. sp. ? juv. ♀. Burmite ..... Cretaceous

*Spinasilia* n. gen. ♂. Burmite..... Cretaceous

– \**Spinasilia dissoluta* n. sp. ♂. Burmite ..... Cretaceous

Hersiliidae indet.: Probably ad. ♀. Burmite ..... Cretaceous

**Superfamily ARANEOIDEA** LATREILLE 1806 s. l..... Triassic – extant  
(= „Orbiculariae“ WALCKENAER 1802, incl. Deinopoidea)

Unsure relationships (see also above):

Family JURARANEIDAE ESKOV 1984 (?cribellate; ?Araneoidea; ?= Araneidae):

See above, the paragraph „Erroneous determinations“. ?subad. ♂. **S**..... Jurassic

– \**Juraraneus rasnitsyni* ESKOV 1984. ?subad. ♂. **S**. Transbaikalia ..... Jurassic

(*Triasaraneus*: See above, Araneomorpha with unsure relationships and below).

(a) **Cribellate ARANEOIDEA** C. L. KOCH 1851 (= “**DEINOPOIDEA**”) ..... Cretaceous – extant

Remark on the Jurassic genus *Zhizhu* SELDEN et al. 2015: This genus in stone from China was regarded as a taxon of the superfamily Deinopoidea. Its thickened male pedipalpal tibia and the existence of a probably well sclerotized epigyne are quite unusual in the Deinopoidea – and may even exclude *Zhizhu* from this superfamily. – See the family Mongolarachnidae.

(Family **MONGOLRACHNIDAE** SELDEN et al. 2013: See above: Haplogynae: Lepto-  
neoidea, unsure relationships).

(Family **DEINOPIIDAE** C. L. KOCH 1850: No Mesozoic report. *Palaeomicromenneus*  
PENNEY 2003: See directly below, the family Salticoididae (**n. relat.**)).

Family **SALTICOIDIDAE** WUNDERLICH 2008. ♂♀. Diverse ambers ..... Cretaceous

*Burmadietyna* WUNDERLICH 2008. ♂♀. Burmite. (**n. relat.**)..... Cretaceous  
– *Burmadietyna clava* **n. sp.** ♂. Burmite..... Cretaceous  
– *Burmadietyna excavata* **n. sp.** ♂. Burmite ..... Cretaceous  
– \**Burmadietyna pecten* WUNDERLICH 2008. ♀. Burmite..... Cretaceous  
? *Burmadietyna* sp. indet. ♀ (nov.). Burmite ..... Cretaceous

*Palaeomicromenneus* PENNEY 2003. ♂. Lebanese amber (**n. relat.**) ..... Cretaceous  
– \**Palaeomicromenneus lebanensis* PENNEY 2003. ♂. Lebanese amber .. Cretaceous

\**Salticoididus* WUNDERLICH 2008. ♂. Jordanian amber ..... Cretaceous  
– \**Salticoididus kaddumiorum* WUNDERLICH 2008. ♂. Jordanian amber .... Cretaceous  
– ?Salticoididae indet.: WUNDERLICH 2008. Juv. Jordanian amber ..... Cretaceous

Family **ULOBORIDAE** THORELL 1869 ..... Jurassic – extant

*Bicalamistrum* **n. gen.** Subad. ♂. Burmite..... Cretaceous  
– \**Bicalamistrum mixtum* **n. sp.** Subad. ♂..... Cretaceous

*Burmuloborus* WUNDERLICH 2008. ♀. Burmite ..... Cretaceous  
– *Burmuloborus antefixus* **n. sp.** ♀. Burmite..... Cretaceous  
– \**Burmuloborus parvus* WUNDERLICH 2008. ?Ad. ♀. Burmite..... Cretaceous  
– ?*Burmuloborus prolongatus* **n. sp.** Juv. ♀. Burmite..... Cretaceous  
– ?*Burmuloborus* sp. indet. (nov.). ♀-exuvia. Burmite..... Cretaceous

*Jerseyuloborus* WUNDERLICH 2011. Juv. ♀. New Jersey amber ..... Cretaceous  
– \**Jerseyuloborus longisoma* WUNDERLICH 2011. Juv. ♀. New Jersey .... Cretaceous

<i>Microuloborus</i> <b>n. gen.</b> ♂. Burmite .....	Cretaceous
– * <i>Microuloborus birmanicus</i> <b>n. sp.</b> ♂. Burmite .....	Cretaceous
<i>Ocululoborus</i> WUNDERLICH 2011. ♀. Burmite .....	Cretaceous
– * <i>Ocululoborus curvatus</i> WUNDERLICH 2011. ♀. Burmite .....	Cretaceous
<i>Palaeomiagrammopes</i> WUNDERLICH 2008. ?Ad ♀, juv. Burmite .....	Cretaceous
– * <i>Palaeomiagrammopes vesica</i> WUNDERLICH 2008. ?Ad ♀, juv. Burmite....	Cretaceous
Note: Probably a synonym of <i>Paramiagrammopes</i> WUNDERLICH 2008.	
<i>Palaeouloborus</i> SELDEN 1990 <b>n. relat.</b> (= <i>Macryphantes</i> SELDEN 1990, <b>n. syn.</b> ). ♂, ? ad. ♀. <b>S.</b> Spain.....	Cretaceous
– * <i>Palaeouloborus lacasae</i> SELDEN 1990 (= <i>Macryphantes cowdeni</i> SELDEN 1990 ( <b>n. syn.</b> )). But see SELDEN & PENNEY (2003)! ♂, ?ad. ♀. <b>S.</b> Spain.....	Cretaceous
<i>Paramiagrammopes</i> WUNDERLICH 2008. ♂. Burmite .....	Cretaceous
– * <i>Paramiagrammopes cretaceus</i> WUNDERLICH 2008. ♂. Burmite .....	Cretaceous
– <i>Paramiagrammopes longiclypeus</i> . <b>n. sp.</b> ♂. Burmite .....	Cretaceous
– <i>Paramiagrammopes patellidens</i> <b>n. sp.</b> ♂. Burmite.....	Cretaceous
<i>Talbragaraneus</i> SELDEN & BEATTIE 2013. ?Ad. ♀. <b>S.</b> Australia.....	Jurassic
– * <i>Talbragaraneus jurassicus</i> SELDEN & BEATTIE 2013. ?Ad. ♀. <b>S.</b> Australia...	Jurassic
<i>Uloboridae</i> indet. (nov.). ?Ad. ♀. Burmite .....	Cretaceous

(b) **Ecribellate ARANEOIDEA** LATREILLE 1806: sensu stricto .....Triassic – extant

### Unsure relationships:

*Araneoidea* fam. indet.: WUNDERLICH (2008: 644-645). Juv. ♀. Burmite.... Cretaceous

*Macryphantes* SELDEN 1990: See Uloboridae: *Palaeouloborus*.

*Mesaranea* HONG 1984. Juv. ♀. **S.** China ..... Jurassic |

– \**Mesaranea hebeiensis* HONG 1984. Juv. ♀. **S.** China..... Jurassic |

*Seppo* SELDEN & DUNLOP 2014: See Archaeoidea (= Palpimanoidea) and questionable Araneoidea s. str.

*Triasaraneus* SELDEN 1999: See above: Araneomorpha indet ..... Trias |

Family **ARANEIDAE** SIMON 1895.....Eocene – extant

Note: The families Nephilidae and Zygiellidae (see below) were previously included in the Araneidae.

No sure Mesozoic proof of the family; see Zygiellidae and the chapter on erroneous determinations.

Family **NEPHILIDAE** SIMON 1894 ..... Cretaceous – extant

*Cretaraneus* SELDEN 1990. ♂♀. **S.** Brazil, China and Spain ..... Cretaceous

– *\*Cretaraneus vilaltae* SELDEN 1990. ♂. **S.** Spain..... Cretaceous

– *Cretaraneus laoningensis* CHENG et al. 2008. ♂. **S.** China.....Cretaceous

– *Cretaraneus martensnetoi* MESQUITA 1996. ?Juv. ♀. **S.** Brazil ..... Cretaceous

Note: In my opinion the generic and even the familiar assignment of the letter two species have to check.

*Nephila jurassica* SELDEN et al. 2011 has been described from the Jurassic of China, based on an adult female. SELDEN et al. (2013) transferred the species to the genus *Mongolarachne* of the family Mongolarachnidae, see above.

*Nephila* sp. indet. from Brazil: See DUNLOP & PENNEY 2012: Fig. 93.

In my opinion the generic assignment of these two species has to check.

The dubious taxon *Huergina diazromerali* SELDEN & DUNLOP 2003 – based on a badly preserved questionable adult female spider in Lower Cretaceous stone from Spain – was placed in the family Nephilidae (under Tetragnathidae: Nephilinae). It appears impossible to assign the taxon to a family level, and I do not want to exclude that it may be a member of the family Uloboridae. See below, the family Nephilidae.

There is no sure report of the Nephilidae from Burmite or other kinds of amber. *Gerateonephila burmanica* POINAR & BUCKLEY: See above: The chapter on erroneous determinations.

Family **ZYGIELLIDAE** SIMON 1929.....Cretaceous – extant

Family status: See WUNDERLICH (2008: 926). Most recent authors include this raxon as a subfamily of the Araneidae.

*Mesozysiella* PENNEY & ORTUNO 2006. ♂. Spain..... Cretaceous

– *\*Mesozysiella dunlopi* PENNEY & ORTUNO 2006. ♂. Spain..... Cretaceous

The genus *Seppo* SELDEN & DUNLOP 2004: See above, e. g. the chapter on erroneous/unsure determinations.

?Zygiellidae (under Linyphiidae) indet.: PENNEY & SELDEN 2002 (♀, fig. 394) in Lower Cretaceous Lebanese amber: It may be a member of the family Zygiellidae, see WUNDERLICH (2008: 645) and below: the family Linyphiidae.



Family **THERIDIOSOMATIDAE** SIMON 1833..... Cretaceous – extant

(*Hypertheridiosoma* WUNDERLICH 2012: See the family Praeterleptonetidae).

*Eocoddingtonia* SELDEN 2010. ♂♀. **S.** Russia..... Cretaceous

– \* *Eocoddingtonia escovi* SELDEN 2010. ♂♀. **S.** Russia..... Cretaceous

*Leviunguis* WUNDERLICH 2012. ♂, ?juv. ♀. Burmite..... Cretaceous

– \* *Leviunguis bruckschi* WUNDERLICH 2012. ♂, ?juv. ♀. Burmite..... Cretaceous

– *Leviunguis* sp. indet. (nov.). ♂, ?juv. ♀. Burmite..... Cretaceous

Family **THERIDIIDAE** SUNDEVALL 1833..... Cretaceous – extant

*Cretotheridion* n. gen. ♂. Burmite..... Cretaceous

– \* *Cretotheridion inopinatum* n. sp. ♂. Burmite..... Cretaceous

Previously a quite doubtful „?Theridiidae gen. et sp. indet.“ in MCALPINE & MARTIN (1969) has been published in Upper Cretaceous Canadian amber.

Family **LINYPHIIDAE** BLACKWALL 1959..... ?Cretaceous – extant

I do not know a sure Cretaceous report of the Linyphiidae or a strongly related family, see above, the chapter on dubious or erroneous determinations and the family Zygellidae.

A quite dubious member of the family Linyphiidae (gen. & sp. indet.) has been listed in MCALPINE & MARTIN (1969) in Lower Canadian amber.

I do not want to exclude that the single male of a male linyphiid indet. in alleged Cretaceous Ethiopian amber – see in SCHMIDT et al. (2010) – is actually preserved in Cenozoic amber but no recent paper has been published on the age of this amber.

PENNEY (2002: 216-217, t. 2, fig. 3; fig. 5) described a male under Linyphiidae gen. & sp. indet. in Upper New Jersey amber. In my opinion the badly preserved specimen does not allow an assignment to a family, and no indication exists that its paracymbium is a free sclerite.

PENNEY & SELDEN (2002) – see WUNDERLICH (2008: 645) and below – described the alleged oldest Linyphiidae (indet.), a female (fig. 394) in Lower Cretaceous Lebanese amber. In my opinion the stout legs and the partly thick tibial bristles may indicate strong relationships to the families Araneidae and Zygellidae. Zygellidae are known from the Cretaceous (see above) in contrast to Araneidae and Linyphiidae.

To my present knowledge the family Linyphiidae has to be removed from the list of Mesozoic spiders.

## **Branch RTA-CLADE:**

Members of this clade are reported from the Eocene, see WUNDERLICH (2004) but no sure Mesozoic proof exists; see the chapter on erroneous determinations. Alleged Dictynidae: See Deinopoidea: Salticoididae.

I now regard the questionable member of the RTA-clade (remains of an exuvia): WUNDERLICH (2008: 652) not as a member of this clade but of a more ancient taxon.

## **The Mesozoic spider faunas: Composition, changes, the Cretaceous-Paleogene extinction events, biogeography etc.**

See WUNDERLICH (2011: 541-543) and (2012: 162-168).

See also above, the partly overlapping chapter on the evolution of spiders, e. g. the paragraph on „Lebensformtypen“.

### **Spider families from selected Mesozoic deposits and epochs:**

Currently the fauna of the Mid Cretaceous amber forest of Myanmar (Burma) is by far best studied, see the list. The families Archaeidae, Uloboridae, Oecobiidae, Oonopidae (only Orchestininae) and Segestriidae are known from all Mesozoic epochs and even from today; Pholcochyroceridae has been reported from the Jurassic and the Cretaceous only. The extinct and very diverse family Lagonomegopidae had the widest known distribution of all families in the Cretaceous: North America, Siberia, Myanmar (Burma), Spain and the Near East, see WUNDERLICH (2008: 543, fig. 2).

### **The oldest proofs of spider families of three Mesozoic epochs are:**

TRIASSIC: Probably Atypidae, probably Hexathelidae and three fam. indet., see below.

JURASSIC: Juraraneidae (extinct), Mogolarachnidae (extinct and also known from the Cretaceous), Plectreuridae (members survived as relicts), Archaeidae, Uloboridae and fam. indet., see below.

CRETACEOUS: More than 30 families, but apparently many more existed (\*); see the lists of the families.

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(\*) Most Mesozoic taxa are known from the Mid Cretaceous Burmese amber. Most frequent spiders preserved in amber are dwellers of higher strata of the vegetation but not of the ground. Therefore ground/soil living spiders of the Mesozoicum are not well represented/known although some of these animals may have been blown by wind or as ballooners to the fossil resin or may have climbed on trees as juveniles; see WUNDERLICH (2004).

Diversity of the faunas and extinctions: See the list of the families below and before the key to the families as well as the annotated list.

Based on remains of plants and animals THE BURMESE AMBER FOREST WAS MAINLY A TROPICAL RAIN FOREST; a strictly tropical animal is the spider of the suborder Mesothelae (see below). Amber inclusions like Trichoptera and remains of (boring) Bivalvae indicate the existence of brooks and/or rivers as well as a nearshore marine environment, see CRUIKSHANK & KO KO (2003). The existence of Solifugae may point to certain dry and sunny areas within the forest, see the paper on „New and rare arachnids in Cretaceous Burmese amber“ in this volume. The diverse spider fauna preserved in Burmese amber – Mesothelae, Mygalomorpha, Haplogynae, Araneoidea and cribellate capture web dwellers – is doubtless the result of diverse biotopes and habitats of the ancient forest.

The very longlived segmented ancient members of the MESOTHELAE were probably the only spiders of the Palaeozoicum; they survived as relicts up to now. A single small juvenile is reported here from the tropical Mid Cretaceous Burmese amber forest, see fig. 5 and the photos 10-13.

To my knowledge there are currently about 1200 described fossil spider species, representing ca. 3 % of all described spider species.

One third (12) of the Mesozoic families is extinct, see below. (Eocene families: See WUNDERLICH (2004): 4 or 5 families are extinct).

The results of my (preliminary) studies of the Mesozoic (mainly Cretaceous) spider faunas are as follows:

- 39 families are reported, the determination of 7 or 8 of these is unsure, only 9 (less than one quarter) of the surely reported 30 families are entelegyne.
- Almost all of these families are reported from the Cretaceous; the Juraraneidae are only known from the Jurassic, the Mongolarachnidae from the Jurassic to the Cretaceous, Spatiatoridae from the Cretaceous to the Eocene (Baltic amber). Mesothelae – probably the only spiders of the Palaeozoicum and surviving with a single family up to now – are reported here from Mid Cretaceous Burmese amber (Burmite).
- 12 (more than one third) of the surely reported families are extinct; only one of these, the Spatiatoridae, survived up to the Eocene. Besides the mygalomorph Fossilcalcaridae all the extinct families are members of the Haplogynae.
- ca. 110 genera are reported: 1 of the Mesothelae, 11 of the Mygalomorpha, ca. 100 of the Araneomorpha: Ca. 75 of the Haplogynae (incl. the Archaeoidea) and ca. 25 of the Entelegynae = 1/4 of the Araneomorpha.
- Most genera are only known from the Cretaceous; 5 from the Triassic: *Ambiortipha-gus* (?Atypidae), *Argyrarachne* (Araneomorpha indet.), *Mesaranea* (Araneoidea in-

- det.), *Rosamygale* (?Hexathelidae) and *Triasaraneus* (Araneomorpha indet.); 5 from the Jurassic: *Eoplectreurus* (Plectreuridae), *Juraraneus* (Juraraneidae), *Jurarchaea* (Archaeidae), *Sinaranea* (fam.?) and *Tatbragaraneus* (Uloboridae): the only genus of the Entelegynae.
- Members of only very few genera – all members of the Haplogynae – survived probably up to now: *Orchestina* (Oonopidae), *Leclercera* (Psilodercidae) and *Scytodes* (Scytodidae).
  - Cribellate genera: (a) Araneomorpha: ca. 25% in the Cretaceous but only ca. 10% in the Eocene Baltic amber forest; (b) Araneoidea: > 50% in the Cretaceous but only ca. 7% in the Eocene (in which ecribellate members of the RTA-clade dominate). A strong removal of cribellate genera occurred during more than 100 million of years.
  - > 140 Mesozoic species have been described; no Mesozoic species survived up to nor or is known to have survived up to the Eocene (e. g. to the Baltic amber forest).

The most diverse superfamilies and selected families of the Araneomorpha (\*) (mainly preserved in Burmite):

Segestriidae (Dysderoidea): 8 genera (at least 2 subfamilies);  
 Lagonomegopidae (Archaeoidea): 14 genera (probably a single subfamily);  
 Archaeidae (Archaeoidea): 8 genera (several subfamilies);  
 ?Mongolarachnidae: At least 3 genera (at least 3 subfamilies!),  
 Note: This family is probably not monophyletic; a revision and more fossils are needed);  
 ?Praeterleptonetidae (Leptonetoidea): 11 genera,  
 Note: This family is probably not monophyletic and the number of genera has to be reduced;  
 Oecobiidae (Oecobioidea): at least 4 genera (3 or 4 subfamilies!);  
 Uloboridae (Araneoidea s. l.: deinopoid branch): 8 genera (unknown number of subfamilies).

Archaeoidea is the most diverse superfamily known in Burmite and from the whole Mesozoic. Oecobiidae and Uloboridae are the only diverse families of the Entelegynae, the remaining families are members of the Haplogynae.

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 (\*) Because of their life style (mainly in tubes in the earth) members of the Mygalomorpha are only weakly known as fossils in amber. (soil-living Dipluridae is an exception; they are not too rare in Burmite).

Most frequent species: I found several conspecific specimens mainly of *Burmorchestina pulcher* (Oonopidae), *Burmesarchaea grimaldii* (Archaeidae) and *Micropalpimanus poinari* (Micropalpimanidae), both Archaeoidea.

## Competition and extinction, remarks on the biogeography

The Burmese amber forest existed in a remarkable area (Southeast Asia) and era (Mid Cretaceous) in which spiders of various families, of similar „ecotypes“ („Lebens-

weisetypen“) existed – they were frequently similar in size and shape of the body, chaetotaxy and certain other structures may be similar, too -; not rarely they may have been competitors. Examples are members of the families Praeterleptonetidae (extinct, superfamily Leptonetoidea, haplogyne) and Theridiosomatidae (Cretaceous to extant, superfamily Araneoidea, entelegyne). Members of both families existed in the old amber forest, both were dwellers of higher strata of the vegetation and built capture webs. Praeterleptonetidae were frequent and diverse in the Mid Cretaceous amber forest at least of Myanmar (Burma) and became extinct during the Cretaceous. Members of the Theridiosomatidae were rare and not diverse in that era, were diverse in the Eocene Baltic amber forest – see WUNDERLICH (2004) -; the family survived and is still fairly diverse today. Probably the Theridiosomatidae – and later the Theridiidae and Linyphiidae, too – displaced the Praeterleptonetidae during the Lower Cretaceous and/or Early Palaeogene. – Why did this happen? As in other members of the superfamily Araneoidea in the Theridiosomatidae sticky droplets on their capturing threads exist in contrast to members of the ancient Praeterleptonetidae. Probably this „innovative“ evolutionary advantage was the (main) reason for the success of the Theridiosomatidae and the extinction of their competitors, the Praeterleptonetidae. Also the haplogyne Pholcidae evolved capture threads which bear sticky droplets; members of this family are unknown from the Mesozoic but existed already in the Eocene – see WUNDERLICH (2004) – and are very diverse today. They may well have replaced Cretaceous spider families. See WUNDERLICH (2008: 553) and the chapter on spider evolution.

Probably certain members of the superfamily Araneoidea displaced their capture web dwelling haplogyne competitors of higher strata of the vegetation – like the extinct cribellate family Pholcochyroceridae – for the same reason during the Lower Cretaceous.

Did the entelegyne Sparassidae replace the extinct haplogyne Lagonomegopidae at the beginning of the Paleogene?

The vicariance of patterns especially in Archaeoidea (= Palpimanoidea) was recently shown impressively by WOOD et al. (2013: 264): „... the diversification of the northern and southern archaeid lineages was congruent with the breakup of Pangaea into Laurasia and Gondwanaland.“

About forty million years ago, when India pushing northwards crashed with Asia, it should have taken along „south-dwelling“ spider families like Archaeidae, Cyatholipidae and Synotaxidae. These families – dwellers of higher strata of the vegetation – were diverse in the Eocene Baltic amber forest, see WUNDERLICH (2004), the Archaeidae in the Mid Cretaceous Burmese amber forest, too but no report of the Cyatholipidae and the Synotaxidae exists in Burmite. These three families are missing today in India and the whole Eurasia. Up to now a report is also missing in the Eocene Indian amber. How can that be explained? Why did the three families in Europe survived at least up to the Eocene? Why does no report of the Cyatholipidae and the Synotaxidae in Burmese amber exist but Archaeidae were diverse? Why did the three families became extinct on the whole Northern Hemisphere (with the exception of a single genus of the Synotaxidae in Central America)? Probably the „young“ families Pholcidae, Linyphiidae, Theridiidae and Theridiosomatidae displaced the three families in question. These four families were quite rare or even absent in the Cretaceous but radiated strongly after the end of the Cretaceous at the latest.

## Changes of the faunas

The changes of the spider faunas from the Triassic to the Upper Cretaceous (that means during almost 200 million years) appear less than the dramatical change from the Upper Cretaceous to the Late Palaeocene or Early Eocene (a time span of only about 15 million years (!).

PENNEY et al. (2003) „provide the first evidence that spiders suffered no decline at the family level during these <Cretaceous – Tertiary> mass extinction events.“ and „it is unlikely that we will discover many, if any, more strictly fossil spider families in the Cretaceous.“ I know 10 strictly Cretaceous spider families (see the lists) – a similar situation (extinct Cretaceous families) exists to my knowledge in several insect orders like Diptera and Hymenoptera -, and clearly a huge decline of – haplogyne – spider families exists after the end of the Cretaceous.

In the following I will give an example of wrong conclusions which are based on errors of determination as well as of misunderstandings of the relationships of higher spider taxa:

In 2008 – see WUNDERLICH (2008: 547, fig. 3; see also fig. 4) – I concluded that the Mesozoic may have been dominated by haplogyne spider families, and this conclusion is fully confirmed by the present investigation: I now know more than half of the surely reported spider families of the Araneomorpha from the classical Haplogynae (16) but only 7 of the Entelegynae. DUNLOP & PENNEY (2012: 123) – apparently without a close knowledge – doubted this composition of the ancient fauna.

Previously I compared the proportion of Haplogynae and Entelegyne in different epochs based on the number of genera, see WUNDERLICH (2011: Fig. p. 543). After numerous new reports of – mainly haplogyne spiders (\*), see above – I modify herewith the left bar diagram of the fig. 543 (EC): The number of the Haplogynae genera is  $\frac{3}{4}$  and the number of Entelegynae is only  $\frac{1}{4}$  of the Araneomorpha in the Cretaceous (= 3 : 1). In the Eocene the proportion is more than 1 : 8. So the proportional growth of the Entelegynae in that time span is around 24 times (!) (\*). THE CENOZOICUM IS CLEARLY THE AGE OF THE ENTELEGYNAE within the evolution of araneomorph spiders in which members of the Araneoidea s. str. and members of the RTA-clade strongly dominate.

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(\* ) The relationships of 5 genera of the Praeterleptonetidae: Zarqaraneini are still unsure: Here they are regarded as members of the Haplogynae but further studies (with the help of micro-CT by J. DUNLOP) they probably may turn out as Entelegynae. If so – 5 haplogyne genera less and 5 entelegyne genera more – the previous result by fig. 543 (see above) would still be valid and the proportional growth would only be around 16 instead of 24 times.

### How many extinct spider species did exist?

Today ca. 1200 fossil/extinct spiders species have been described and more than 42 000 extant species but much more – 50 000? – extant species are still waiting for descriptions. If 99 to 99.9 percent of all spider species are extinct, ca. 100 000 extant species exist, and we know only 0.1 to 1 promille of the extinct species – as some authors assume – we may expect between ca. 1.2 and 100 million fossil/extinct spider species; that means: at least few millions but probably even about 50 million fossil species did exist! Probably only few tenthousand fossil spider species are (fairly well) preserved and may be available for studies in the future.

## Early origin of the RTA-clade?

The alleged origin of the family Sparassidae 186 million years ago reported by MORADMAND et al. (2014) – based on a molecular clock analysis – strongly contradicts the absence of members of this family in Mid Cretaceous amber (100 million years old) and in all other Mesozoic ambers. Were the most primitive sparassid members – of the subfamily Heteropodidae – ground dwellers which only very rarely were captured by the fossil resin and are therefore not yet reported? Interestingly not a single sure Mesozoic report of a member of the whole RTA-clade exists, and so the above supposition appears quite unlikely to me. It is remarkable that investigators of the extant spider faunas usually ignore results regarding the Mesozoic faunas. Probably the entelegyne Sparassidae replaced the extinct haplogyne Lagonomegopidae – see below – at the end of the Mesozoic or in the Lower Palaeocene.

Relict taxa are e. g.:

- Mesothelae; a single Mesozoic taxon in Burmite is described below;
- Archaeoidea (= Palpimanoidea) which extinct taxa – e. g. of the Families Archaeidae and Lagonomegopidae were quite diverse, and even the extinct families Micropalpididae and Spatiatoridae existed;
- the taxa of the Segestriidae: The number of Cretaceous genera is about four times the number of extant genera (but the extant genera will probably split up in the future);
- the taxa of the cribellate Deinopoidea like Uloboridae which are still not well studied (e. g. taxa of Liaoning, China).

Selected striking gaps of families of the Mesozoic faunas which probably will be found in the future:

Ctenizidae,  
Theraphosidae,  
Hypocheilomorpha (see Leptonetoidea: Mongolarachnidae),  
Filistatidae,  
Oonopidae: Other subfamilies than Orchestininae,  
Dysderidae,  
Caponiidae,  
Pholcidae,  
Ochyroceratidae s. str. (see the strongly related Psilodercidae, key no. 27),  
Sicariidae, especially Loxoscelinae (see the related Epsilodercidae, key no. 27),  
families which became extinct in the Eocene (Baltic amber) like Ephalmatoridae or  
families of the superfamily Araneoidea, e. g. Baltsuccinidae and Protheridiidae, see  
WUNDERLICH (2004),  
Theridiosomatoids like Anapidae, Comaromidae and Mysmenidae,  
members of the RTA-clade (Trionycha and Dionycha as well).



Urgently „wanted“ taxa – males – of the Cretaceous faunas (see also above):

Mesothelae: Liphistiidae: Adults,

Mygalomorpha: Surely determined Atypidae; more adults of different families,

Oonopidae (besides Orchestiniinae): Males of Gamasomorphinae and Oonopinae,

Plumorsolidae: Males,

Pholcoidea: *Furcembolus andersoni* WUNDERLICH 2008: Both sexes,

Huttoniidae (doubtful mesozoic reports): Adults, surely determined members/males,

*Autototomiana* n. gen. (Praeterleptonetidae): More adult spiders including spinnerets and leg IV,

*Triasaraneus*: Adult males,

Zygiellidae: More and surely determined members/males,

Nephilidae: Surely determined members/males,

Theridiidae: More and surely determined members/males,

Linyphiidae: Surely determined adult members/males.

## IV. TAXONOMY

### IDENTIFICATION KEY to the Mesozoic spider families

with remarks, a list of the families and with remarks on related extant families

Spiders with **striking characters** or a remarkable combination of characters:

Remarks: (1) A determination to the family may be quickly successful if peculiar characters are combined, e. g. (A) very long and diverging basal cheliceral articles + existence of a diastema + existence of cheliceral peg teeth (see b), and (B) the complete absence of leg bristles (see c). – (2) Several characters are not well or incompletely developed in juvenile spiders. – (3) Most families of the Mygalomorpha (key no. 3f) are excluded in this list of characters because most taxa are only known from juveniles.

**(a) Characters of the eyes:**

Only six (probably even only four) eyes: See the key nos. 11, (12), 16, 23f.

Eight-eyed Cretaceous „Haplogynae“ are members of the PLECTREURIDAE, LEPTONETOIDEA (except the six-eyed *Palaeoleptoneta*), and most or even all ARCHAEOIDEA (= Palpimanoidea).

Note: All described Cretaceous Entelegynae – e. g. Araneidae and Uloboridae (cribellate) – as well as all (other) cribellate spiders are eight-eyed.

The combined existence of eight eyes + cribellum/calamistrum: See below (f).

Huge eyes in a lateral position which are directed more sideways (as well as – in all taxa? – three pairs of tiny and indistinct eyes, figs. 231-233, photos 92 f.) . . . . (a) ecribellate: LAGONOMEGOPIIDAE (no. 12); (b) cribellate: Certain ULOBORIDAE like *Microuloborus* (fig. 377) (no. 28).

Large eyes which are directed anteriorly: *Salticoididus* of the SALTICOIDIDAE (fig. 340) (no. 21).

NOTE: Members of the family Salticidae (less distinct Lycosidae) possess huge anterior or posterior median eyes but are unknown (apparently absent) from the Cretaceous.

Long and/or quite wide eye field (e. g. fig. 367); usually with femoral trichobothria (fig. 387), cribellate. . . . . ULOBORIDAE (nos. 9, 17, 29); without femoral trichobothria, ecribellate. . . . . e. g. certain ARCHAEOIDEA (no. 13).

**(b) Other characters of the prosoma, the chelicerae and the clypeus:**

A distinctly wrinkled prosomal cuticula (figs. 43f, 118-121, 131) exists mainly in most ARCHAEIDAE (no. 13), SPATIATORIDAE: Spatiatorinae (no. 19) and TETRABLEMMIIDAE (no. 16).

A strongly domed prosoma exists in certain Oonopidae: *Burmorchestina* (*Burmorchestina* has strongly thickened femora IV, Sctytodidae and certain Oecobiidae: *Retroecobius* (figs. 314, 322) (Oecobiidae has a „nose-shaped“ clypeus, fig. 313).

Huge AND horizontally protruding basal cheliceral articles, fangs in a longitudinal position (fig. 2, 13). Key no. 3f . . . . .clade MYGALOMORPHA (no. 3f).

Distinctly obliquely protruding chelicerae (figs. 33f, photos 25f). . . . .  
. . . . .Some SEGESTRIIDAE (no. 24), TELEMIDAE (no. 27)

Very long and diverging basal cheliceral articles AND a diastema (a distinct gap behind the chelicerae) (figs. 199f, photos 118f. . . . . ARCHAEIDAE s. l. (no. 23).

Very small basal cheliceral articles . . . . . OONOPIIDAE (nos. 11, 16, 26); (weak articles, e. g., in the Oecobiidae, too, no. 22).

Existence of cheliceral „peg teeth“ (fig. 244, photo 128) (modified thickened and blunt hairs on the anterior margin of the fang furrow), e. g. ARCHAEIDAE and LAGONOMEGOPIIDAE. . . . . superfamily ARCHAEOIDEA (= PALPIMANOIDEA) (no. 12).

Retrolateral cheliceral stridulatory files or edge (fig. 202) in Cretaceous spiders (they are hard to observe in fossil spiders): Most ARCHAEOIDEA (= PALPIMANOIDEA) (nos. 12, 13, 19), SICARIIDAE: LOXOSCELINAE (no. 26) (no Cretaceous proof), certain OCHYROCERATIDAE (no Cretaceous proof), and NEPHILIDAE (no. 32).

Clypeus ventrally strongly protruding (fig. 97): PSILODERCIDAE (no. 27) SICARIIDAE: Loxoscelinae (no. 26) (no Cretaceous proof) and OECOBIIDAE (fig. 313).

**(c) Characters of the legs:**

Extremely long and slender legs: Most Leptonetoidea like MONGOLARACHNIDAE (no. 29) (photos 65f), PHOLCOCHYROCERIDAE (photos 70f) (no. 29) and PSILODERCIDAE (photo 55f) (no. 27). Quite long and slender legs also exist in the EOPSILODER-

CIDAE (photo 53) (no. 27), in the LOXOSCELINAE of the SICARIIDAE (no Cretaceous proof) (no. 26) in which a paired tarsal claw is absent (no Cretaceous proof), in the HERSILIIDAE (photo) (no. 10) which have very long spinnerets, and in certain LAGONOMEGOPIDAE (no. 12) which have huge eyes in a lateral position.

Leg bristles are absent in most Archaeoidea like ARCHAEIDAE s. l. (nos. 12, 13, 19), most PHOLCOIDEA (no. 27), in certain OONOPIDAE (nos. 11, 16, 26), in certain ULOBORIDAE (no. 29) and in male Burmascutidae (no. 15).

Distinctly thickened femora of the posterior jumping legs: Tiny, six-eyed and frequent spiders: subfamily ORCHESTININAE of the OONOPIDAE (no. 11).

Leg III directed forwards (fig. 33, photos 24f) (the „segestriid leg position“) (the natural position may be modified in some fossils, and an unnatural similar position exists in some other taxa, too): PLUMORSOLIDAE with 2 tarsal claws and distinct claw tufts (no. 20) and SEGESTRIIDAE with 3 tarsal claws but no claw tuft (no. 24).

Unpaired tarsal claw absent: Six-eyed. . . . LOXOSCELINAE of the SICARIIDAE (no. 26) (still no proof for the Cretaceous), OONOPIDAE (no. 11, 16, 26), most frequent are the Orchestininae which have strongly thickened posterior femora, probably tiny EOPSILODERCIDAE (no. 27), as well as PLUMORSOLIDAE (no. 20) which have distinct claw tufts of long hairs (figs 76-77).

NOTE: Members of the diverse extant branch „Dionycha“ like Clubionidae and Thomisidae – in which an unpaired tarsal claw is absent, too – are unknown from the Cretaceous.

Existence of distinct claw tufts (figs. 76-77, photo), six-eyed: PLUMORSOLIDAE (no. 20); eight eyed: Fossilcalcaridae. See also the following two lines.

Existence of prolateral spatulate leg I-II hairs. . . . . several members of the superfamily Archaeoidea.

Existence of femoral trichobothria (fig. 387); cribellate....most ULOBORIDAE (no. 29). See also the ecribellate genus *Autotomiaria* (Praeterleptonetide).

Existence of several tarsal trichobothria as well as several metatarsal trichobothria (fig. 245, photo 112) besides Mesothelae and Mygalomorpha: MICROPALPIMANIDAE (no. 19), and some – or even all – LAGONOMEGOPIDAE (no. 12). – REMARK: Several tarsal trichobothria exist also in the Caponiidae (see below: Dysderoidea) which are not known from the Mesozoic.

Existence of feathery hairs (fig. 189) (they are hard to recognize in the fossils). . . . .  
. . . . *Plumorsolus* of the PLUMORSOLIDAE (no. 20), HERSILIIDAE (no. 10), some SALTICOIDIDAE (no. 21), and some ULOBORIDAE (no. 29).

Striking (very long/dense hairs of spiders in Burmite): Some LAGONOMEGOPIDAE (no. 12) and *Autotomiaria* of the PRAETERLEPTONETIDAE (no. 35) in which patella-tibia autotomy exists.

#### (d) **Characters of the opisthosoma** (excl. (e) and (f)):

Existence of distinct scuta including an entire large dorsal one: Tiny spiders of the BURMASCUTIDAE (no. 15), GAMASOMORPHINAE of the OONOPIDAE (not yet reported from the Mesozoic), TETRABLEMMIDAE (fig. 126, photos 43f) (no. 16), as well as certain larger members of the MYGALOMORPHA (no. 3f).

A laethery/hardened opisthosoma exists in certain members of the superfamily Archaeoidea; a small anterior opisthosomal scutum exists in the SPATIATORIDAE (no. 19)

Several transverse dorsal scuta (fig. 5, photo. 10). . . . . LIPHISTIIDAE (no. 1)  
(Several dorsal opisthosomal scuta may also exist in Mygalomorpha like Antrodietidae (no. 6)).

Two pairs of lungs and lung covers (they are hard to recognize in fossil spiders). . . . .  
. . . . . LIPHISTIIDAE (no. 1) and the clade MYGALOMORPHA (nos. 3f).

**(e) Characters of the spinnerets, the colulus and the anal tubercle:**

Posterior spinnerets unusually long: Certain MYGALOMORPHA (nos. 3f) (figs. 13-14, 20) like FOSSILCALCARIDAE (fig. 21 (no. 3) and DIPLURIDAE (photo 18) (no. 8).

Spinnerets in an advanced position. . . . . LIPHISTIIDAE (fig. 7) (no. 1), BURMASCUTIDAE (no. 15), and certain ULOBORIDAE (figs. 357f) (no. 15).

Pairs of spinnerets: 4 in LIPHISTIIDAE (fig. 7) (no. 1), 2 in DIPLURIDAE (no. 8) and NEMESIIDAE (no. 4), and others of the Mygalomorpha, 3 in the remaining families.

Spigots of the posterior spinnerets are absent in the family PHOLCIDAE which is still unknown from the Cretaceous.

Colulus very large/wide, e. g. taxa in Burmite: TELEMIDAE, and – fig. 305 – (it may be called „pseudocribellum“). See directly below . . . . . certain OECOBIIDAE (no. 22).

Anal tubercle peculiar, huge and setose (fig. 305): Most...OECOBIIDAE (no. 22).

**(f) Characters of cribellum/calamistrum** (see the questionable pseudocribellum directly above):

Described cribellate Cretaceous/Mesozoic families are: MONGOLARACHNIDAE (no. 9), PHOLCOHYROCERIDAE (no. 29), certain OECOBIIDAE (no. 22), ULOBORIDAE (nos. 9 and 29) and SALTICOIDIDAE (nos. 17, 21). The existence of a „spinning field“ (cribellum, fig. 185) is linked basically and most often with the existence of a comb of metatarsus IV (calamistrum, figs. 372, 373, 385, photo 164) which may be absent, untypical or indistinct in males, e. g. in certain Dictynidae (extant), and in the Longissipalpinæ of the Mongolarachnidae. In all families listed here in (f) eight eyes exist.

NOTE: If the spinning field of the cribellum is hidden the existence of a cribellum is indicated usually by the position of the anterior spinnerets which are widely spaced at their base and usually distinctly converging distally (fig. 185).

**(g) Characters of the male pedipalpus:**

Thickened articles exist in most MYGALOMORPHA (nos. 2-8) and most „HAPLOGYNÆ“ (e. g. figs. 19, 36). Pedicular long articles exist e. g. in the family MONGOLARACHNIDAE (figs. 184, 186, photos 165-166). Simple and globular bulbi which usually bear only an embolus but no additional sclerites like a conductor (e. g. figs. 19, 36, 84) exist in the EOPSILODERCIDAE (no. 27), certain OONOPIIDAE (nos. 11, 16, 26), PLECTREURIDAE (no. 30), probably PLUMORSOLIDAE (no. 20; ♂ unknown), SCYTODODAE (no. 27), SEGESTRIIDAE (no. 24) and SICARIIDAE (no. 26). In *Furcembolus* (probably Pholcoidea) exists a bifurcated embolus (no. 27).

**(h) The body size:**

Tiny spiders (most adult males only about 1-1.3 mm long): Members of the families TELEMIDAE (no. 27), EOPSILODERCIDAE (no. 27), PSILODERCIDAE (no. 27), BURMACSUTIDAE (no. 15), MICROPALPIMANIDAE (no. 19), OONOPIIDAE (no. 11, 16, 26), TETRABLEMIDAE: Tetrablemminae (no. 16), certain ULOBORIDAE (no. 29) and certain THERIDIOSOMATIDAE (no. 35).

Larger spiders, body length of ADULT spiders at least 5 mm: *Mongolarachne* of the MONGOLARACHNIDAE, *Autotomiana* of the PRAETERLEPTONETIDAE, certain LAGONOMEGOPIDAE (key no. 12), *Cretaraneus* of the NEPHILIDAE (no. 32), mem-

bers of the MYGALOMORPHA (no. 3f), and most probably of the LIPHISTIIDAE (no. 1) of which adults in amber are still unknown.

A distinct sexual size dimorphism – up to giant females and dwarf males – exists in extant members of the families ARANEIDAE and NEPHILIDAE in contrast to related families like Tetragnathidae (no Cretaceous proof) or Zygellidae.

**REMARK:** Besides the up to 38 families known today from the Cretaceous **I expect proofs for the future** of the following – apparently (in the geological sense) old – families:

- Mygalomorpha: CTENIZIDAE and THERAPHOSIDAE (as well as sure members of the ATYPIDAE).
- Members of the HYPOCHILOMORPHA, key no. 9.
- Several haplogyne families of the Dysderoidea/Pholcoidea (most have only six eyes) like CAPONIIDAE (they possess several tarsal trichobothria, see below), DYSDERIDAE (in which the patellae are unusually long), OCHYRO CERATIDAE s. str. (they possess a row of small teeth on the promargin of the cheliceral fang furrow in contrast to the strongly related Psilodercidae), ORSOLOBIDAE (similar to the Oonopidae but with a parallel position of the gnathocoxae in contrast to the converging gnathocoxae in the Oonopidae, and similar to the Plumorsolidae, too, in which the „segestriid“ leg position and the leg bristles are different), and the six- or eight-eyed PHOLCIDAE which possesses a peculiar position of the eyes (fig. 83), widely fused chelicerae, and in which leg bristles are absent (rarely exist femoral bristles) in contrast to the cribellate Pholcochyroceridae which may be similar (see also the questionable \*Pholcoidea indet. from Liaoning below), and finally members of the SICARIIDAE: LOXOSCELINAE which male pedipalpus is similar in Cretaceous Eopsilodercidae but which have an almost laterigrade leg position and different structures of the chelicerae. – See the key to the families no. 27.
- The FILISTATIDAE which are cribellate and in which a tibia-patella autotomy exists
- Families of the superfamily Araneoidea s. str.: PROTHERIDIIDAE and the BALT-SUCCINIDAE (both extinct families preserved in Eocene Baltic amber) as well as families strongly related to the Theridiosomatidae like ANAPIDAE and MYSMENIDAE which are known from Eocene Baltic amber; they have the tarsi usually longer than the metatarsi and sternal pits are absent.

Alphabetic order of the families listed and their nos. in the key:

Remarks: (1) The Mesozoic proof of six or even seven families appear questionable to me, see the question marks; well preserved adult males are needed for closer studies. (2) Synonymy: Juraraneidae may be related to or identical with the Araneidae. (3) Previous erroneous Mesozoic reports of families like Clubionidae, Deinopidae, Dictynidae, Linyphiidae, Pisauridae, Salticidae, Tetragnathidae and Thomisidae: See the paragraph „Erroneous determinations“ above. (4)

Extinct (sub)families are underlined. Besides the Salticoididae they are reported from Burmite: Spatiatorinae are additionally reported from the Paleogene: from Eocene Baltic amber. (5) In brackets: Taxa without a mesozoic report up to now.

Antrodietidae .....	6
?Araneidae .....	32
Archaeidae s. l. ....	13
?Atypidae .....	5
<u>Burmascutidae</u> .....	15
Dipluridae .....	8
<u>Epsilodercidae</u> .....	27
<u>Fossilcalcaridae</u> n. fam. ....	3
Hersiliidae .....	10
?Hexathelidae .....	8
?Huttoniidae .....	19
(Hypochilomorpha) .....	9
<u>Juraraneidae</u> .....	32
<u>Lagonomegopidae</u> .....	12
Leptonetidae: <u>Palaeoleptonetinae</u> .....	23
?Linyphiidae .....	33
Liphistiidae .....	1
Mecicobothriidae .....	7
<u>Micropalpimanidae</u> .....	9
<u>Mongolarachnidae</u> .....	9, 29
<u>Longissipalpinæ, Mongolarachninae,</u> <u>Pedipalparaneinae</u>	
?Nemesiidae .....	4
Nephilidae .....	32
Oecobiidae, incl. <u>Retroecobiinae</u> .....	22
Oonopidae: <u>Orchestininae</u> : 11; see 16, 26	
(Pholcidae) .....	27
?Pholcoidea: <u>Furcembolusini</u> .....	27
<u>Pholcochyroceridae</u> .....	29
Plectreuridae .....	30
Plumorsolidae .....	20
<u>Praeterleptonetidae</u> .....	35
(five diverse higher taxa – tribes?)	
Psilodercidae .....	27
<u>Salticoididae</u> .....	17, 21
Scytodiidae .....	27
Segestriidae .....	24
(Sicariidae) .....	26
<u>Spatiatoridae</u> .....	19
<u>Spatiatorinae, Vetiatorinae</u>	
Telemidæ .....	27
Tetrablemmidae .....	16
(?)Theridiidae .....	34
Theridiosomatidae .....	35
Uloboridae .....	9, 29
Zygiellidae .....	32



Notes on the key below: In this key mainly such characters are used which may be more easily observable in fossils; certain important characters like the dentition of the chelicerae or the spigots or the characters of the respiratory system – e. g. the tracheal openings – are most often hidden or deformed in the fossils. – The most often described Cretaceous spiders are taxa of the SIX-EYED Haplogynae – see below (a) – in contrast to the predominantly EIGHT-EYED taxa of today's Entelegynae. Remarks on six-eyed extant families which are (still?) unknown from the Cretaceous: See the key no. 27. – A separate key is given to the families of the ARCHAEOIDEA and the ARANE- OIDEA s. l.: DEINOPOIDEA s. str., see below. – For an easier determination the diverse family OONOPIDAE is keyed three times, see the nos. 11, 16 and 26, and the family ULOBORIDAE two times, see the nos. 9 and 29. – The most often described Cretaceous members of the Mygalomorpha are preserved in stone, marked with a „\*“ or both – in stone as well as in amber – marked with „(\*)“. Most members of the Araneomorpha are preserved in deposits of the Cretaceous (C) (usually in ambers), few in Triassic (T) or Jurassic (J) kinds of deposits. – Extinct families are underlined. – For further characters and notes on extant families: See JOCQUE & DIPPENAAR (2007) and WUNDERLICH (2012). – In certain extinct taxa of some families – see Oecobiidae and Uloboridae – typical family characters are absent.

Hint: Usually only few of the important taxonomical structures are (well) observable in the fossils. The determination to the family level may be verified with the help of peculiar characters of the list above; see e. g. the remark on the cribellum.

1 Opisthosoma segmented and bearing several transverse dorsal scuta (fig. 5, photo 10), position of the (four pairs of) spinnerets almost in the middle of the opisthosoma (fig. 7, photo. 11). MESOTHELAЕ. *Cretaceothele* n. gen. C. Burmite. . . . . **Liphistiidae**, p. 101

- Opisthosoma not segmented, usually soft (except certain Mygalomorpha, no. 3f; see also no. 15, position of the (three or less pairs of) spinnerets at the end of the opisthosoma (e. g. figs. 216, 394 ) (except the Burmascutidae (no. 15) and few taxa of the cribellate Uloboridae, no. 29). OPISTOTHELAЕ. . . . . 2, p. 103

2(1) Basal cheliceral articles strongly protruding (figs. 12, 15), fangs very long and in a more longitudinal position if not spread off (fig. 29). Eyes small, frequently in a compact group of eight (figs. 10, 15, 20). MYGALOMORPHA (see also Mygalomorpha indet.). Note: The identity of some Mesozoic families is unsure, see the list above . . . . . 3, p. 103

- Basal cheliceral articles not or obliquely protruding (certain Segestriidae and Archaeoidea, figs. 41, 57, e. g. nos. 13, 24), fangs shorter and in a more transverse position (figs. 62, 93). Six or eight eyes, their size and position variable. ARANEOMORPHA. . . . . 9, p. 111



3(2) ♂ (♀ unknown): Metatarsus and tarsus I-II bear a dense scopula. Tibia I bearing a peculiar nippers-shaped clasping spine (figs. 23-24), pedipalpal tibia with a peculiar pointed retrolateral spur (fig. 27). *Fossilcalcar* n. gen. C. Burmite. . . . . **Fossilcalcaridae**, p. 107

- Usually no (dense) scopula on metatarsus and tarsus I-II. Tibia I clasping spine different, pedipalpal tibial spur absent. . . . . 4

4(3) Paired tarsal claws wide, bearing two rows of teeth (usually similar fig. 11). Tibia I of the adult male with a clasping spur. Isle of Wight. . . . . **\*Nemesiidae**, p. 103

- Paired tarsal claws slender, bearing a single row of teeth. Clasping spur absent or existing. . . . . 5

5(4) Posterior spinnerets of medium length (photo 20). Gnathocoxae strongly prolonged anteriorly (fig. 29). Subfamily *\*Ambiortiphaginae* from Lower Cretaceous of Central Mongolia (fig. 12): The correct determination of this taxon as a member of the *Atypidae* has been questioned by WUNDERLICH (2011: 481) mainly because of its unknown gnathocoxae and spinnerets. A quite questionable confamilial member (photo 20) in Burmite is reported below. (C). . . . . (\*)**?Atypidae**, p. 104

- Posterior spinnerets short to long. Gnathocoxae not or only slightly prolonged. . . . 6

6(5) Posterior spinnerets short (fig.10), cheliceral rastellum existing (fig. 10). Lower Cretaceous of Mongolia. . . . . **\*Antrodietidae**

- Posterior spinnerets long (figs. 13, 20), cheliceral rastellum absent. . . . . 7

7(6) Fovea a short longitudinal slit (fig. 13), posterior spinnerets rather long, cymbium long, bulbus large. Lower Cretaceous of Transbaikalia. . . . . **\*Mecicobothriidae**

- Fovea pit-like to transverse, posterior spinnerets long to very long (figs. 20-21), cymbium short or long, bulbus small. . . . . 8

8(7) Posterior spinnerets very long, frequently about as long as the opisthosoma, apical segment slender and pointed (figs. 20-21). Labium without cuspules. C. Burmite. Most frequent fossil Mygalomorpha in the Cretaceous. Brasil and Burmite. . . . . (\*)**Dipluridae**, p. 104

- Posterior spinnerets about half the opisthosomal length, apical segment digitiform. Labium with numerous cuspules. Triassic, France. . . . . (?)**\*Hexathelidae**

9(2) Cribellum and calamistrum existing (calamistrum with TWO rows of setae in the family Hypohilidae). TWO pairs of lungs and lung covers in contrast to the following families. No fossil proof up to now. . . . . . HYPOCHILOMORPHA, p. 111

- Cribellum and calamistrum (fig. 360) existing, calamistrum WITH TWO ROWS OF SETAE close together, besides a large depression. Subad. ♂. C. Burmite. Genus *Bicalamistrum*. . . . . **Uloboridae** (part.), p. 318

- Notes: (1) for the case that the cribellum is difficult to recognize: The anterior spinnerets are widely spaced basally and usually distinctly converging in cribellate taxa, see fig. 185.  
 (2) A large/deep depression on metatarsus IV (the calamistrum) exists also in *Zhizhu* SELDEN et al. 2015 (Mongolarachnidae?, Deinopoidea? See below) in Mid Jurassic stone of China.
- Cribellum existing or absent; if existing (see nos. 17 and 28) the calamistrum bears a single row of setae only or seemingly two rows (*Burmuloborus*, fig. 375) or it is absent/indistinct: in the Longissipalpinae of the Mongolarachnidae, see no. 28. A single pair of lungs and lung covers (few lungless taxa exist in extant spiders and Eocene spiders like Telemidae). DIPNEUMONOMORPHA (= ARANEOCLADA). . . . . 10
  - 10(9) Posterior spinnerets very long (photo 143). C. Burmite. . . . . **Hersiliidae**, p. 303
  - Posterior spinnerets short. . . . . 11
  - 11(10) Posterior femora strongly thickened. Tiny six-eyed spiders (not much longer than 1 mm). Frequent in most Cretaceous ambers (as well as in Eocene ambers and extant). Subfamily Orchestiniinae. . . . . **Oonopidae** (part.), p. 140
  - Posterior femora not strongly thickened, not distinctly thicker than the remaining femora. Tiny or larger spiders, six (see nos. 12 – number unsure –, 16 and 23) or eight eyes. . . . . 12
  - 12(11) A pair of huge eyes in a lateraal position which are DIRECTED SIDEWARDS (figs. 231-233, photos 92f) as well as ?always three additional pairs of tiny and indistinct eyes. Tarsal trichobothria (figs. 245-246, 259) existing, frequently hard to recognize mainly in juvenile spiders. C. Frequent in most kinds of Cretaceous ambers. . . . . **Lagonomegopidae**, p. 236
  - No huge eyes in a lateral position which are directed sideways. Tarsal trichobothria rarely existing: in the Micropalpimanidae (no. 19). . . . . 13
  - 13(12) Basal cheliceral articles very long and diverging, anterior margin of the fang furrow bearing „peg teeth“ (blunt and thick bristles) and with a large gap to the gnathocoxae (diastema) (fig. 244, photos 118f); the cephalic part frequently strongly raised and wrinkled. Leg bristles absent. Various kinds of Cretaceous ambers. . . . . (\*) **Archaeidae s. l.**, p. 211
  - Basal cheliceral articles not very long and diverging, „peg teeth“ existing only in the Micropalpimanidae, Spatiatoridae and questionable Huttoniidae (no. 19), diastema absent. Cephalic part rarely raised/wrinkled (in *Spatiator*). Leg bristles absent or existing . . . . . 14
  - 14(13) Opisthosoma strongly/completely armoured dorsally and ventrally. . . . . 15
  - Opisthosoma soft, rarely leathery (the epigaster may be sclerotized). . . . . 17
  - 15(14) Spinnerets in a distinct anterior position, see WUNDERLICH (2008: 669, fig. 106). 8 eyes in two rows. Unpaired tarsal claw existing. C. Burmite . . **Burmascutidae**, p. 289

- Position of the spinnerets at the end of the opisthosoma (fig. 82) (except few cribellate and eight-eyed Uloboridae. 6 eyes (fig. 117) in the known fossils but their number is different in various extant Tetrablemmidae (!). Unpaired tarsal claw absent or existing . . . . . 16
- 16(15) Unpaired tarsal claw and lateral opisthosomal scuta absent (dorsal and ventral scuta exist). Leg bristles usually existing. Subfamily Gamasomorphinae. Not yet reported from the Mesozoic. . . . . **Oonopidae** (part.), p. 140
- Unpaired tarsal claw as well as LATERAL opisthosomal scuta besides dorsal and ventral scuta existing (fig. 126, photos 43f). Leg bristles absent. C. Burmite. . . . . **Tetrablemmidae**, p.157
- 17(14) Embolus very long and spirally, describing about a dozen loops (fig. 351). *Burmadictyna* in Burmite. Cribellum and calamistrum existing. See no. 21. . . . . **Salticoididae** (part.), p. 310
- Embolus much shorter; if spirally describing at most 2 loops (see no. 21). Cribellum and calamistrum absent or existing (no. 28). . . . . 18
- 18(17) Cheliceral „peg teeth“ existing (fig. 275) (they may be hidden!). Leg bristles usually absent (few may exist in the Huttoniidae). Prolateral flattened/spatulate hairs may exist on tibiae, metatarsi and tarsi of legs I-II. . . . . 19
- Cheliceral „peg teeth“ absent. Leg bristles usually existing (see no. 23). Flattened/spatulate hairs absent. . . . . 20
- 19 (18) Tarsal trichobothria existing (fig. 267) but hard to recognize. Cephalic part distinctly raised (photo 134). C. Burmite. . . . . **Micropalpimanidae**, p. 266
- Tarsal trichobothria absent. C. Burmite. Spatiatorinae (prosoma distinctly wrinkled, cephalic part distinctly raised, similar to photo 134) and Vetiatorinae (prosoma indistinctly corniculate, cephalic part flat, fig. 285). . . . . **Spatiatoridae**, p. 269
- Tarsal trichobothria absent. Cephalic part not raised. Extants known from New Zealand. Adults unknown from the Cretaceous. C. Canadian and New Jersey ambers. . . . . QUESTIONABLE **Huttoniidae**, p. 234
- 20(18) Existence of conspicuous claw tufts of long and flattened hairs (fig. 76). 6 eyes. Feathery hairs existing or absent. Adult male unknown. C. Lebanese and Burmese ambers. . . . . **Plumorsolidae**, p. 136
- Claw tufts usually absent (existing only in most Oonopidae which are also six-eyed and have WIDE tooth-bearing paired tarsal claws which usually possess TWO rows of teeth in contrast to the Plumorsolidae). Feathery hairs existing (Salticoididae, some Uloboridae) or absent. . . . . 21
- 21(20) Embolus describing ca. 3 loops (figs. 339, 341). Cribellate. Legs with numerous feathery hairs. Anterior median eyes quite large (fig. 340): *Salticoididus* in Jordanian

- amber; anterior median eyes not enlarged (fig. 338): *Palaeomicromenneus* in Lebanese amber, as well as probably in New Jersey (indet. juv). See no. 17. .... **Salticoidae** (part.), p. 310
- Embolus different, describing less than 2 loops (a single loop probably in *Palaeouloborus*). Cribellate or ecribellate. Feathery hairs absent or indistinct in some Uloboridae (no. 29). .... 22
- 22(21) Anal tubercle usually quite large and bearing a fringe of hairs (fig. 298, 305; but see fig. 318). Clypeus ventrally protruding to even „nose-shaped“ (fig. 300). Tarsi III-IV with ventral bristles (figs. 304, 323). Cribellate or ecribellate (most Cretaceous taxa). C. Various kinds of amber. .... **Oecobiidae**, p. 292
- Anal tubercle of normal size, without a fringe of hairs. Clypeus protruding or not, not „nose-shaped“. Tarsi III-IV usually without ventral bristles. Ecribellate or cribellate. With ventral tarsal III-IV bristles (questionable Dictynidae, no. 29, and most Uloboridae, no. 29) or without such bristles. .... 23
- 23(22) Six eyes (figs. 34a, 39, 51, 61). Legs besides the Segestriidae (no. 24) (they possess well developed bristles and a special leg position) with few thin bristles or even bristleless. ♂-pedipalpus with thickened article(s) and simple structures of the bulbus (e. g. figs. 36f) or partly complex structures (figs. 94f). .... 24
- Six eyes (fig. 34a). Legs with numerous bristles. ♂-pedipalpus (fig. 34c) with slender articles and complicated structures of the bulbus. C. Burmite. Subfamily *Palaeoleptonetinae*. (A single Cretaceous species). .... **Leptonetidae**, p. 173
- Eight eyes (e. g. figs. 160, 342, 367). Legs with numerous distinct bristles. ♂-pedipalpus with slender articles and complicated structures of the bulbus. Burmite and other kinds of amber/deposits. .... 28
- 24(23) Legs with long bristles, e. g. well developed ventrally on tibiae I-II (fig. 45). Chelicerae frequently distinctly protruding (figs. 41, 57, photos 25f). Leg III directed forward (photos 25f) (its position may be unnatural in the fossils). C. Several kinds of amber. . . . **Segestriidae**, p. 115
- Legs bristleless or with few thin bristles (probably in Oonopidae, see no. 26). Chelicerae not (distinctly) protruding. Leg III directed backwards (photos) like in most spiders except Plumorsolidae (no. 20). .... 25
- 25(24) Unpaired tarsal claw completely absent. STILL UNKNOWN FROM THE MESOZOIC. .... 26
- Unpaired tarsal claw existing, reduced or even absent (apparently in the Eopsiloderidae), it is indistinct in some Praeterleptonetidae (no. 35). .... 27
- 26(25) Legs very long and very slender, their position more or less laterigrade, teeth-bearing part of the paired tarsal claws narrow and with a single row of teeth. Larger spiders, body length 8-19 mm. Subfamily Loxoscelinae: Quite similar to members of the

Eopsilodercidae (no. 27) as well as certain extant members of the families Psilodercidae and Ochyroceratidae. STILL NO CRETACEOUS PROOF (!). . . . . **Sicariidae**, p. 142

- Legs not VERY long, their position prograde, teeth-bearing part of the paired tarsal claws usually wide and bearing two rows of teeth. Tiny to small spiders, body length up to 4 mm. Subfamily Oonopinae. STILL NO CRETACEOUS PROOF (!). . . . . **Oonopidae** (part.), p. 140

27(25) Clypeus not protruding, thoracic area usually distinctly raised (fig. 99), chelicerae fused basally, fangs very short/stout. Bulbus simple, more basally attached on the long cymbium. Female genital area in extant members with a pair of „clasping grooves“ (unknown in the fossils). C. Jordan. . . . . **Scytodidae**, p. 157

- Clypeus ventrally strongly protruding (fig. 97, 99), thoracic area flat, chelicerae not fused basally, fangs quite long (fig. 91). Bulbus complicated (in most of the known fossils, and attached more basally on the cymbium, ?*Leclercera*, figs. 95f) or simple (globular, fig. 100). Existence of „clasping grooves“ most probably absent. C. Burmite. . . . . **Psilodercidae**, p. 149  
Remark: Still no Cretaceous proof of members of the partly similar family Pholcidae.

- Clypeus fairly protruding, thoracic area not raised (domed). Chelicerae fused basally, bearing a long medial lamina and a peculiar long retroapical bristle, fangs fairly long (figs. 85-86). Bulbus simple, globular, attached apically on the cymbium (fig. 84). (RETROLateral bristle-shaped hairs may exist on tibia I, fig. 87). C. Burmite. . . . . **Eopsilodercidae**, p. 145

- Clypeus long and vertical, prosomal cuticula wrinkled, embolus distinctly bifurcated. *Furcembolus andersoni* WUNDERLICH 2008: 582, figs. 20-22 (family unsure). C. Burmite. . . . . **Furcembolusini**, p. 143  
Remark: Still no Cretaceous proof of members of the more or less similar Ochyroceratidae, Pholcidae and Sicariidae: Loxoscelinae (no. 26). During printing this paper I got a male of the family Telemidae (indet.) in Burmite which is only 0.85 mm long. In this taxon exist a huge colulus and a long and slender cymbium, see p. 171.

28(23) Cribellum (fig. 180, 185 ) and calamistrum existing (figs. 184, 361 372, 375, 380, 384) (the calamistrum may be absent or indistinct in the male sex: In the Longispalpiniae of the Mongolarachnidae). . . . . 29

- Cribellum and calamistrum absent. . . . . 30

29(28) Metatarsus IV frequently distinctly CONCAVE DORSALLY & compressed laterally (figs. 361 372, 375, 380, 384). Tarsi III-IV usually with ventral bristles (fig. 388). Femora most often WITH TRICHOBOTHRIA (figs. 379, 386), (feathery hairs may also exist). Eye field very long and wide, with anterior and posterior lateral eyes widely separated (fig. 367, 377, photos 267f). C. frequent e. g. in Burmite; see also nos. 9 and 17. . . . . **Uloboridae** (part.), p. 318

- Metatarsus IV straight dorsally, never depressed laterally (the following 2 taxa). Femoral trichobothria absent (the following two taxa). Usually very long leg I. Frequently spiny articles of the male pedipalpus (figs. 178, 182). C: Burmite. . . . . **Pholcochyroceridae**, p. 197
- Similar but pedipalpal articles extremely long (leg-shaped) and bulbus very small (figs. 184, 186). Jurassic (in stone, Mongolia): Mongolarachninae and in Cretaceous Burmite: Longissipalpinae and Pedipalparaneinae. See no. 9. . . . . **Mongolarachnidae**, p. 201
- 30(28) ♂: A „clasping spine“ exists on tibia I in *Eoplectreurys* (fig. 32) or on femur I (*Montsecarachne*). Number of eyes unknown in the fossils, 8 eyes in extant spiders. Fine retrolateral cheliceral stridulatory files – existing in extant taxa – are unknown in the fossils. Simple structures of the bulbus. *Eoplectreurys*: J (China) and *Montsecarachne*: C (Spain) (both in stone). . . . . **\*Plectreuridae**, p. 114
- ♂: „Clasping spine“ of the tibia I or femur I absent, retrolateral cheliceral files usually absent (a small and indistinct field in the Nephilidae; probably existing in the questionable Cretaceous Linyphiidae). Complex structures of the bulbus . . . . . 31
- 31(30) Clypeus distinctly shorter than the field of the median eyes. Numerous leg bristles. . . . . 32
- Clypeus about as long as the field of the median eyes or longer. Few to numerous leg bristles. . . . . 33
- 32(31) Eye field rather narrow or only fairly wide, median and lateral eyes only fairly wide spaced. ♂-Pedipalpus e. g. as in figs. 192-193; structures of the bulbus complex. Probably: Jurassic (*Seppo*); C: Spanish amber and probably Lebanese amber. . . . . **Zygiellidae**, p. 337
- Eye field wide, with median and lateral eyes widely spaced. ♂-Pedipalpus different: Structures of the bulbus not complex, figs. 390-391. ?J – C. . . . . **\*Nephilidae**, p. 337 (no sure proof of the Mesozoic . . . . . Ananeidae, p. 336)
- 33 (31) Metatarsal bristles absent or very rare and thin. Coxa-trochanter leg autotomy . . . . . 34
- Dorsal metatarsal bristles existing (as well as femoral bristles). Paracymbium sickle-shaped and close to the bulbus. Tibia-patella leg autotomy. ??C (probably Cenozoic: Ethiopian amber). . . . . questionable **Linyphiidae**, p. 345
- 34(33) All femora bristleless, lateral tibial bristles absent. Labium not rebordered apically (fig. 398) in contrast e. g. to the Linyphiidae and Theridiosomatidae (no. 35). ♂-pedipalpus (figs. 403-406): Tibia quite long in the single known Mesozoic genus *Cretotheridion*, tibial and cymbial outgrowths or spines absent. Photo 175. C. Burmite. . . . . **Theridiidae**, p. 340

- At least femur I bears at least a single bristle, at least tibiae I-II bear lateral bristles. Labium in the Theridiosomatidae with an indistinct transverse apical border. Pedipalpal tibial or cymbial outgrowths/spines existing in the Praeterleptonetidae . . . . . 35

35(34) Pedipalpus (figs. 396-397) large, patellar or tibial apophyses as well as cymbial spines/bristles absent, paracymbium small. C. Preserved in Burmite (only *Leviunguis bruckschi*, photos 171-174) and in stone of Russia. . . . (\*)**Theridiosomatidae**, p. 338

- Pedipalpus (figs. 138f) smaller, tibial or patellar and/or cymbial apophyses/bristles or humps exist, paracymbium large and frequently standing widely out. Shape of body and legs as well as the varying chaetotaxy frequently quite similar to the Theridiosomatidae. (photos 74-91). C. Burmite (frequent and diverse) and Jordanian amber: *Zarqaraneus hudei*. (This is probably not a monophyletic family) . . . . .  
 . . . . . **Praeterleptonetidae**, p. 174

Remarks on changings of diagnostic characters of families regarding space (regions) and time (eras) based on the example of the family Theridiosomatidae (see also above, e. g. the families Archaeidae, Spatiatoridae, Praeterleptonetidae and Uloboridae):

Connected receptacula seminis have been regarded as one of the main diagnostic characters of the family up to latest times. Only four years ago – see WUNDERLICH (2011) – the extant theridiosomatid genera *Luangnam* and *Chthonopes* of the new subfamily Luangnaminae were described from South East Asia in which – at least in *Luangnam* – the receptacula seminis are clearly spaced, and which I regard as a „primitive“ taxon (connected receptacula seminis is surely an apomorphic character). In 2010 SELDEN described the Early Cretaceous theridiosomatid genus *Eocoddingtonia* from Russian Asia (in stone) in which the receptacula are also clearly not connected, which may be a member of the subfamily Luangnaminae, too. The Cretaceous genus *Leviunguis* WUNDERLICH 2012 (female unknown) – and some relatives – in Cretaceous Burmese amber may also be members of this subfamily. – Because of these new findings the character of connected receptacula seminis cannot be regarded as a family character but only as a – the main! – diagnostic character of the subfamily Theridiosomatinae. Furthermore the paracymbium of certain questionable/ doubtful Cretaceous taxa is distinctly larger than in extant or Eocene Theridiosomatidae, see the extinct family Praeterleptonetidae. These patterns demonstrate that a family diagnostic character may have to be emended after the discovery of extant taxa (in this case of a tropical region) or probably of fossils (in this case of extinct Cretaceous taxa in Burmese amber); see the provisional cladogram of the suprageneric taxa of the Theridiosomatidae, WUNDERLICH (2011: 439).



# DESCRIPTIONS AND REVISIONS OF FOSSIL SPIDER TAXA IN MESOZOIC AMBER, with remarks on taxa preserved in stone

## Infraorder **MESOTHELAE**

### Family **LIPHISTIIDAE**

See also the chapter on the infraorder Mesothelae above.

#### **Cretaceothele** n. gen.

Etymology: The name is based on creta (latin) = cretaceous, and part of the name Mesothelae. – The gender of the name is feminine.

**Type species** (by monotypy): *Cretaceothele lata* n. sp.

**Diagnosis** (juv., probably second instar): Eye field (fig. 6) wide, anterior lateral eyes very widely spaced from each other.

**Further characters**: 8 Eyes (fig. 6), coxa IV (fig. 7) probably not modified (compare fig. 9), median spinnerets (fig. 7) well developed, anal tubercle (A in fig. 7) large. Pedicel and retromarginal cheliceral teeth are unknown (their areas are hidden).

Remark: A posteriorly narrow sternum (fig. 9) exists in adult and older instars of extant Liphistiidae, but – according to P. SCHWENDINGER (e-mail) – in very young extant Liphistiidae it is wide posteriorly, similar to the quite young spiderling of *Cretaceothele* (fig. 7).

**Relationships**: In extant mesothelid members of the only known family Liphistiidae SCHIÖDTE 1849 – see the chapter on the Infraorder Mesothelae above – the eye field is distinctly narrower and the anterior lateral eyes are close together (fig. 8), even in young spiderlings to my knowledge. Therefore I regard *Cretaceothele* as a member of the family Liphistiidae only provisionally, and a genus of its own; I do not want to exclude that *Cretaceothele* may represent the extinct member of an undescribed family related to the Liphistiidae or to *Palaeothele* SELDEN 2000. In the Carboniferous „mesothele“ plesion genus *Palaeothele* which is preserved in stone from France (family unknown) the

position of the eyes is unknown, and – in contrast to extant Mesothelae – the posterior cheliceral margin bears teeth; unfortunately the posterior margin is hidden in *Cretaceothele*. *Palaeothele* is the only other sure fossil Mesothelae besides *Cretaceothele*. In the Carboniferous „mesothele“ families (they are preserved in stones) Arthrolycosidae, Arthromygalidae and Pyritaraneidae the position of the eyes is unknown or different, in a narrow field.

**Distribution:** Mid Cretaceous Burmese (Myanmar) amber forest.

***Cretaceothele lata* n. gen. n. sp.** (figs. 5-7, compare figs. 8-9, photos 10-13)

Etymology: The name points to the wide eye field, *latus* (latin) = wide.

**Material:** Holotype (juv., probably a second instar) in Mid Cretaceous Burmese amber, F2447/BU/CJW.

**Preservation and syninclusions:** The spider is completely preserved in a yellow-orange piece of mainly clear amber which has a size of 18 x 14 x 7 mm. The opisthosoma and the prosoma anteriorly-laterally and posteriorly (photos) are strongly inclined/depressed dorsally. The pedicel is hidden. A transverse fissure runs ventrally through the spider and the piece of amber. – There are numerous syninclusions: Ca. 10 Acari of at least 4 families (5 are close to the spider), badly preserved remains of an Araneae indet. near the margin of the piece of amber, 2 Isopoda, 2 Diptera, 2 Coleoptera, 2 insect larvae (Coleoptera?), legs and excrements of insects, questionable Nematoda and Bacteria, some pear-shaped remains of burrows of questionable boring Bivalvia at the margin of the piece of amber, hairs and other remains of plants.

**Diagnosis** (juv.): See the genus.

### **Description:**

Measurements (in mm): Body length 1.6 (the adult spider would have been probably 1 to 2 cms long); prosoma: Length 0.6, width 0.6; opisthosoma: Length 0.8, width 0.6; femora about 0.45 (I slightly shorter, IV slightly longer), leg IV: patella ca. 0.18, tibia 0.35, metatarsus 0.4, tarsus 0.3; tarsus of the pedipalpus 0.26.

Colour light grey-brown.

Prosoma (figs. 5-7 and photos; the posterior area is deformed) as long as wide, cuticula fairly wrinkled, 8 eyes in a wide field on a low tubercle, anterior medians tiny, anterior laterals largest, laterals widely spaced from each other. Basal cheliceral articles large, only fairly protruding, in a vertical position, fangs stout, tips fairly converging, anterior margin of the cheliceral furrow with ca. 4 teeth, posterior margin hidden. Labium and sternum wide, sternum not protruding posteriorly but wide, deeply sloping at its margin, gnathocoxae without modifications. – Pedipalpus (fig. 5) large, with long and thin bristles, tarsal claw very long and apparently toothless. – Legs (fig. 5, photos) stout, IV longest, bristles thin, most of them are almost hair-shaped. In second instars

strong (almost spine-shaped) megabristles are not yet developed to my knowledge. The metatarsi bear at least two trichobothria which are not club-shaped, trichobothria of other leg articles have been not studied more closely. A modification of coxa IV is not observable and may be absent. – Opisthosoma (figs. 5, 7, photos; it is depressed dorsally) 1.33 times longer than wide, bearing dorsally at least 5 wide scuta (tergites) which cuticula is finely wrinkled. The deformed tergites bear a dozen longer bristles. Ventrally with two wide scuta covering the lungs. 4 pairs of spinnerets, the medians slender, well developed, not segmented, the laterals large and segmented, the right ones shortened and deformed in an unnatural way, anal tubercle large, apparently two-partite. The pedicel is hidden.

**Relationships and distribution:** See the genus.

## Infraorder **OPISTHOTHELA**

### Subinfraorder **MYGALOMORPHA**

See the list of Mesozoic spiders under Opisthotelae: Mygalomorpha above.

Seven families have been reported from the Mesozoic, the determination of three of them appears unsure to me. The present males of *Fossilcalcar praeteritus* and *Phyxioschemoides collembola* are the first described adult mygalomorph males in Cretaceous ambers. More adult mygalomorph males are needed for closer determinations of the juveniles and of various conclusions.

Members of the ancient Mygalomorpha in Burmite and other ambers are rare, juvenile Dipluridae are not extremely rare. In Burmite I studied specimens/remains of a dozen juveniles and two adult males of two families (as well as the juvenile of an unsure family). Because of their relative large size adults are extremely rarely preserved. Most Mygalomorpha in Burmite are members of the family Dipluridae which build sheet capture webs with funnel-shaped retreats. Adult male mygalomorph spiders like Nemesiidae (and probably Fossilcalcaridae) may left their tube – which is closed with a trapdoor – when searching for sessile females.

Two specimens of unknown genera in Burmite were described by WUNDERLICH (2011: 169-171). See also Mygalomorpha indet. below.

Superfamily **ATYPOIDEA**; questionable **ATYPIDAE**:

(a) A „possible member of the mygalomorph superfamily Atypoidea“ – *Friularachne rigoi* – has recently been described by DALLA & SELDEN (2013) „as possible member of the Atypoidea.“. The weakly preserved male holotype is preserved in Triassic stone of Italy. A membership of the family Atypidae THORELL 1870 cannot be excluded.

(b) Subfamily Ambiotiphaginae from Lower Cretaceous of Central Central Mongolia: The correct determination of this taxon as a member of the Atypidae has been questioned by WUNDERLICH (2011: 481) mainly because of its unknown gnathocoxae and spinnerets. In my opinion the taxon may be the member of a family of its own.

(c) A quite questionable confamiliar juv. member in Burmite is reported below.

## Family **DIPLURIDAE**

Members of this family are not rare in SE-Asia today, see e. g. SCHWENDINGER (2009). A typical character of the Dipluridae are their very long posterior spinnerets (shorter in juveniles) with a long and pointed apical segment (fig. 20); see the key to the fossil families above and RAVEN (1985).

Juveniles of this family are not extremely rare in the Mesozoic, especially in Burmite; they frequently are strongly deformed. See the list of Mesozoic spiders under Opisthothelae: Mygalomorpha: Dipuridae above. In an institution which is not designated here I saw two more juvenile Dipluridae.

### ***Phyxioschemoides* n. gen.**

Etymology: The species name refers to the related genus *Phyxioschema* SIMON 1881; -oides = similar. – The gender of the name is neuter.

Type species (by monotypy): *Phyxioschemoides collembola* n. sp.

**Diagnosis** (♂; ♀ unknown): Metatarsus II with a small but distinct proventral hump in the middle of the article (fig. 17), patella I with 3 long retrolateral megaspines which are

bent (fig. 18), tibia I: Fig. 16, tibia II (fig. 17) with a spur which bears a long clasping spine, pedipalpus: Fig. 19.

Further characters: Body length only 4.5 mm, tarsal bristles (at least on I-III; IV is lost) absent besides weak ventral bristles on II and III, spinules (of femora I-II and tibia II) absent, metatarsal III preening comb absent, structures of the spinnerets as well as the existence of labial and gnathocoxal cuspules unknown, cymbium spinose and apparently bilobed, bulbus (fig. 19) deformed, probably long.

**Relationships**: According to the absence of a cheliceral rastellum and leg scopulae, the large anterior median eyes as well as the structures of the cymbium I regard the new genus as a member of the family subfamily Euagrinae of the Dipluridae. Apparently Dipluridae are by far the most frequent mygalomorph spiders in Burmite. Although the spinnerets of the holotype are lost, the existence/absence of an australotheline crescent is unknown and the absence of gnathocoxal cuspules is not quite sure I consider the new genus as a member of the Euagrinae.. A well developed tibial II mating spur exist in *Allothele*, *Australothele*, *Euagris*, *Namirea* and *Phyxioschema*, see RAVEN (1985: 53). In the African genus *Allothele* TUCKER 1920 tarsal IV (and III?) bristles are absent. In *Namirea* RAVEN 1984 tarsus II bears several bristles, *Australothele* RAVEN 1984 is only known from the Australian Region, *Euagrus* AUSSERER 1875 is known from Africa and America, and tibia II bears more than a single megaspines. In *Phyxioschema* SIMON 1881 the strong retroventral bristles of patella II are well developed like in *Phyxioschemoides* but they are bent two times (slightly s-shaped), the ventral hump of metatarsus II is larger, and its position is near the basis of the article, spinules exist on legs I-II, the bulbus is more compact, pear-shaped.

**Distribution**: Mid Cretaceous amber forest of Myanmar (Burma).

***Phyxioschemoides collembola* n. gen. n. sp.** (figs. 15-19) photos 15-17

Etymology: The species name refers to the huge number of Collembola near the holotype.

**Material**: Holotype ♂ in Mid Cretaceous amber from N-Myanmar (Burma), F2720/BU/CJW.

**Preservation and syninclusions**: The spider is fairly well preserved in a yellow piece of amber, strongly pyritized; both legs IV are lost beyond the coxa by autotomy, the mouth parts are hidden, the pedipalpi are well preserved. – Syninclusions: Numerous Collembola and Acari, some Diptera, 1 Hymenoptera, 2 Psocoptera, 1 questionable tiny Coleoptera, insect's excrement and plant hairs.

**Diagnosis** (♂; ♀ unknown): See above; pedipalpus as in fig. 19.

**Description (♂):**

Measurements (in mm): Body length ca. 4.5, prosoma: Length 2.0, width 1.6; leg I: Femur 1.7, patella 0.9, tibia ca. 1.4, metatarsus ca. 1.2, tarsus 1.0, tibia II 1.3, tibia III 1.2, pedipalpal femur 1.0.

Colour (the spider is pyritized) dark grey brown.

Prosoma (fig. 15, photo) 1.25 times longer than wide, widest near the middle, low, 8 eyes in two fairly wide rows, anterior median eyes largest, posterior median eyes widely spaced, fovea well developed, deformed, basal cheliceral articles small, bearing longer anterior hairs, teeth of the fang furrow hidden, fangs fairly long and converging, mouth parts hidden, coxae IV spaced by ca. half of their diameter. – Legs (figs. 16 – 18, photo) (IV is lost) fairly long and slender, hairs partly long, scopulae absent, trichobothria indistinct, not closely studied, bristles partly long, existing on femora, patellae, tibiae and metatarsi (as well as weak bristles ventrally on the tarsi II-III), tibia II 8, tibia III 7, metatarsus III 9. Legs I and II are modified; I: Patella with 3 long and bent retrolateral megaspines, tibia with 8 long ventral and lateral bristles in the distal half; II: Tibia with a distinct ventral spur in the middle which bears a long clasping spine, metatarsus with a small but distinct proventral hump in the middle. Paired tarsal claws with several long teeth in a single row, unpaired claw well developed. – Opisthosoma (it is deformed, the distal half is cut off) soft, hairs of medium length. – Pedipalpus (fig. 19, photo): Tibia long and fairly thickened, cymbium long, apparently bilobed, spiny apically, bulbous deformed, long-oval, embolus long, thin and almost straight.

**Relationships and distribution:** See above.

**Reports on juvenile Dipluridae indet. in Burmite:**

F2629/BU/CJW (photo 18): Body length almost 3.5 mm, prosomal length ca. 1.5 mm, leg IV about 4.5 mm long. The spider is decomposed as demonstrated by two protrusions of gas on the opisthosoma as well as deformations of the basal cheliceral articles which are distinctly widened retrodistally, the left leg is cut off beyond the femur, the ventral mouth parts are hidden. Prosoma low, distinctly longer than wide, 8 eyes in a compact group. Basal cheliceral articles distinctly widened retrodistally (apparently deformed). Legs (photo) slender, bearing hair-shaped bristles, IV probably longest, 3 long tarsal claws, 2 pairs of spinnerets, the posteriors long and slener, 0.8 times the length of the opisthosomal length. – Syninclusions: A small juvenile araneomorph spider below the mygalomorph spider, two tiny insects, few Diptera, two tiny insect's larvae, a small Myriapoda, insect's excrements and a gas bubble which is movable in fluid (water?).

F2714/BU/CJW: Body length 1.1 mm, completely preserved, partly hidden by bubbles and an emulsion. – Syninclusions: 1 Acari, 1 large insect larva, 1 Collembola, remains of a questionable Blattoidea.

F2716/BU/CJW: Body length 1.8 mm, completely preserved, opisthosoma strongly deformed. – Syninclusions: 4 Crustaceae, 1 Diplopoda, 1 questionable insect larva and the larva of a Blattoidea.

F2718/BU/CJW (photo 19): Body length 4.0, completely preserved on a larger particle of a plant and behind a snail-shell. Prosoma including the apparently slender chelicerae distinctly deformed, prosoma twice as long as wide (this is apparently not its original shape; see below, Mygalomorpha indet. 2, F2610/BU/CJW), a pseudosegmentation of the apical article of the posterior spinnerets is not observable. – Further syninclusions: Few Acari and plant hairs.

F2719/BU/CJW: Body length 2.2 mm, completely preserved, opisthosoma displaced almost above the prosoma, the spinnerets are relatively short. – Syninclusions: Some Acari and 2 insects.

### **Family FOSSILCALCARIDAE n. fam.**

Etymology: From fossil = extinct, and calcar (lat.) = spur, referring to the tibial I and pedipalpal tibial spurs/outgrowths.

Type genus (by monotypy): *Fossilcalcar* n. gen.

**Diagnosis** (♂; ♀ unknown): Length of the posterior spinnerets about one third of the opisthosomal length (fig. 21), TIBIA I PROAPICALLY WITH A BIPARTITE NIPPERS-SHAPED CLASPING STRUCTURE (figs. 22-24); PEDIPALPUS (fig. 27): TIBIA WITH A STRONG, BENT, POINTED AND TOOTH-LIKE RETROLATERAL SPUR, cymbium and bulbus small, conductor probably absent.

Further important characters: Cephalic part low, cheliceral rastellum absent, legs fairly slender, order IV/I/II/III, leg bristles slender (photo) and numerous, tarsi not pseudosegmented, tarsi and metatarsi I-II bear a dense scopula, ventral tarsal bristles existing (fig. 25), metatarsal III-IV preening combs and club-shaped trichobothria absent, tarsi bearing a dorsal-apical „brush“ of hairs and weak claw tufts (fig. 25), paired claws slender, bearing a single row of teeth. Number and position of the eyes and the existence of labial and gnathocoxal cuspules are unknown (these structures are hidden). Number – only two pairs? –, position (in the ventral aspect) and segmentation of the spinnerets are unknown.

**Ecology and behaviour**: The absence of a cheliceral rastellum, the modifications of the legs as well as legs which are relatively long and slender may indicate that these spiders did not live in tubes with trap-doors but construct capture webs.



The **relationships** are unsure: Certain characters – especially the shape of the clasping structures of tibia I and the pedipalpal tibial outgrowth which bears a spine – fit in none of the extant families. Nemesiidae is probably most related, see RAVEN (1985); the posterior spinnerets of the present male are relatively long as in most Nemesiidae (and certain other mygalomorph families), the bipartite tibial I clasping structure reminds a bit of structures present in the genus *Brachythele* AUSSERER 1871 (Nemesiidae), but in the Nemesiidae the paired tarsal claws are wide and bear TWO rows of teeth, tibial clasping SPINES exist, a pedipalpal spine-bearing tibial outgrowth is absent, the cymbium is usually spinose, and the shape of the fovea is usually different, in a transverse position, more or less straight. See also above: Ecology and behaviour. – In members of the family Dipluridae leg scopulae are absent, the posterior spinnerets are longer, mating spurs of the male anterior legs are different; and a pedipalpal tibial spur is absent.

Remark: Blunt apical clasping structures of the male anterior tibia and spiny outgrowths of the male pedipalpal tibia exist also in several members of the Liphistiidae (Mesothelae). Are these characters plesiomorphic in *Fossilcalcar*?

**Distribution:** Mid Cretaceous amber forest of N-Myanmar (Burma).

### ***Fossilcalcar* n. gen.**

Etymology: See above.

The gender of the name is masculine.

**Type species** (by monotypy): *Fossilcalcar praeteritus* n. sp.

**Diagnosis, relationships and distribution:** See the new family.

### ***Fossilcalcar praeteritus* n. gen. n. sp. (figs. 21-27) photo 14**

Etymology of the species name: From praeteritus (lat.) = gone, in the sense of extinct.

**Material:** Holotype ♂ in Burmite from N-Myanmar (Birma), F2607/AR/CJW.

**Preservation and syninclusions:** The male is almost completely preserved in a muddy piece of amber which includes numerous tiny droplets, body and legs are partly covered with an „emulsion“ including numerous questionable decomposing fugi (hyphae), and thus are difficult to observe. Because of the existence of hyphae the spider

has surely been preserved as a dead organism. The left leg III has been lost beyond the coxa by autotomy, the opisthosoma is dorsally depressed longitudinally; this depression/damage may have been the reason for the death of the spider. – Parts of a large leaf are preserved left below the spider and hide parts of it. Near the surface of the piece of amber, e. g. above the right tibia/metatarsus III several – more or less deformed – „objects“ are preserved which appear somewhat similar to Tardigrada; their body length is only 0.1-0.17 mm.

**Diagnosis, relationships and distribution:** See above.

**Description (♂):**

Measurements (in mm): Body length 6.7, prosoma: Length 3.4, width 3.2; opisthosoma: Length ca. 3.6, width 2.2; leg I: patella ca. 1.9, tibia ca. 2.6, tarsus ca. 1.7; leg IV: tibia 3.4, tarsus 1.9; observable length of the posterior spinnerets in the dorsal aspect 1.1.

Colour: Prosoma and legs dark brown, legs not annulated, opisthosoma dark grey.

Prosoma (fig. 21, photo) slightly longer than wide, cephalic part not raised, hairs short, fovea a round depression, eyes hidden, clypeus short, basal cheliceral articles small, rastellum absent, gnathocoxae, labium and sternum hidden. – Legs (figs. 22-26, photo) fairly long and slender, covered with longer hairs, order IV/I/II/III, club-shaped trichobothria absent, tarsi not pseudosegmented, bearing ventral bristles, metatarsi and tarsi I-II bear dense scopulae, bristles slender and partly long, existing on femora, patellae, tibiae, metatarsi and tarsi (ventrally). Metatarsal III-IV preening combs absent (few long bristles exist in this position). Tarsi with long (brushlike) dorsal-apical hairs. Unpaired tarsal claw hidden but most probably existing in my opinion, paired claws slender, bearing long teeth, see the diagnosis. Tibia I proapically with a bipartite nippers-shaped clasping structure. – Opisthosoma (fig. 21) oval, bearing short hairs, dorsal scutum absent; probably two pairs of spinnerets, length of the posteriors about one third of the opisthosomal length. – Pedipalpus (fig. 27): Femur and patella slender, tibia long, bearing a strong, bent, pointed and tooth-like retrolateral spur, cymbium and bulbus small, cymbial bristles absent, conductor probably absent.

**Mygalomorpha indet.** (??Atypidae) (figs. 29), photo 20

**Material:** 1 juv. in Burmite, F2608/BU/CJW.

**Preservation and syninclusions:** The spider is completely and well preserved in a clear yellow piece of amber (photo). Two and three mm behind the spider an Acari and a peculiar larva of an insect – of a questionable Mantispodea: Mantispidae: Mantispinae (Neuroptera) (fig. 28, photo 21) – are preserved. The larva is 2.2 mm long, slender, possesses two triads of eyes, and quite remarkable questionable secretions dorsally (!) near the end of all tarsi (fig. 28).

Remark: The presence of the larva of the questionable Mantispidae is probably not an accident but it may be considered in connection with the spider nearby: Did the larva

search for a transporting spider like today's mantispinae larvae? See WUNDERLICH (2012). A questionable specimen of the Mantispidae in Burmite has recently been described by POINAR & BUCKLEY (2010).

**Description and relationships:** Measurements (in mm): Body length 2.2, prosoma: Length 1.15, width 0.9, opisthosoma: Length 1.0, width 0.7, length of the posterior spinnerets ca. 0.4.

The prosoma is distinctly convex, the eye tubercle is well developed, the fovea is a divided transverse groove, probably three pairs of spinnerets exist, the apical articles of the posterior spinnerets are only fairly pointed. Most ventral parts of the prosoma are hidden by an emulsion and a large bubble. Therefore the gnathocoxae (fig. 29) are observable only in a quite restricted way; they may be prolonged and thus I do not want to exclude that the spider probably is a member of the family Atypidae.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

### **Mygalomorpha indet. 1**

**Material:** Part of remains of an exuvia without peltidium and opisthosoma in Burmite, F2609/BU/CJW.

Tibia I is 1.1 mm long, the pedipalpi are long, its tibia is 0.8 mm long.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

### **Mygalomorpha indet. 2 (figs. 30-31) photos 22-23**

**Material:** 1 juv. in Burmite, F2610/BU/CJW.

**Preservation:** The prosoma is laterally fairly deformed, the opisthosoma and especially the spinnerets are strongly deformed.

**Diagnosis** (juv.): Prosoma (figs. 30-31, photos) extraordinary slender, 1.9 times longer than wide.

**Description** (juv.):

Measurements (in mm): Body length 3.7, prosoma: Length 1.6, width 0.85, tibia IV 0.85.

Prosoma 1.9 times longer than wide (in my opinion the deformation does not fully cause its slenderness), raised, glabrous, 8 eyes on a distinct tubercle in a fairly wide field, fovea procurved, chelicerae large, rastellum absent, gnathocoxae, labium and

parts of the sternum hidden. Legs slender and fairly long, I longest, scopulae, club-shaped trichobothria, metatarsal preening combs and claw tufts absent, bristles long, ventral tarsal bristles existing, some trichobothria very long, unpaired tarsal claw existing, paired claws slender and with a single row of long teeth. Opisthosoma and spinnerets strongly deformed.

The **relationships**: are unsure; an adult specimen is needed for further conclusions. The very slender prosoma is quite unusual within mygalomorph spiders. I do not want to exclude with certainty that the juvenile spider may be a member of the family Dipluridae, see above, F2718/BU/CJW.

**Distribution**: Mid Cretaceous amber forest of Myanmar (Burma).

## SUBINFRAORDER ARANEOMORPHA

ARANEOMORPHA with unsure relationships:

*Argyrarachne* SELDEN in SELDEN et al. 1999. Juv. **S.** USA: Virginia, Triassic.

*Argyrarachne solitus* SELDEN in SELDEN et al. 1999. Juv. **S.** USA: Virginia, Triassic.

*Triassaraneus* SELDEN in SELDEN et al. 1999. Juv. **S.** Africa. Triassic

*Triassaraneus andersonorum* SELDEN in SELDEN et al. 1999. Juv. **S.** Triassic

See SELDEN et al. (2009)

## SUBINFRAORDER ARANEOMORPHA (1):

## MICROORDER HYPOCHILOMORPHA MARX 1888

Although members of this branch must have existed since the Palaeozoic (see fig. C) not a single sure fossil proof exists up to now. The monotypic extinct Triassic genera *Argyrarachne* SELDEN 1999 and *Triassaraneus* SELDEN 1999 (preserved in stones of

North America resp. South Africa) may be related to this branch; probably both were not cribellate (the opisthosoma is unknown in *Triassaraneus*). – See also below: Leptonetoidea: The family Mongolarachnidae which may be related.

**Taxonomy:** In this paper I provisionally regard Hypochilomorpha MARX 1888 (\*) – see FORSTER (1955: 177), GERTSCH (1958) and PETRUNKEVITCH (1939: 154) and above – in a wide sense, including with little hesitation the advanced Austrochiloidea ZAPFE 1955. In both nominal superfamilies the advanced plagiognathy as well as a cribellum (lost in certain Gradungulidae), large basal cheliceral articles, and basically two pairs of lungs exist (one pair is lost in certain Gradungulidae), see above and fig. B. I suppose that the endocephalic venom glands (and certain other characters) in the Austrochilidae + Gradungulidae (both are included in the Austrochiloidea sensu FORSTER et al. (1987)) evolved convergently to the branch Dipneumonomorphae PETRUNKEVITCH 1933 (\*\*). A single row of teeth of the gnathocoxal serrula evolved within the Hypochiloidea (in the traditional sense) (see fig. B) convergently in the (a) Austrochilidae + Gradungulidae, and (b) in the branch Dipneumonomorphae. – LOPARDO et al. (2004) regard Austrochilidae (is its superfamily level really justified?) – based on their web building behaviour of South American taxa – as more evolved than in the Hypochilidae but probably being the sister group of entelegyne spiders. See also DIMITROV et al. (2012).

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(\*) Erroneously attributed to PETRUNKEVITCH 1933 by FORSTER and PETRUNKEVITCH, but introduced by MARX (1888), see IRZN, art. 36.1.

(\*\*) If Austrochiloidea is included in the Hypochilomorpha the term Neocribellata is superfluous.

**Diagnostic characters** of the Hypochilomorpha s. l.: **Apomorphies:** Plagiognathy, a more posterior position of the posterior pair of lungs, and probably a restricted length of the calamistrum up to the basal third of metatarsus IV. **Plesiomorphies:** (see the key to the families, and the characters of the subinfraorder Araneomorpha): Large basal cheliceral articles in a vertical position, existence of two pairs of lungs and cribellum, tarsal bristles (\*), (partly – basically?) wide eye field which may include triads, long/slender articles of the male pedipalpus, a quite slender/long cymbium (it is short in the Hypochilidae) which does not cover most parts of the, no leg autotomy, and probably basically existence of retrolateral cheliceral stridulatory files. The extant spiders are large, its body length is 7-22 mm (fossils are still not identified, see below).

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(\*) Ventral tarsal bristles – at least on legs III-IV -, is an ancient character of spiders, existing in Mesothelae but also, e.g., in the more derived Oecobiidae and Uloboridae.

**Relationships:** A strongly widened superfamily Hypochiloidea sensu LEHTINEN (1967) – including e.g. Leptonetidae AND Pholcidae (!) – appears not justified to me, but the basically cribellate superfamily Leptonetoidea – including Mongolarachnidae and Pholcochyroceridae may well be related, see below.

**Note:** The body length of the probably related Leptonetoidea (usually 2-4 mm; the more than 16 mm long members of the genus *Mongolarachne* are an exception) is smaller than the body length of extant Hypochiloidea (7-22 mm)..

**Diversity, biogeography and fossils:** (1) Known from the SOUTHERN Hemisphere and extant only: Austrochiloidea: Austrochilidae (South America) and Gradungulidae (Australia, New Zealand). – (2) Known from the NORTHERN Hemisphere: Hypochiloidea: Hypochilidae (extant, North America and South East Asia). – (3) Quite unsure Triassic fossils: the insufficiently known genera *Argyrarachne* and *Triassarachne* may be related, and are not included in the key below.

**Key to the families of the Hypochilomorpha s. l.:**

1 Unpaired tarsal claw absent, proclaw of tarsi I-II modified and very large, cheliceral stridulatory files existing, cribellate or ecribellate, one or two pairs of lungs. – Australia and New Zealand. . . . . Gradungulidae

- Unpaired tarsal claw existing, tarsal proclaw unmodified, cheliceral files existing or absent, cribellate, two pairs of lungs at least in the Austrochilidae (their number is unknown in the Palaeochilidae). . . . . 2

2(1) Calamistrum biseriate (double-rowed), occupying up to the BASAL THIRD of metatarsus, cheliceral files absent, medial concavity of the basal cheliceral articles existing, see PLATNICK (1977: Fig. 8), gnathocoxal serrula consisting of a field of teeth (several rows) (unique in its kin), bulbus attached near the end of the truncate cymbium which bears a spine-shaped paracymbium. – North America and South East Asia . . . . . Hypochilidae

- Calamistrum uniseriate and existing in the CENTRAL third of metatarsus IV, cheliceral files or nodules (♀) existing, a single row of the gnathocoxal serrula. – South America, Tasmania. . . . . Thaididae (= Austrochilidae)

## ARANEOMORPHA (2):

### MICROORDER DIPNEUMONOMORPHA (all remaining taxa) (= ARANEOCLADA)

#### SUPERFAMILY DYSDEROIDEA s. l.

The limit and the closest relationships of this superfamily are still unsure.

#### Family PLECTREURIDAE s. l.

In 2004: 671-672 I regarded the six-eyed Diguettidae GERTSCH 1949 as a subfamily of the eight-eyed Plectreuridae BANKS 1898 s. l.

See the key to the families no. 30.

Diagnosis of the family in the wide sense: See WUNDERLICH (2004: 671). The chelicerae bear fine retrolateral stridulatory files and are medially partly connected with a membrane, the gnathocoxae are strongly converging; in the Plectreurinae an article of the anterior male leg usually bears a „clasping spine“: The metatarsus in *Palaeoplectreurys* WUNDERLICH 2004, the tibia in *Plectreurys* SIMON 1893 and *Eoplectreurys* SELDEN & HUANG 2010 (fig. 32), the femur in *Montsecarachne* SELDEN 2014.

Related are the cribellate Filistatidae and the ecribellate Segestriidae. In several taxa of the Segestriidae (most Ariadninae) exists also clasping spines of the male anterior legs (the metatarsus) but the third pair of legs is directed forward, cheliceral files and a medial cheliceral membrane are absent, the gnathocoxae are not converging above the labium.

Distribution: Plectreuridae is a „primitive“ and non-diverse relict spider family; today it is only known from North and Central America, see WUNDERLICH (2004: 670). In former times the family had a wide distribution at least on the Northern Hemisphere: *Pa-*



*laeoplectreurys baltica* WUNDERLICH 2004 has been reported from the Eocene Baltic amber forest, *Montsecarachne* from the Cretaceous of Spain, *Eoplectreurys* from the Jurassic of China, see below.

Mesozoic fossil taxa: The following two taxa – preserved in stone – have been published from the Mesozoic, and are regarded as members of the family Plectreuridae by SELDEN, although the (number of) eyes is/are unknown:

(1) *Eoplectreurys gertschi* SELDEN & HUANG 2010, Jurassic, ♂ ♀, from Inner Mongolia, China. The ♂-tibia I bears a retroventral „clasping spine“ (fig. 32), the embolus is very long (longer than the prosoma).

(2) *Montsecarachne amicorum* SELDEN 2014, Cretaceous, ♂, El Montsec, Spain. The ♂-femur I bears a strong spine at its end (it may be a „clasping spine“), the embolus is short.

Remark: In the abstract the species name is spelled *amicus*.

**Family SEGESTRIIDAE** SIMON 1893 figs. 33-70, photos 24-35, family key no. 40

I thank A. M. GIROTI (Sao Paolo) – who is working on the genus *Ariadna* in Brasil – for helpful comments and discussions, and Prof. A. LISE (Porto Alegre) for the loan of specimens of *Ariadna* from Brasil.

Segestriidae is an old relict family which has been diverse in former geological periods: Seven genera from Mesozoic ambers have been described up to now (although only few deposits have been studied), compared with probably only two or three genera of today: *Ariadna* and *Segestria*; *Gippsicola*: See below.

**Diagnostic characters** (\*) (\*\*): The unique family besides the extinct Plumorsolidae – see below – in which the third pair of legs is directed forwards like the anterior two pairs (apomorphy; the „segestriid leg position“) (photos). In certain fossil spiders an unnatural position exists, see the photos. Probably also unique is the light (hairless) longitudinal opisthosomal band at least in the extant taxa, see WUNDERLICH (2011: 632, fig. 81); in certain extant specimens and especially in fossils it may be indistinct, probably even absent in fossils.

Further important external diagnostic characters besides the plesiomorphic pattern of the Dysderoidea: Six eyes in three diads (figs. 33, 39, 51) (similar to several related families), chelicerae: lamina absent, retromargin with 0-3 teeth, onychium usually well developed (figs. 46, 64-65), unpaired tarsal claw existing (\*\*\*) and claw tufts absent, all paired tarsal claws with a single row of teeth, metatarsal III/IV preening comb frequently well developed, tendency to modifications of male leg I in the Ariadninae: Spurs, spines, thickened and/or bent metatarsi and/or (rarely) tibiae. Slender pedipalpal tarsus of the subadult male. Conductor usually absent but see (\*\*) below in the key (*Gippsicola* and *Microsegestria*). The (extant) spiders hide in tubes from whose openings signal lines originate; the females have a long life-span of several years in contrast to the short-living males which live at most few month (both are old plesiomorphic characters, similar to some Mygalomorpha and Filistatidae).

(\*) The behaviour as one of the best diagnostic family character analogous to the Pisauridae in which the female carries its egg sac with the help of the chelicerae under the sternum.

(\*\*) The limits – and therefore the real diagnostic characters – of this family are quite unclear if the Cretaceous taxa are included. The very variable characters within the Segestriidae in their mosaic intrafamilial distribution (as well as apparently their numerous convergences) cause problems. The limits may be subjective: In the enigmatic genera *Gippsicola* and *Microsegestria* a conductor exists in contrast to all remaining taxa of the Segestriidae.

(\*\*\*) In the studied Cretaceous taxa the unpaired tarsal claw is thinner and inserted more basally on a longer onychium than in the extant genera *Ariadna* and *Segestria*; see the figs.

The **relationships** are unsure, see above (\*\*). The extinct Plumorsolidae WUNDERLICH 2008 – see below – may be most related; it possesses the same „segestriid leg position“; this peculiar leg position is apparently unique in spiders and may be a synapomorphy of Plumorsolidae + Segestriidae, but I do not want to exclude with certainty that this character evolved probably convergently in these families – important other differences exist: An unpaired tarsal claw is absent, and well developed claw tufts exist in the Plumorsolidae like (both characters) in the Orsolobidae, which may be related, but which possesses usually bipectinate paired tarsal claws – like the strongly related Oonopidae –, and does not possess a light lateral opisthosomal band which apparently is unique in the Segestriidae. – Probably Periegopidae is strongly related, too, see the key below: Tarsal claws, leg bristles. In Orsolobidae and Periegopidae the third pair of legs is not directed forwards, but see fig. 528 of *Tangata nigra* (Orsolobidae) in FORSTER & PLATNICK (1985: 144) in which the left leg III is directed forwards (the right leg III is missing in the specimen shown). – See also above, the family Plectreuridae.

**Distribution:** Cosmopolitical (extant and most probably the fossils, too; fossil proofs of the Southern Hemisphere are needed but fossils/deposits are still very rare in this region), especially amber deposits.

**Evolution of the body size:** The body size of extant Segestriidae lies usually between 5 and 15 mm, up to 22 mm in females. Cretaceous fossils: We do not know the largest spiders (probably they were not or very rarely captured by the fossil resin) but we know tiny spiders which are only half or one third of the tiniest extant spiders: The

body length (male sex) of *Microsegestria* is 1.35 mm, of *Denticulosegestria* and *Parvosegestria* about 2 mm. The largest Cretaceous Segestriidae known to me – *Jordariadna amissicoli* (= *Ariadna a.*) and *Myansegestria engin* possess a body length of 4 and 3 mm; the body length of *Palaeosegestria lutzii* is 3.75 mm. Small and even tiny Segestriidae are also known from the Eocene Baltic amber: The body length of *Vetsegestria quinquespinosa* WUNDERLICH 2004 (both sexes) is only 2.1-2.6 mm, most members of *Segestria* are about 3 mm long, the largest Eocene *Segestria* (females) are up to about 8 mm long. Dwarfism is apparently a very old pattern in certain spider families. In various other taxa – like in the subfamily Erigoninae of the Linyphiidae (known from the Miocene onwards) – dwarfism is younger than Eocene. Eocene Zygellidae were on average only half the size compared with extant spiders of this family, see WUNDERLICH (2004: 261).

Did a tendency exist to evolve a larger body size within 100 million years – probably in co-evolution with larger prey? Or did the tiniest species and genera die out during the Tertiary? Why did they die out?

**Behaviour and ecology:** EXTANT SPIDERS: The habitats of extant spiders are quite diverse: In Southern Europe I found most populations living in tubes from whose openings signal lines originate, see the photos. Such tubes are only few cms long, and apparently – at least some – spiders use small natural holes. I discovered most tubes in shaddy localities at steep slopes (a) in Southern Portugal *Ariadna algarvensis* WUNDERLICH 2011 inhabiting tubes in the earth; the earth is not too hard, covered with moss and lichens (no grass or other higher plants), (b) on Menorca (Balears) in tubes at steep rocks and under stones and (c) less frequently in tubes on tree trunks. Recently I discovered *Ariadna inops* WUNDERLICH 2011 in Southern Portugal living in the sand of dunes within scarce lower plants. In captivity I observed a female hidden in sand as well as between low plants near the ground, spinning some threads. In cities of Brazil A. M. GIROTI (person. commun.) found *Ariadna* sp. in rolled leaves as well as in cracks on walls. COSTA & CONTI (2013) report Ariadninae (sub *Ariadna*) from a desert of Namibia constructing burrows „with a circular entrance surrounded by a ring of small pebbles, sometimes they close their burrows by a small stone“ as a plug after a heavy rainfall. – FOSSILS: In Cretaceous members of the family Segestriidae the third pair of legs was already directed forwards like in confamilial spiders of today. This leg position may indicate their tube-living behaviour like in extant relatives although such tubes are still unknown from that time. Tubes of silk are known from Eocene Segestriidae, see WUNDERLICH (2004). Segestriidae (species and specimens) were not rare in the Eocene Baltic amber forest, and one may conclude, that at least some of these species lived under the bark of trees, probably of the resin-producing needle trees.

**Biogeography and diversity** of extant and fossil/extinct taxa: Members of the old family Segestriidae were diverse in the Cretaceous and rather frequent, 8 genera are known from 5 kinds of amber, see below. Cretaceous members of four subfamilies have been reported, while members of only two subfamilies survived besides the enigmatic genus *Gippsicola* (see below the key to the genera): Ariadninae and Segestriinae.

The genera *Ariadna* SAVIGNY & AUDOUIN 1827 (Ariadninae) and *Segestria* LATREILLE 1804 (Segestriinae) are the only accepted EXTANT genera of this family besides *Gippsicola*. *Ariadna* and *Segestria* are also reported from the best known Eocene European amber forests (the Baltic, Bitterfeld and Ukrainian forests) in which additionally the extinct genus *Vetsegestria* WUNDERLICH 2004 (Segestriinae) existed. The proof of the

extant genera *Ariadna* and *Segestria* from Cretaceous ambers are quite unsure and appear unlikely to me; both have been reported – partly with a question mark – from the Cretaceous but these reports are most probably misidentifications in my opinion.

*Ariadna monticola* THORELL 1897 (Ariadninae) has been described from Myanmar (Burma) as an EXTANT species. In Burmese amber I found only members of the Segestriinae but not of the Ariadninae up to now. I determined surely Cretaceous Ariadninae only in Jordanian amber. In Lebanese amber I found only taxa of the enigmatic subfamilies Lebansegestriinae and Microsegestriinae.

To our present knowledge the Cretaceous amber fauna of the Middle East represents the most diverse fauna regarding the SUBFAMILIES: The DOUBLE number of subfamilies is known compared with the extant fauna, most diverse in Jordanian amber, although only very few specimens have been found in this kind of amber up to now.

Not a single Cretaceous member of the Segestriidae is known up to now in amber from Spain according to P. SELDEN, person. commun. in X 20013.

Segestriidae is apparently a relict family which has a large number of Mesozoic genera; I suppose the discovery of much more taxa in Cretaceous ambers, e. g. in Spain.

#### List of the taxa of the family Segestriidae in Cretaceous ambers:

?Segestriidae indet.: ESKOV & WUNDERLICH (1995: 99), juv. ....	Siberia (Taimyr)
?Segestriidae indet.: WUNDERLICH 2008, juv. ....	Myanmar (Burma)
? <i>Segestria</i> sp. indet.: PENNEY 2002, juv. ....	New Jersey
<i>Denticulsegestria</i> n. gen., ♂. ....	Myanmar (Burma)
<i>Denticulsegestria rugosa</i> n. sp., ♂. ....	Myanmar (Burma)
<i>Jordariadna</i> n. gen., ♂. ....	Jordan
<i>Jordariadna</i> (= ? <i>Ariadna</i> ) <i>amissiocoli</i> (WUNDERLICH 2008)(n. comb.), ♂ ...	Jordan
<i>Jordansegestria</i> n. gen., ♂. ....	Jordan
<i>Jordansegestria detruneo</i> n. sp., ♂. ....	Jordan
<i>Lebansegestria</i> WUNDERLICH 2008, ♂. ....	Lebanon
<i>Lebansegestria azari</i> WUNDERLICH 2008, ♂. ....	Lebanon
<i>Microsegestria</i> WUNDERLICH & MILKI 2004, ♂. ....	Lebanon
<i>Microsegestria poinari</i> WUNDERLICH & MILKI 2004, ♂. ....	Lebanon
<i>Myansegestria</i> n. gen. ♂. ....	Myanmar (Burma)
<i>Myansegestria caederens</i> n. sp., ♂. ....	Myanmar (Burma)
<i>Myansegestria engin</i> n. sp., ♂. ....	Myanmar (Burma)
<i>Palaeosegestria</i> PENNEY 2004, ♂. ....	New Jersey
<i>Palaeosegestria lutzii</i> PENNEY 2004, ♂. ....	New Jersey
<i>Parvosegestria</i> n. gen., ♂. ....	Myanmar (Burma)
<i>Parvosegestria longitibialis</i> n. sp., ♂. ....	Myanmar (Burma)
<i>Parvosegestria obscura</i> n. sp., ♂. ....	Myanmar (Burma)
<i>Parvosegestria pintgu</i> n. sp., ♂. ....	Myanmar (Burma)
<i>Parvosegestria triplex</i> n. sp., ♂. ....	Myanmar (Burma)

List of the subfamilies of Cretaceous Segestriidae, their distribution and selected sub-taxa:

- (1) Ariadninae WUNDERLICH 2004: *Jordariadna* n. gen. (= ?*Ariadna*) *amissiocoli* (WUNDERLICH 2008) in Jordanian amber;
- (2) Segestriinae SIMON 1893 (?): *Jordansegestria detruneo* n. gen. n. sp. in Jordanian amber (relationships not quite sure, see below); three genera (*Denticulsegestria*, *Myansegestria*, and *Parvosegestria*) in Burmite, *Palaeosegestria* in New Jersey amber;
- (3) Lebansegestriinae WUNDERLICH 2008: *Lebansegestria azari* WUNDERLICH 2008 in Lebanese amber;
- (4) Microsegestriinae WUNDERLICH 2004: *Microsegestria poinari* WUNDERLICH & MILKI 2004 in Lebanese amber.

Provisional **Key** to the extant and fossil taxa of the family Segestriidae and selected extant as well as similar or related haplogyne six-eyed fossil taxa:  
See the key on all Cretaceous families above.

Remarks: (1) Orsolobidae and Periogopidae as well the genera *Ariadna* and *Segestria* of the Segestriidae are not reported from the Cretaceous up to now (erroneous identifications exist). – (2) Most taxa of the segestriid branch are based on the male sex only but the male of the Plumorsolidae is unknown. – (3) The determination of taxa of the Segestriidae (no. 5f, 9f) is partly based on their distribution as an easy (but not sure) way for the identification. – (4) See the key above to the Mesozoic spider families which includes the six-eyed families, and the previous key by WUNDERLICH (2008: 571) which is obsolete. – (5) Families and subfamilies known from the Cretaceous are printed in heavy letters.

- 1 FEMUR IV STRONGLY THICKENED. Body length usually 1-1.5 mm. Cretaceous (frequent apparently in all kinds of amber, e. g. *Burmorchestina* in Burmite) to extant (very diverse). . . . . **Oonopidae: Orchestinae**
- Femur IV not distinctly thickened. Tiny to larger spiders. . . . . 2
- 2(1) Claw tufts well developed (figs. 76-77). . . . . 3
- Claw tufts absent. . . . . 4

3(2) Leg III directed forwards (photos 37-42) like in the Segestriidae (fig. 33). Paired tarsal claws with a single row of teeth. Feathery hairs existing or absent. Adult male unknown. Cretaceous: Burmite (*Burmorsolus* and probably *Plumorsolus*) and Lebanese amber (*Plumorsolus*). . . . . **Plumorsolidae**

- Leg III directed backwards (the position may be different in fossil spiders). (See fig. 528 of *Tangata nigra* FORSTER & PLATNICK (1985: 144) from New Zealand). Paired tarsal claws usually with a double row of teeth. Feathery hairs absent. Extant. Australian Region and South America. . . . . **Orsolobidae**

4(1) Leg bristles absent. Paired claws of the anterior tarsi bipectinate (like most Orsolobidae and Oonopidae). Legs I-II directed forwards, legs III-IV directed backward like in most spiders. Cheliceral lamina existing. Eyes small, their diads widely spaced. Gnathocoxae strongly converging. The spiders hide in retreats e. g. under stones. EX-TANT, Australia and New Zealand. Only *Periegops* SIMON 1893. . . . . **Periegopidae**

- Leg bristles existing (fig. 42). All paired tarsal claws bear a single row of teeth. Third pair of legs directed forwards like legs I-II (the „segestriid leg position“, fig. 33, photos). See no. 2: Plumorsolidae. Cheliceral lamina absent. Eyes larger, their diads less spaced. Gnathocoxae parallel (fig. 41). Most extant and Eocene spiders are known to hide in tubular retreats from which signal lines originate. Extant and fossil. **Segestriidae** (1). . . 5

5(4) Tibiae I-II bear a single pair of ventral bristles besides apical ones. Deformed structures of the ♂-pedipalpus: See WUNDERLICH (2008: 659, figs. 8-9). Cretaceous amber from Lebanon. **Lebansegestriinae**. . . . . *Lebansegestria azari*

- Tibiae I-II bear usually at least 2 pairs of ventral bristles besides apicals; *Denticulosegestria* in Burmite (no. 19) is an exception. Lebanese amber: *Microsegestria*, see directly below, and other kinds of amber. . . . . 6

6(5) Body length (♂) only 1.35 mm, clypeus strongly projecting, opisthosoma egg-shaped short, bulbus globular, BEARING A CONDUCTOR and attached in the distal half to the short cymbium, see WUNDERLICH & MILKI (2004: 1873, figs. 1-4). Cretaceous, Lebanese amber. **Microsegestriinae**. . . . . *Microsegestria poinari*

- Body length at least 2 mm, clypeus not distinctly projecting, opisthosoma longer oval, conductor absent. Ariadninae and Segestriinae, see the tab. below. . . . . 7

7(6) FANGS STOUT (fig. 35), position of the median eyes USUALLY more between the posterior lateral eyes, articles of the ♀-pedipalpus stout; attachment of the GLOBULAR bulbus near or at the end of the always short cymbium (fig. 37). **Ariadninae**. . . . . 8

- FANGS LONG AND SLENDER (fig. 34), position of the median eyes USUALLY more between the anterior median eyes (fig. 39), articles of the ♀-pedipalpus slender; attachment of the PEAR-SHAPED bulbus often in the basal half of the frequently long cymbium (fig. 36). **Segestriinae** (1). . . . . 9

8(7) Labrum only about as long as the labium, distinctly shorter than the gnathocoxae. Cretaceous, Jordanian amber (= ?*Ariadna a.*) . . . . . *Jordariadna amissiocoli*



- Labrum distinctly longer than the labium, about as long as the gnathocoxae. Extant and Eocene: Baltic, Bitterfeld and Ukrainian ambers. . . . . Ariadna s. l. (2)
- 9(7) Extant and Eocene. Cymbium distinctly widened basally (fig. 36) . . . . . 10
- Cretaceous. Cymbium not distinctly widened basally (figs. 50, 55). . . . . 11
- 10(9) Cephalic part wide, eye field narrow, cheliceral retromargin with a single large tooth, tibiae I-II with 4 pairs of ventral bristles and none laterals. Eocene – e. g. Baltic – amber forest. . . . . Vetsegestria quinquespinosa WUNDERLICH 2004
- Cephalic part narrow, eye field wide, cheliceral retromargin with two large teeth, tibiae I-II most often with not more than 3 pairs of ventral bristles and with laterals. Extant and Eocene amber forests. . . . . Segestria
- 11(9) Tibia of the ♂-pedipalpus slightly longer than wide (fig. 57). . . . . 12
- Tibia of the ♂-pedipalpus ca. 2-4 times longer than wide (fig. 44). . . . . 13
- 12(11) The ♂-chelicerae bear distinct long anterior setae (fig. 57). New Jersey amber. . . . . Palaeosegestria lutzii
- The ♂-chelicerae bear only few anterior setae. Burmite. *M. ceaderens* and *engin*. . . . . Myanseggestria
- 13(9) Body length almost 3.5 mm, embolus widened apically (fig. 44). Jordanian amber. . . . . Jordanseggestria detruneo
- Body length usually 2.0-2.2 mm (3.2 mm in *Parvosegestria triplex*), embolus not widened apically (figs. 38, 59, 67). Burmite. . . . . 14
- 14(13) Basal cheliceral articles with retrolateral denticles (fig. 38), gnathocoxae with strong medial denticles (fig. 40), bulbus relatively longer (fig. 38). . . . . Denticulseggestria rugosa
- Basal cheliceral articles without retrolateral denticles, gnathocoxae without medial teeth (only with longer hairs). Bulbus (figs. 58-59, 67) more stout. Parvosegestria . . 15
- 15(14) ♂-pedipalpus (fig. 58): Tibia very long and very slender, embolus distinctly longer than the quite small bulbus. . . . . Parvosegestria longitibialis
- ♂-pedipalpus (figs. 67-69): Tibia long and fairly thickened, embolus strongly bent, as long as the bulbus. Body length 3.2 mm. . . . . Parvosegestria triplex
- ♂-pedipalpus (figs. 59-60, 66): Tibia more stout, embolus relatively shorter: not or only slightly longer than the larger bulbus. Body length 2-2.2 mm. . . . . 16
- 16(15) Embolus fairly bent (figs. 59-60). . . . . Parvosegestria obscura
- Embolus straight (except it tip) (fig. 66). . . . . Parvosegestria pintgu



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(1) The enigmatic extant genus *Gippsicola* HOGG 1900 from the Australian Region has erroneously been regarded as a synonym of *Segestria* by ROEWER (1954: 1516), Katalog der Araneae, 2b. The complicated distal structures of its bulbus indicate at least the existence of a separate genus which relationships are quite unsure, see FORSTER & PLATNICK (1985: 213, fig. 828), but in my opinion it well may be the member of an unnamed subfamily or even family. – Usually a conductor is absent in the members of the Segestriidae but – besides *Gippsicola* – it exists also in the enigmatic Cretaceous genus *Microsegestria* WUNDERLICH & MILKI 2004 (Microsegestriinae WUNDERLICH 2004, see the key no. 6), which relationships appears also unsure. Hopefully more material will be discovered in the future.

(2) The genus *Ariadna* will be split up in the future, *Segestriella* PURCELL 1904 of Namibia (currently regarded as a synonym of *Ariana*) may well be a genus of its own.

### Comparison of fossil and extant Segestriinae and Ariadninae:

CHARACTER	SEGESTRIINAE	ARIADNINAE
teeth of the chelicer- al retromargin	0-3 larger teeth usually 2 large teeth	a single tiny tooth near the base of the fang or none
<b>fangs</b>	<b>long and slender,</b> fig. 34	<b>stout,</b> fig. 35
USUAL (!) position the median eyes	more in front, between the anterior lat. eyes	more between the poste- rior lateral eyes
♂-metatarsus I	<b>unmodified, straight</b>	<b>most often modified:</b> bent and/or bearing <b>clasp- ing spines or spurs</b>
ventral ♀-tibial I- II bristles	longer	shorter
ventral tibial bristles I-II (♀), II (♂)	usually up to 3 pairs	usually > 3 pairs
<b>articles of the ♀-pedipalpus</b>	<b>long and slender,</b> tarsus 4-5 times lon- ger than wide	<b>stout,</b> tarsus usually 2.5-3 times longer than wide
<b>bulbus</b>	usually <b>pear-shaped</b> & attached <b>more basally</b> on the <u>frequently long</u> <u>cymbium</u> , figs. 36, 67	almost <b>globular,</b> attached naer or at the end of the <u>always short</u> <u>cymbium</u> , fig. 37

Remarks on differences of extant and extinct taxa: (a) In contrast to most Cretaceous taxa the labrum is as short as the labium in today's Segestriinae but distinctly longer, and about as long as the gnathocoxae in extant Ariadninae.

(b) The sexual dimorphism of the Ariadninae – e. g. the modification of the ♂-tibia I – may be less developed (or even absent) in Mesozoic taxa than in extant taxa.

(c) The life span of the Cretaceous spiders is unknown; to my knowledge in extant ariadnine males the life span is – much? – shorter than in segestriine males.

## **DESCRIPTIONS OF THE TAXA**

### **Subfamily ARIADNINAE**

***Ariadna*** AUDOUIN 1826: See *Jordariadna* below. No sure Cretaceous report of this genus exists.

### ***Jordariadna* n. gen.**

Etymology: The first part of the name refers to Jordan, the country in which the amber containing the generotype was collected, the second part originates from the nominate genus name *Ariadna* of the subfamily Ariadninae.

The gender of the name is feminine.

Type species (by monotypy): ?*Ariadna amissiocoli* WUNDERLICH 2008 = *Jordariadna amissiocoli* (WUNDERLICH 2008) (**n. comb.**).

**Material:** Holotype ♂ F2014/JB/CJW. Further material: ?*Ariadna amissiocoli*: WUNDERLICH (2011: 544), exuvia, probably conspecific, F2205/JB/CJW.

**Diagnostic characters** (♂; ♀ unknown): Labrum short, not longer than the labium, distinctly shorter than the gnathocoxae (exuvia), tibia I with 2 pairs of ventral bristles besides apicals (plus a single prolateral one in the probably conspecific exuvia), metatarsus I: 3 ventral pairs + apicals. Metatarsal III-IV preening combs well developed. Pedipalpus with stout tibia and cymbium, embolus long and strongly bent.

Notes: (1) *J. amissiocoli* is the only species of the subfamily Ariadninae which is surely reported from the Cretaceous. The short life span of male Ariadninae may be the reason for the rareness of these fossils. – (2) The body length of the male holotype of *amissiocoli* is really 4 mm. – (3) The pedipalpal tarsus of the exuvia of *?amissiocoli* is three times longer than wide.

**Relationships:** See WUNDERLICH (2008 and 211). In *Ariadna* AUDOUIN 1826 the labrum is distinctly longer than the labium, about as long as the gnathocoxae.

**Distribution:** Early Cretaceous Jordanian amber forest.

## Subfamily SEGESTRIINAE

### *Denticulsegestria* n. gen.

Etymology: Derived from dens (lat.) = tooth, according to the relatively small gnathocoxal teeth (denticles), and the related genus *Segestria*, the nominal genus of the family Segestiidae.

The gender of the name is feminine.

Type species (by monotypy): *Denticulsegestria rugosa* n. sp.

**Diagnostic characters** (♂; ♀ unknown): Basal cheliceral articles with denticles (figs. 38, 40), gnathocoxae with long medial teeth (figs. 38, 40–41), tibia I (fig. 42) with 2 pairs of ventral bristles besides 1 prolateral one and apicals; pedipalpus (fig. 38): Tibia very long, fairly thickened, cymbium oval relatively long, position of the alveolus quite distally, bulbus oval, long and slender, embolus long. Body length only 2.0–2.2 mm.

**Relationships:** See *Parvosegestria* n. gen.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

***Denticulsegestia rugosa* n. gen. n. sp.** (figs. 38-42) photos 25-26

**Etymology:** The species is named after its retrolaterally rugose basal cheliceral articles.

**Material:** Holotype ♂ and a separated piece of amber in Mid Cretaceous amber from Myanmar (Burma), F2622/BU/CJW.

**Preservation and syninclusions:** The spider is excellently and almost completely preserved in a yellowish piece of amber, only the tip of the right tarsus II is lost within the amber. The opisthosoma is distinctly deformed, probably eaten out ventrally. – Right behind the spider a tiny insect (a wasp?) is preserved. Remains of plants exist in the separated piece of amber. A Diptera and a Collembola are preserved in another piece which has been separated.

**Diagnosis** (♂; ♀ unknown): See the new genus.

**Description** (♂):

Measurements (in mm): Body length ca. 2.2, prosoma: Length 1.12, width 0.8; length of a basal cheliceral article 0.45; leg I: Femur 1.1, patella 0.35, tibia 1.2, metatarsus 1.0, tarsus 0.45, tibia II 1.0, tibia III 0.7; pedipalpus: Tibia: Length 0.47, height 0.1, length of the embolus 0.2.

Colour: Prosoma dark brown, legs medium brown, apparently not annulated, opisthosoma light brown.

Prosoma (figs. 38-41, photos) 1.4 times longer than wide, smooth, anteriorly distinctly narrowed, fovea absent, 6 eyes, position of the median eyes in front of the middle of the eye field, basal cheliceral articles long and slender, distinctly protruding, laterally rugose, fangs long and fairly slender, anterior margin of the fang furrow with 5 teeth, posterior margin probably toothless, gnathocoxae quite long, medially bearing at least three long teeth, serrula well developed, labium long, labrum hidden, apparently short, sternum 1.25 times longer than wide, anteriorly wide, the coxae IV spacing by about only their diameter. – Legs (fig. 42, photos) fairly long and slender, order I/II/IV/III, I-III directed +/- forwards, bristles not numerous, the femora bear a dorsal one in the basal half, additional bristles exist distally, e. g. 2-3 dorsally and prolaterally on I, tibia I-II bear two ventral pairs besides apical ones and a prolateral one, metatarsus I-II with a ventral pair in the basal half besides an apical pair, legs III-IV bear some more bristles, metatarsus III-IV without an apical preening comb but with few long ventral bristles, position of the metatarsal I-II trichobothrium in ca. 0.85, onychium well developed, three tarsal claws which are well developed, paired claws with long teeth. – Opisthosoma (photo; it is strongly deformed and incompletely preserved) oval, covered with short hairs. – Pedipalpus: See the genus. The embolus is slightly bent.

**Relationships and distribution:** See above.

### **Jordansegestria n. gen.**

**Etymology:** From Jordan, the country in which the the holotype of the new species has been collected, and the segestriine genus *Segestria*.

The gender of the name is feminine.

**Type species** (by monotypy): *Jordansegestria detruneo* n. sp.

**Diagnosis** (♂; ♀ unknown ): Pedipalpus (figs. 43-44): Cymbium very long and slender, basally not widened, embolus thickened and strongly bent apically.

Further diagnostic characters: Alveolus in a basal position, bulbus pear-shaped. (Tibia I and the position of the eyes are unknown).

**Relationships:** According to the basal position of the alveolus at the long cymbium and the pear-shaped bulbus *Jordansegestria* may well be a member of the subfamily Segestriinae, see WUNDERLICH (2004: 658). In the remaining known Cretaceous Segestriinae the cymbium is only slightly elongated, beyond the bulbus/alveolus, in *Segestria* LATREILLE 1804 and *Vetsegestria* WUNDERLICH 2004 (Palaeogene, Baltic amber) the cymbium is widened basally and the embolus is needle-shaped (pointed) apically. The absence of a clasping spine of tibia I in the present taxon – as in other members of the subfamily Segestriinae – is unknown because the anterior tibiae are lost in the single known specimen of the type species). See also *Parvosegestria*.

**Distribution:** Early Cretaceous amber from Jordan, Zarqa river basin. If the holotype is assigned correctly *Jordansegestria detruneo* is the first Cretaceous report of the subfamily Segestriinae.

***Jordansegestria detruneo* n. gen. n. sp.** (figs. 43-44) photo 24

**Etymology** of the species name: From detruneo (lat.) = multilated, according to the injured/cut right pedipalpal tibia and the incompletely preserved legs.

**Material:** Male holotype in Early Cretaceous amber from Jordan, Zarqa river basin, F2463/JB/CJW, ex coll. H. KADDUMI (Amman), ERMNH 1001.

**Preservation and syninclusions:** The piece of amber has been embedded in a larger piece of artificial resin by its collector H. KADDUMI before the year 2012. The spider (photo) is strongly darkened and incompletely preserved; cut off are the posterior three

quarter of the opisthosoma and most articles of the legs including all tarsi, the right leg IV is lost, the right leg II is lost beyond the coxa probably by autotomy, the right femur I has been broken and empty at the end and probably dissected like parts of the opisthosoma, both pedipalpal tibiae are cut off dorsally, parts of body and legs, especially the eye field are deformed and darkened by the pressure during the long time of preservation. – A tiny questionable mite, larger parts of leafs as well as numerous tiny bubbles/droplets and parts of detritus are also preserved.

**Diagnosis** (♂; ♀ unknown): See the new genus.

**Description** (♂):

Measurements (in mm): Body length probably almost 3.5, prosoma: Length 1.7, width ca. 1.4; femur II and IV ca. 2.5, femur III ca. 1.9, patella IV ca. 0.6, tibia IV >2.0; pedipalpus: Tibia ca. 0.6, cymbium ca. 0.6.

Colour dark brown (almost black).

Prosoma anteriorly distinctly smaller, fairly hairy, feathery hairs probably absent, apparently 6 eyes in a strongly deformed field, basal cheliceral articles long, slender and fairly diverging medially-distally, condylus and most probably lateral files absent. Most parts of the fangs, other mouth parts and sternum are hidden. – Legs (photo) long, I longest, III shortest, the articles of III beyond the femur are directed forward, hairs fairly short, bearing fairly long bristles; observable are: A dorsal and a retrolateral one in the distal third of femur II, a retrodorsal one near the base of the left femur III, tibiae III and IV bear few bristles. – Opisthosoma: Only the dissected basal part exists. – Pedipalpus (figs. 43-44): Femur slender, patella short, tibia long and only slightly thickened, cymbium long, slender and not widened basally, position of the alveolus near its base, bulbous pear-shaped, embolus fairly thick, thickened and bent apically.

**Relationships and distribution:** See the new genus.

**Myansegestia n. gen.**

**Etymology:** „Myan“ is taken from the country in which the the fossils in question have been found, „segestia“ refers to the name of the type genus of the family Segestriidae.

The gender of the name is feminine.

Type species: *Myansegestia engin* n. sp.

Further species: *Myansegestia caederens* n. sp.

**Diagnosis** (♂; ♀ unknown): Tarsi with a „girlande“ of long hairs which originate above the claws and surround them, onychium quite large and sclerotized (figs. 46-47) (it is less developed in *caedarens*), tibia I with about three pairs of ventral bristles besides apical ones (fig. 45); pedipalpus (figs. 48, 52) with stout tibia and cymbium.

Further characters: Gnathocoxae not elongated, no preening comb on metatarsus III-IV but few long bristles in this position (ventrally-apically).

**Relationships:** In *Palaeosegestria* PENNEY 2004 in Cretaceous amber from New Jersey the cymbium is also short but the basal cheliceral articles bear anterior-basally a brush of long and downwards projecting setae, and the gnathocoxae are elongated quite long, see the remark below.

Remark: The alleged conical setae-bearing outgrowths of the basal cheliceral articles of the holotype of *Palaeosegestria lutzii* PENNEY 2004 (fig. 57) are in my opinion nothing else than the misinterpreted tip of the long gnathocoxae (see the fig. 78 of the *Plumorsolobidae* below).

In *Vetsegestria* WUNDERLICH 2004 (preserved in Eocene Baltic amber) tibia I-II bear at least 4 pairs of ventral bristles besides apical ones and the cymbium is much longer.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

### ***Myansegestria engin* n. gen. n. sp. (figs. 45-51) photo 28**

Derivatio nominis: The species is dedicated to ENGIN NI in Myanmar (Burma), our native guide during a trip to Myanmar in I-II 2013. Her kind help included the proof and purchase of important fossil spiders in amber from North Myanmar (Burma).

**Material:** Holotype ♂ and two separated pieces of amber in Mid Cretaceous amber from Myanmar (Burma), F2620/BU/CJW.

**Preservation and syninclusions:** In most parts the spider is excellently preserved, parts of the right legs I and II are cut off, the right part of the opisthosoma is cut off within the resin, the eyes are strongly deformed. – The peltidium of an exuvia (fig. 51), 1.3 mm long, 1.1 mm wide, probably remains of the holotype's exuvia, is preserved in the smaller separated piece of amber. Remains of a small spider's opisthosoma and leg articles as well as some stellate plant hairs are preserved in the larger separated piece of amber.

**Diagnosis** (♂; ♀ unknown): Metatarsus I bristleless besides apical bristle, pedipalpus as in figs. 48-50, 55-56; embolus only slightly bent distally.

### **Description** (♂):

Measurements (in mm): Body length 3.2, prosomal length 1.5; leg I: Femur 1.5, patella 0.5, left tibia 1.6, right tibia (a regeneration?) 1.25, metatarsus 1.35, tarsus 0.6, tibia II 1.45, tibia III 1.3, tibia IV 1.4; opisthosoma: Length 2.1, height 1.2.

Colour: Prosoma and legs dark grey brown, legs not annulated, opisthosoma light grey. Prosoma (fig. 51, of the exuvia, photo) probably 1.18 times longer than wide, most hairs are short, fovea absent, 6 eyes which are strongly deformed in the male holotype but are well preserved in the exuvia in which the position of the median eyes is about in the



middle of the eye field. Basal cheliceral articles rather slender, not protruding and only slightly diverging, bearing long anterior hairs in the basal half, fangs long and slender, anterior margin of the fang furrow with two or three teeth, posterior margin probably with two teeth. – Legs (figs. 45-47, 53-54, photo) fairly long, their position unnatural, order I/II/IV/III, III relatively long. Bristles long and numerous, existing on femora, tibiae and metatarsi; leg I: Femur 4 dorsally, tibia 3 ventral pairs, few laterals and apicals, metatarsus I only with an apical-ventral pair, remaining metatarsi with several bristles. Metatarsal trichobothria near the end of the articles. Unpaired tarsal claws long, paired claws with long teeth, surrounded by long hairs, onychium with a long sclerotized outgrowth. – Opisthosoma (photo) 1.75 times longer than high, hairs short, lateral light band not recognizable or absent, spinnerets and anal tubercle short. – Pedipalpus (figs. 48-50, 55-56): Femur and patella slender, tibia stout, cymbium short, position of the alveolus in the distal half, bulbus pear-shaped, embolus long and apparently straight (its tip is hidden).

**Relationships:** In *M caederens* n. sp. the embolus is distinctly bent near its end.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

***Myansegestia caederens* n. gen. n. sp.** (figs. 52-56) photo 27

**Etymology:** From caedes (lat.) = killing.

**Material:** Holotype ♂ in Burmite from N-Myanmar (Burma), Kachin State, F2706/BU/CJW; paratype ♂ in Burmite, Tanai (= Tanaing) Township, Myitkyina Distr., Kachin State; coll. HUANG, without a number. Note: The male has originally provisionally been labeled as holotype by me); 1 probably conspecific ♂ in Burmite, F2619/BU/CJW.

**Preservation and syninclusions:** Holotype: The male is well preserved in a yellow piece of amber, the right leg III is lost beyond the coxa by autotomy, the right tarsus and metatarsus IV are cut off. A larger fissure within the piece of amber runs across the right legs I and II – The paratype is partly well but incompletely preserved: The eye region and the bulbi are distinctly deformed; except the basal part the opisthosoma is cut off, leg III and most articles of leg IV are cut off. The left metatarsus I is a shortened malformation, probably broken in the distal half and healed. – The probably conspecific ♂ is badly preserved, strongly heated and deformed. A tiny Diptera is preserved above the spider.

**Diagnosis** (♂; ♀ unknown): The tip of the embolus is strongly bent (figs. 52, 56).

**Description** (♂):

Measurements (in mm): Holotype: Body length ca. 2.5, prosoma: Length 1.2, width ca. 0.8; leg I: Femur 1.2, patella 0.25, tibia 1.2, metatarsus 0.85, tarsus 0.5, tibia II 1.15, tibia III 0.9, tibia IV 1.0. – Paratype: Body length unknown, prosomal length 1.15; leg I:

Femur 1.2, patella 0.45, tibia (left/right) 1.25/1.45, metatarsus 1.35, tarsus 0.65, tibia II 1.4, tibia III 1.2, tibia IV is lost. – Male F2619/BU/CJW: Body length 2.2, tibia I 1.2. Colour dark grey brown, legs not annulated.

Prosoma (photo) ca. 1.3 times longer than wide, hairs short, fovea a small depression in a posterior position, 6 strongly deformed eyes in a „segestriid position“ (three diads), basal cheliceral articles long and slender, distinctly protruding, bearing anteriorly long and bristle-shaped hairs, fangs long and slender, both margins of the fang furrow are hidden, gnathocoxae not elongated beyond the basal cheliceral articles. – Legs (figs. 53-54, photo) long and slender, order I/II/IV/III, III relatively long, the left legs I and II and the right legs I-III of the paratype are directed forwards. Bristles long, existing on femora, tibiae and metatarsi, the right femur I bears 3 dorsal bristles and a prodistal one (further bristles are probably broken off), the left femur I bears only a single dorsal and a single prodistal bristle. Tibia I bears 3 ventral pairs, an apical pair and some laterals, metatarsi I-II ventrally bristleless, metatarsus I bears a prolateral bristle (in the paratype), and a pairs apically-ventrally, the remaining metatarsi bear several bristles. – Position of the metatarsal trichobothria near the end of the articles, onychium well developed, paired tarsal claws surrounded by some long hairs, bearing long teeth, the retroclaw I bears ca. 10 teeth, unpaired claw long in the paratype but indistinct in the holotype. – Pedipalpus (figs. 52, 55-56): Femur long and slender, patella, tibia and cymbium stout but patella slender (deformed?) in the paratype, bulbus pear-shaped (the left one of the paratype is deformed), embolus long, slender and strongly bent near the end. In the probably conspecific male F2619/BU/CJW the long embolus of the strongly deformed pedipalpus is less bent.

**Relationships:** See *M. engin* n. sp.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

Segestriidae: Segestriinae indet.

**Material:** 1♂ in Burmite, F2621/BU/CJW.

The male is almost completely preserved, only some right leg articles are cut off. Body and legs are strongly deformed and darkened apparently by heating and pressure. The left and right legs I and II are stretched forwards, the remaining legs sideways. The body length is 2.5 mm, tibia I is 1.2 mm long. The pedipalpen tibia and the cymbium are stout, the bulbus is pear-shaped, the embolus is long, partly decomposed. similar to *Myansegestria engin*.

## ***Palaeosegestria* PENNEY 2004**

The only known species is *P. lutzii* PENNEY 2004, a single male preserved in Cretaceous amber from New Jersey, fig. 57, see the key above and *Myansegestria* n. gen. According to the more oval shape of the bulbus which is attached not at the end of the cymbium (the shape of the fangs is unknown) I regard *Palaeosegestria* as a member of the subfamily Segestriinae.

The genus is diagnosed by its numerous long antero-basal bristles on the basal chelical articles. The body length is 3.75 mm.

Note: The alleged conical and setae-bearing apical outgrowths of the chelicerae of the holotype are in my opinion nothing else than the misinterpreted tips of the long gnathocoxae which exist in certain Segestriidae and in the Plumorsolidae as well, see fig. 78.

## ***Parvosegestria* n. gen.**

Etymology: The first part of the name of these tiny spiders is based on parvus (lat.) = small; the second part is taken from the segestriine genus *Segestria*.

The gender of the name is feminine.

**Type species:** *Parvosegestria obscura* n. sp.

**Diagnostic characters** (♂; ♀ unknown): Body length usually only 2.0-3.2 mm (3.2 mm in *triplex*), tibia I with 2 pairs of long and thin ventral bristles besides usually 1 prolateral one and apicals (photos); pedipalpus (figs. 58-60, 66-69): Tibia long to very long, slightly or fairly thickened, cymbium short, alveolus in its distal half, bulbus relatively stout, embolus distinctly bent but usually almost straight.

**Relationships:** According to the long fangs and the oval shape of the bulbus I regard *Parvosegestria* as a member of the subfamily Segestriinae. According to the small body length and the structures of the male pedipalpus *Denticulosegestria* n. gen. is similar; in *Denticulosegestria* the basal chelical articles bear retrolateral denticles, the gnathocoxae bear long medial teeth, the cymbium is relatively longer, the bulbus is longer and its attachment more near the tip of the cymbium. – In the Eocene genus *Vetsegestria* WUNDERLICH 2004 in which the small body is 2.1-2.6 mm long, the cephalic part is wide, tibia I bears 4 pairs of ventral bristles, and the cymbium is very long and widened basally. – In the Early Cretaceous genus *Jordansegestria* n. gen. the body is almost 3.5 mm long and the embolus is widened apically.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

***Parvosegestria obscura* n. gen. n. sp.** (figs. 59-60) photos 30-31

Etymology of the species name: The species is named after its darkened body and legs in a darkened piece of amber.

**Material:** 2♂ in Mid Cretaceous Burmite; holotype and two separated pieces of amber, F2615/BU/CJW; paratype and a separated piece, F2732/BU/CJW.

**Preservation and syninclusions:** (a) Holotype: The spider is almost completely and fairly well preserved in a darkened red-brown piece of amber, its right leg III is lost beyond the coxa by autotomy, the left tarsus is cut off, body and legs are darkened by natural pressure and heating, the eyes are distinctly deformed; a tiny droplet is preserved at the tip of the left embolus (fig. 58). – A Diptera and some stellate plant hairs are preserved in the same piece of amber, and in the separated pieces as well. (b) Paratype: The spider is completely and excellently preserved in a clear yellow piece of amber. An emulsion covers the anterior median eyes which therefore appear distinctly larger than these eyes of the holotype.

**Diagnosis** (♂; ♀ unknown): Pedipalpus: Tibia only fairly thickened in the heated male (fig. 59) but thick in the not deformed male (fig. 60), embolus fairly bent, as long as the bulbus, less than 0.2 mm long.

**Description** (♂):

Measurements (in mm): Body length 2.2, prosoma: Length 1.0-1.15 (paratype), width 0.7; leg I: Femur 1.3, patella 0.4, tibia ca. 1.2, metatarsus 1.1, tarsus 0.3, tibia II 1.1, tibia III 1.0, tibia IV ca. 1.1, embolus 0.2.

Colour dark brown.

Prosoma (photos 30-31) 1.4 times longer than wide, 6 eyes, median eyes close together and in a more anterior position, small in the heated holotype but seemingly large in the paratype in which they bear an emulsion, fovea indistinct, few long anterior hairs, basal cheliceral articles long and slender, bearing some long anterior hairs, fangs long and slender, anterior margin of the fang furrow with few small teeth, posterior margin probably with a single lateral tooth. Mouth parts deformed, labrum hidden, not longer than the short labium, gnathocoxae distinctly shorter than the basal cheliceral articles. – Legs (photos) fairly long, order I/II/IV/III, III relatively long and directed forwards in the holotype. Bristles: Femora with few ones, tibia I and II bear two ventral pairs and apicals, legs III-IV bear numerous bristles. Metatarsi III-IV with some long ventral-apical bristles (no true preening comb), position of the metatarsal trichobothrium IV (holotype) in 0.8, onychium and unpaired tarsal claws well developed, paired tarsal claws with long teeth. – Opisthosoma (photos) twice as long as wide, covered with short hairs. – Pedipalpus (figs. 59-60): See the diagnosis; bulbus oval, embolus fairly bent.

**Relationships:** In *P. longitibialis* the pedipalpal tibia is longer and more slender, the embolus is distinctly longer than the small bulbus. In *P. pintgu* the embolus is straight (except its tip).

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

***Parvosegestria longitibialis* n. gen. n. sp.** (fig. 58) photo 29

**Etymology:** The species name refers to its long pedipalpal tibia, from longus (lat.) = long.

**Material:** Holotype ♂ and two separated pieces of amber in Mid Cretaceous Burmite, F2614/BU/CJW.

**Preservation and syninclusions:** The spider is incompletely and not well preserved in a clear yellow piece of amber, deformed and apparently decomposed; the right margins of body, the right legs and the right pedipalpus are cut off, most legs are partly transparent. – Some stellate plant hairs are preserved in one of the separated pieces of amber.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (fig. 58): Tibia very long and slender, embolus distinctly longer than the small bulbus, ca. 0.22 mm long.

**Description** (♂):

Measurements (in mm): Body length 2.0; prosomal length 1.1; leg I: Femur 1.0, patella 0.4, tibia 1.1, metatarsus ca. 0.75, tarsus 0.35, tibia III 0.7; embolus ca. 0.22.

Colour medium grey brown (apparently the spider has been decomposed).

Prosoma (photo; it is strongly deformed): Six eyes, median eyes in a more anterior position, similar to *P. obscura*. – Legs (photo) slender and fairly long, order I/II/IV/III, I-III directed forwards, IV directed backwards, bristles and metatarsal trichobothria as in *P. obscura*. – Opisthosoma strongly deformed, bearing short hairs. – Pedipalpus (fig. 58): Femur, patella and tibia very long and slender (the tibia is slightly deformed), cymbium short, bulbus small and oval, attached in the distal half of the cymbium, embolus long and almost straight.

**Relationships:** See *P. obscura* and *P. pintgu*.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

***Parvosegestria pintgu* n. gen. n. sp.** (figs. 61-66) photos 32-34

**Etymology:** Pintgu is the Burmese word for spider.

**Material:** Holotype ♂ in Mid Cretaceous Burmite, F2655/BU/CJW.

**Preservation and syninclusions:** The spider is almost completely preserved in a clear yellow piece of amber, only the right leg I is lost beyond the coxa by autotomy, the prosoma as well some leg and pedipalpal articles are deformed. – A movable gas bubble in fluid is preserved left of the spider between the legs II and III, another bubble exists on

the spiders's body between pro- and opisthosoma. A small Diptera is preserved in front of and in contact to the spider (photo). It has not been the prey of the spider: As shown by the position of the wings of the midge – they possess an unnatural position anteriorly of the Diptera's head and are directed to the spiders' body – the flow of the fossil resin transported this animal to the anterior part of the spider at the left leg II. A Thysanoptera exists left above the spider. More bubbles and several plant hairs are also preserved. A tiny wingless arthropod has been separated, F2657/BU/CJW.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (fig. 66) straight except at the tip, at least as long as the bulbus. – Basal cheliceral articles (fig. 62, photo) with distinct inclinations retrobasally as well as medially which may be caused by the preservation.

**Description** (♂):

Measurements (in mm): Body length 2.0, prosoma: Length 0.9, width 0.7; opisthosoma: Length 1.2, width 0.55; tibia I 1.1, tibia III 0.73, metatarsi I and IV ca. 1.0.

Colour: Prosoma dark brown, legs medium brown, opisthosoma light grey brown.

Prosoma (figs. 61-62, photos) 1.3 times longer than wide, anterior part abruptly narrowed, hairs probably rubbed off, fovea hidden, six widely spaced eyes in a very wide field, median eyes spaced by more than their radius. Clypeus very short, basal cheliceral articles long and obliquely protruding (anterior inclinations may be deformations, see above), fangs long, posterior margin of the fang furrow apparently with three teeth, gnathocoxae not longer than the chelicerae, labium free, sternum longer than wide, separating the coxae IV by more than their diameter. – Legs (figs. 63-65, photos) fairly long, order I/II/IV/III, III relatively short, directed mainly sideways (photo; the spider is situated flat on a layer of the fossil resin), tarsi and metatarsi III and IV are directed forwards, hairs rather indistinct, bristles long and thin, femora with 3 dorsally, I and II additionally with a distal-lateral pair, patellae none, tibia I-II ventrally probably two pairs as well as laterals and apicals; metatarsi I-II at least with a single ventral pair, metatarsi III-IV with at least 7 bristles, metatarsal preening combs indistinct. Position of the metatarsal IV trichobothrium in 0.85, paired tarsal claws with long teeth, unpaired claw very thin, bent in a right angle. – Opisthosoma (photos) 2.2 times longer than wide, hairs short and indistinct, anterior and posterior spinnerets fairly long and slender, median spinnerets short. – Pedipalpus (fig. 66, photos): Articles quite similar to *P. obscura*, embolus almost straight (the tip is slightly bent apically), at least as long as the oval bulbus.

**Relationships:** In *P. longitibialis* the pedipalpal tibia is more slender and the bulbus is smaller, in the strongly related *P. obscura* the embolus is fairly bent.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

***Parvosegestria triplex* n. gen. n. sp.** (figs. 67-69) photo 35

Etymology of the species name: Triplex (lat.) = triple, according to the discovery of three specimens of this species.

**Material:** 3♂ in Mid Cretaceous Burmite; holotype and one paratype F2675/BU/CJW, second paratype F2676/BU/CJW.

**Preservation and syninclusions:** F2675, a clear yellow piece of amber: The holotype is fairly well preserved, the left leg II has been separated within the fossil resin beyond its coxa by autotomy and is preserved in front of the spider, its sides and dorsal parts are hidden by layers of the amber, the left pedipalpus is a malformation: The cymbium is shortened, the bulbus (partly hidden) is quite slender. – The paratype in the same piece of amber is completely and well preserved; the leg position is as in the holotype and the second paratype. – Left of the holotype remains of a small arthropod – of an exuvia of a ricinulei? – are preserved, furthermore exist 2 Coleoptera, 1 Collembola, 1 ½ Diptera, 1 slender insect larva (Blattoidea?), Acari of four taxa, 1 Psocoptera, 1 Thysanoptera, and a huge number of tiny, spherical to oval brown ordark (pollen?) grains (some are touching each other, others are partly clumped), diameter 0.03 – 0.04 mm, 6 „organic objects“ similar to diatomees (insects eggs?), 0.1 mm long, insects excrements, numerous plant hairs, small ?gas bubbles and pyrite. – The paratype F2676 is fairly well preserved in a clear yellow piece of amber, the right leg I and the left leg III are lost by autotomy. Syninclusions: 1 Cicadina, remains of two Blattaria larvae (the larger one is in contact with the spider), some Acari of different taxa, including the larva of an Erythraeidae, Collembola, 3 Coleoptera (one with eggs), some Diptera, 1 Thysanoptera, 1 Hymenoptera, insects excrements, plant hairs, remains of leafs, gas/water bubbles and some small particles of amber.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (figs. 67-69): Tibia long and fairly thickened, embolus strongly bent. Body length 3.2 mm.

### **Description** (♂):

Measurements (in mm): Body length 3.2, prosoma: Length 1.5-1.7, width 1.2-1.3; opisthosoma: Length 1.5-1.8, width 0.8-1.0; legs: I (holotype): Femur 1.6, patella 0.65, tibia 1.75, metatarsus 1.4, tarsus 0.45, tibia II 1.7, tibia III 1.15, tibia IV 1.3, pedipalpal tibia (holotype) 0.6; tibia I F2675 1.6, F2676 1.5.

Colour light, prosoma and legs (they are not annulated) brown, opisthosoma grey.

Prosoma (photo) 1.3 times longer than wide, abruptly narrowed anteriorly, hairs short, fovea indistinct or even absent, 6 small eyes in a wide field as in *P. pintgu*, clypeus very short, basal cheliceral articles long and obliquely protruding, fangs long, anterior margin of the fang furrow probably with 4 teeth (holotype), gnathocoxae shorter than the basal cheliceral articles, other mouth parts hidden, sternum longer than wide, separating the coxae IV by more than their diameter. – Legs (photo): Order I/II/IV/III, slender and fairly long, III distinctly shortest, all legs directed forward, hairs rather indistinct, bristles and tarsal claws as in *P. pintgu*, position of the metatarsal IV trichobothrium in 0.85 (F2676). – Opisthosoma (photo) 1.8 times longer than wide, hairs short and indistinct, anterior and posterior spinnerets long, median spinnerets short. – Pedipalpus (figs. 67-69, photo) (see the diagnosis): Cymbium long and slightly widened basally.

**Relationships:** *P. triplex* is the largest known species of the genus, and its embolus is (stronger) bent than in its relatives.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).



**Family PLUMORSOLIDAE** WUNDERLICH 2008 figs. 71-78, photos 37-42, family key no. 20

Only a single genus and species of this six-eyed extinct Cretaceous family has been described previously: *Plumorsolus gondwanensis* WUNDERLICH 2008 (?juv.), preserved in Lebanese amber, as well as a questionable member of this family (juv., unnamed) in Burmese amber (see below). Here I describe the new tribe Burmorsolini from Burmite. The discovery of the unknown male in the future may help to clear the relationships of the Plumorsolidae.

**Diagnostic and further characters** (see WUNDERLICH (2008: 595)): Six eyes in a „segestriid“ position, unpaired tarsal claw absent, dense claw tufts of fairly flattened hairs (figs. 76-77), leg bristles usually long and thin in *Burmorsolus nonplumosus*, but strong in *B. crassus* n. sp. and *B. sp. indet.* A „segestriid leg position“ (in which the third leg is directed forwards, photos) exists probably in all taxa of this family, well preserved in *Burmorsolus* n. gen.. Feathery hairs exist in the nominate tribe Plumorsolini but are absent in the second known genus *Burmorsolus* n. gen., the Burmorsolini (\*). In the Burmorsolini exist 4 cheliceral teeth (fig. 71) and a fovea is absent. Both characters are absent in the Plumorsolini.

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(\* ) The existence/absence of feathery hairs within the same family is not unusual in spiders. Plumorsolidae is one of the oldest spider families from which feathery hairs are reported.

Two tribes: The nominate tribe Plumorsolini WUNDERLICH 2008 (under Plumorsolidae), and Burmorsolini n. trib.

**Relationships**: Segestriidae – in which an unpaired tarsal claw exists (\*) but no claw tufts and no feathery hairs – may be most related, see above. According to certain characters – like the position of the six eyes in diads, the absence of an unpaired tarsal claw and the existence of claw tufts – the family Orsolobidae (extant, Southern Hemisphere) is similar. In the Orsolobidae the paired tarsal claws are bipectinate, a distinct onychium exists, feathery hairs are absent and the position of leg III is different (not „segestriid“); furthermore the hairs of the – „true“ – claw tufts are more broadly flattened.

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(\* ) Within very few spider families an unpaired tarsal claw exists or is absent; an example is the genus *Dysdera* (Dysderinae) (two-clawed) within the usually three-clawed Dysderidae.

**Distribution**: Early Cretaceous Lebanese amber forest (Plumorsolini) and Mid Cretaceous Burmese amber forest (Burmorsolini).

## **BURMORSOLINI n. trib.**

Etymology: See the type genus below.

Type genus (by monotypy): *Burmorsolus* n. gen.

**Diagnostic characters** (♀): Feathery hairs absent, tarsal claw of the pedipalpus very long (fig. 72). (Claw tufts existing of two distinct rows (figs. 76-77); this character has not been reported from the Plumorsolini but may exist, too); fovea absent, fang furrow with four teeth (fig. 71).

**Relationships**: In the nominate tribe Plumorsolini WUNDERLICH 2008 (under Plumorsolidae), preserved in Early Cretaceous Lebanese amber – about 40 million years older than Burmite – feathery hairs exist, see WUNDERLICH (2008: 663, fig. 43), the hairs of the claw tufts are stronger flattened and the tarsal claw of the ♀-pedipalpus is shorter.

**Distribution**: Mid Cretaceous amber forest of Myanmar (Burma). – **Remark**: WUNDERLICH (2008: 597) reported feathery hairs of a juv. or ad. female of ?Plumorsolidae indet., MHMLP In. no. 20197. In my opinion the origin of the amber and the real existence of feathery hairs of this specimen have to revise.

## **Burmorsolus n. gen.**

Etymology: The name is a combination of the geological deposit of the type species, the Burmite in North Burma/Myanmar, and the related genus *Plumorsolus* WUNDERLICH 2008.

The gender of the name is masculine.

Type species: *Burmorsolus nonplumosus* n. sp.

Further species: *Burmorsolus crassus* n. sp.

**Diagnosis, relationships and distribution**: See the Burmorsolini n. trib.

***Burmorsolus nonplumosus* n. gen. n. sp.** (figs. 71-73) photos 38-41

**Etymology:** The species name refers to the absence of feathery/plumose hairs, non (lat.) and plumosus (lat.) hairy.

**Material:** Three probably (in my opinion) adult females in Mid Cretaceous amber from Myanmar (Burma): Holotype F2618/BU/CJW, paratypes F2656/BU/CJW and 2733/BU/CJW.

**Remarks:** The relatively length of the legs is largest in the paratype HUANG, the slenderness of the legs of the paratype 2656 is specific, see below.

**Preservation and syninclusions:** The holotype is almost completely preserved, only the right leg II is lost beyond the coxa by autotomy. Most legs are stretched dorsally in an unnaturally position. – Parts of two questionable spider's legs are preserved above and behind the spider. A large Cicada larva and a tiny insect's larva right of it as well as numerous particles of detritus are preserved in the same piece of amber. – The Paratype F2656/BU/CJW is almost completely preserved in a clear yellow piece of amber, only the right leg I is lost beyond the coxa by autotomy. The prosoma is crumbled dorsally, a bubble covers the genital area. – The paratype F2733/BU/CJW is well and almost completely preserved in a flat yellow piece of amber, only the left tarsus I is cut off. A large bubble is preserved on the right side of the opisthosoma, a long and thin spider's thread is preserved right and in front of the spider.

**Diagnosis:** Legs AND leg bristles long and slender (fig. 73, photos), tibia I ca. 33 times longer than high in the middle in the holotype (only ca. 25 times longer than high in the paratype F2656).

**Description (♀):**

Measurements (in mm): Body length 3.0 (holotype and paratype F2733) and ca. 2.4 (paratype F2656), prosomal length 1.25 (holotype and paratype F2733) and 1.1 (paratype F2656); leg I (holotype): Femur 1.9, patella 0.6/, tibia 2.2, metatarsus 1.6, tarsus 0.5; tibia II 2.0, tibia III 0.9, tibia IV (holotype): right 1.5, left 1.3, paratype F2656 1.5, paratype F2733 1.2.

Colour grey brown, legs not annulated.

Prosoma (fig. 71, photos): Six deformed eyes similar to *Plumorsolus gondwanensis* WUNDERLICH 2008, chelicerae long, condyle and lateral files absent, 4 teeth of the fang furrow (fig. 71), fangs long, gnathocoxae long and not converging, labrum not longer than the labium. – Pedipalpus (fig. 72) quite long and slender, tarsal claw very long, slender, bent distally. – Legs (fig. 73, photos) long and slender, order I/II/IV/III, III distinctly the shortest and directed forward in the holotype and in paratype F2656, tarsi short, hairs not distinct, some long erect hairs exist between normal hairs, feathery hairs, scopulae, unpaired tarsal claws and preening combs III-IV absent, dense claw tufts exist, see WOLF et al. (2013), the brush is distinctly divided longitudinally, teeth-bearing part of the paired claws narrow, bearing a single row of up to ten partly long teeth, bristles numerous, long and thin, not standing out from their articles, existing on femora, tibiae and metatarsi (absent on patellae and tarsi), the femora bear dorsal

bristles, usually 4 on III-IV, tibia I bears usually 3 pairs of long ventral bristles and few laterals; coxa-trochanter autotomy. Trichobothria absent on tarsi, a single one exists on all metatarsi (a long trichobothrium in a position of 0.95), few long ones on the tibiae, tarsal organs elevated. – Pedipalpus (fig. 72): articles long and slender, tarsal claw long. – Opisthosoma (photos) about twice as long as wide, hairs short, lateral light band absent or not recognizable, tracheal spiracles not observable, 3 pairs of spinnerets which are well developed.

**Relationships and distribution:** See *B. crassus* n. sp.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

***Burmorsolus crassus* n. gen. n. sp.** (figs. 74-77) photo 37

Etymology of the species name: From *crassus* (lat.) = thick, according to the thick leg bristles and the relatively thick leg articles.

**Material:** Holotype, a most probably adult female in Mid Cretaceous Burmite, F2611/BU/CJW.

**Preservation and syninclusions:** The spider is incompletely preserved and partly decomposed, enclosed in a yellowish (slightly greenish) piece of amber. The opisthosoma is lost, some leg articles are lost or loose, the dorsal part of the prosoma is partly cut off or hidden, most articles of the left legs are preserved, some parts are deformed. – A tiny Acari – body length 0.2 mm – and particles of detritus are preserved in the same piece of amber.

**Diagnosis** (♀; most probably adult in my opinion): Leg bristles well developed/thick (figs. 74-75), tibia I relatively thick, ca. 17 times longer than high in the middle.

**Description** (♀):

Measurements (in mm): Body length ca. 4.0, prosomal length 2.0; leg I: Femur 3.1, patella 1.0, tibia 3.0, tibia II 2.9, tibia III 1.7.

Colour dark grey, legs not annulated.

Legs (figs. 74-77, photo) only fairly long, I-II are distinctly directed forwards, bristles strong and probably more numerous than in *B. nonplumosus*.

**Relationships:** *B. nonplumosus* n. sp. is smaller, its leg bristles are distinctly thinner (see the figs.), its legs are more slender, tibia I is ca. 33 times longer than wide in the middle in the holotype (but only 25 times longer in the paratype F2656).

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

*Burmorsolus* sp. indet. (fig. 78), photo 42

**Material:** A most probably adult female in Mid Cretaceous Burmite, coll. HUANG-HP-1277.

**Preservation and syninclusions:** The spider is excellently and completely preserved in a clear yellow piece of amber, the prosoma is dorsally deformed (the cephalic part is depressed, the thoracic part is elevated), the legs III have a more prolateral position. – Two tiny winged insects are preserved near the surface of the piece of amber.

The prosomal length is about 2 mm, the legs are long and slender, its bristles relatively thick.

**Distribution:** Mid Cretaceous amber from Myanmar (Burma).

**Family OONOPIDAE** SIMON 1890 fig. 79, photo 36, family key no. 11, 16, 26

Members of this family are six-eyed two-clawed tiny spiders, their body length of amber fossils is only 1-2 mm (of extant spiders up to 4 mm). Their opisthosoma is soft (so the taxa known from the Mesozoic known today) or armoured (partly similar to Tetrablemmidae, see below). Like the small (body length 2.5-7 mm), similar and related Orsolobidae – they are unknown from the Mesozoic, see below: *Orchestina rabagensis* and above: The family Segestriidae. Their paired tarsal claws are biserially dentate, too, but a claw of the female pedipalpus is absent (it is almost always existing in the Orsolobidae), the margins of their fang furrow is usually toothless (usually exist two teeth on both margins in the Orsolobidae), and the claw tufts are usually not well developed (they consist of conspicuous spatulate hairs in the Orsolobidae). Furthermore the opisthosoma is soft in almost all Orsolobidae (scutate in *Duripelta* FORSTER), see JOCQUE & DIPPENARSCHOEMAN (2007), and their long legs are covered with long hairs.

Oonopidae is a very diverse and very old spider family which is widely distributed today and was already widely distributed in – probably all – Eocene and Cretaceous amber forests, see WUNDERLICH (2008: 53f).

From the Mesozoic only Cretaceous members of the subfamily Orchestinae are reported up to now, see the list above: *Burmorchestina* WUNDERLICH 2008 from Myanmar (Burma), *Canadaorchestina* WUNDERLICH 2008 from Canada and *Orchestina* from Spain (questionable, see below).

According to PLATNICK et al. the subfamily Gamasomorpinae is included in the Oonopinae. I am in doubt if this inclusion is really justified; such a taxon may be not monophyletic.

### Remarks:

(1) Members of two genera of the family Tetrablemmidae have been erroneously described by me as members of the subfamily Gamasomorphinae of the Oonopidae: (a) *Eogamasomorpha nubila* WUNDERLICH 2008 in Burmite, and (b) *Eoscaphiella ohlhoffi* WUNDERLICH 2011 in Burmite. See WUNDERLICH (2008: 172) and below, the family Tetrablemmidae.

(2) The only known specimen (female or juvenile) described as Oonopidae indet. by PENNEY (2002) in amber from New Jersey is so badly preserved that I am not sure about its family relationships.

### **Subfamily ORCHESTININAE**

This subfamily may easily be recognized by the distinctly thickened femur IV and the „segestriid“ eye position; distinct/long leg bristles are absent. It was widely distributed during the Mesozoic, see the list above and WUNDERLICH (2008).

Remark on *Orchestina rabagensis* SAUPE et al. 2012 – based on a single male in amber from France -: The long legs and the long leg hairs are quite unusual characters of *Orchestina* and even of the Oonopidae but similar in the family Orsolobidae. Therefore I am unsure about the relationships of this species.

***Burmorchestina pulcher*** WUNDERLICH 2008 (fig. 79) photo 36

*Burmorchestina* is the only known orchestinine genus which is known from Burmite. Only a single species – based on both sexes – has been described: *B. pulcher* WUNDERLICH 2008: 69-72, figs. 34-46, photos 66-70 (not figs. 33-43 as noted p. 69). Here I describe shortly or list five further females of this frequent species which may be conspecific:

F2688/BU/CJW, 1♀: The spider is completely preserved in a yellow-orange piece of amber, body and legs are deformed, the hairy legs are long, thinned by the preservation and stretched sideways, the femora IV are distinctly thickened.

Measurements (in mm): Body length 1.1, prosoma: Length 0.6, width 0.55, femur I ca. 0.7, tibia I ca. 0.6.

F2689/BU/CJW and F2690/BU/CJW, 2♀: Both females are 1.25 mm long and show clearly the strongly domed prosoma (fig. 79) as in the holotype, see WUNDERLICH (2008: 77, fig. 34); the opisthosoma of F2689 is twice as long as high.

Female F2689 is completely and very well preserved and observable near the surface of a yellow-orange piece of amber, the female F2690 is completely preserved in a muddy piece of amber, not well observable. Left directly in front of the spider and held by the left legs I and II an irregular and almost globular white object is preserved, 0.5 mm long, which may be a remain of a prey (remains of legs are not observable).

Measurements (F2689): Prosomal length 0.52, opisthosomal length 0.8; leg I: Femur ca. 0.3, patella 0.12, tibia ca. 0.23.

F2704/BU/CJW and F2705/BU/CJW, 2♀: Both females are well and completely preserved in yellow pieces of amber.

## **SUPERFAMILY PHOLCOIDEA (= SCYTODOIDEA)**

Included in this superfamily are the families (\*) Drymusidae, Eopsilodercidae (extinct), Ochyroceratidae s. str. (Ochyroceratinae and Theotiminae but excl. Psilodercinae which I regard as a family of its own), Pholcidae, Psilodercidae, Scytodidae, Sicariidae (Loxoscelinae and Sicariinae) and Tetrablemmidae. Eopsilodercidae is the only extinct family. The families Leptonetidae and Telemididae are excluded from my previous possible cladogram; see WUNDERLICH (2004: 645) and the superfamily Leptonetoidea below.

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(\*)The relationships of the enigmatic monotypic extant family Periegopidae SIMON 1893 (New Zealand) are quite unsure, see below.

Determination of the families: See the key above.

Remarks on three families which are (still) not known from the Cretaceous: Members of the family Pholcidae C. L. KOCH are known from the Eocene but not yet from the Cretaceous although the origin of this family PROBABLY goes back more than 200 million years, see DIMITROV et al. (2012); that is twice the age of the Burmese amber forest. The absence of leg bristles, the special eye position in lateral triads and a pair of small anterior median eyes (fig. 83) (they may be absent), the WIDELY fused chelicerae, the absence of spigots of the posterior (lateral) spinnerets and the existence of a special cymbium (the procurus) are good diagnostic characters of this family; which should be observable in Cretaceous fossils, too. – A Cretaceous proof of the families Drymusidae SIMON 1893 and Sicariidae KEYSERLING 1880 (Sicariinae and Loxoscelinae) are also



missing. The legs of these three families are bristleless, an unpaired tarsal claw is absent in the Sicariidae, and the leg position of this family is laterigrade. While Pholcidae has a complicated male pedipalpus the male pedipalpus of the remaining families is quite simple and the bulbus is located at the tip of the cymbium (like in the Eopsilodercidae and certain members of the Ochyroceratidae and Psilodercidae). In contrast to most Ochyroceratidae the clypeus is not protruding in the Drymusidae and the opisthosoma bears some short stiff setae in this family.

In contrast to these three families, in the extinct Cretaceous family Eopsilodercidae (see below) exists a quite long medial lamina along almost the whole length of the chelicerae, as well as a unique long and strong retroapical cheliceral bristle (fig. 84).

### **Unsure Pholcoidea:**

#### ***Furcembolusini* WUNDERLICH 2008**

The relationships of the extinct monotypic tribe Furcembolusini WUNDERLICH 2008: 582, figs. 20-22, photos 75-76, type species *Furcembolus andersoni* WUNDERLICH 2008, ♂, preserved in Mid Cretaceous Burmite, originally assigned with hesitation to the family Eopsilodercidae (see below) is quite unsure; it is not placed in a specific family of the Pholcoidea. Its prosoma is wrinkled, six eyes exist, the thoracic part is raised, the clypeus is long and vertical, the legs are bristleless, the bulbus is simple, the embolus is strongly bifurcated.

**?Pholcoidea or ?Oecobioidea or Leptonetoidea indet.** (figs. 80-81), photos 62-63

**Material:** 1♂ in stone from Liaoning (China), Cretaceous, without closer locality; F2455/LI/CJW.

**Preservation:** The spider is only fairly well incompletely and deformed – probably in a ventral position – preserved in a stone which is up to 17 cm long, see the photos. I did not recognize bivalved crustaceans (Conchostrata) but needle-shaped structures exist. Most tips of the spider's tarsi, the eyes, the chelicerae and the spinnerets are not preserved or only as remains.

#### **Description (♂):**

Measurements (in mm): Body length less than 4.0, prosomal length ca. 1.6; legs: I ca. 8.3, II ca. 5.8, III ca. 4.5, IV probably 5.0; leg I: Tibia ca. 1.7, metatarsus 2.0, tarsus >1.1; pedipalpal tibia: Length ca. 0.9, height about 0.4.

Colour grey brown.

Prosoma and Opisthosoma are strongly deformed, the chelicerae are probably fused for a long part.

Legs: Order most probably I/II/IV/III, I distinctly longest, III distinctly shortest. Bristles thin and numerous on femora, patellae (few), tibiae and metatarsi (fig. 80). Feathery hairs, leg scopulae and metatarsal preening combs absent. Metatarsus I may be pseudosegmented. Pedipalpus (fig. 81) fairly long, tibia thickened and probably with a strongly sclerotized apical tooth-like apophysis, cymbium fairly large, origin on the bulbus apparently near the middle of the cymbium, bulbus probably expanded, bearing at least three thin and strongly sclerotized sclerites.

The **relationships** are quite unsure. Unfortunately the incomplete preservation – metatarsus IV and the area of the probably existing cribellum – are not preserved. According to the absence of leg scopulae as well as metatarsal preening combs, thin leg bristles, and the thickened pedipalpal tibia the spider may be a member of the superfamily Pholcoidea sensu WUNDERLICH (2004). The existence of numerous leg bristles exclude the taxon from the family Pholcidae. In the families Psilodercidae and Ochyroceratidae – except the Theotiminae of the Ochyroceridae – the legs are distinctly longer and bear no or only few leg bristles. In *Althepus* THORELL 1898 (Psilodercidae), e. g., exists also complicated structures of the bulbus which reminds on the present taxon but the legs are much longer in *Althepus*. The thickened articles of the pedipalpus are similar to the Jurassic genus *Zhizhu* SELDEN et al. 2015 from China which has been published under Deinopoidea and which I regard as probably related to the Oecobioidea or the Mongolarachnidae (Leptonetoidea), see below.

**Behaviour:** According to the absence of leg scopulae and metatarsal preening combs as well as the long leg I and the short leg III the spider should have been a capture web dweller.

**Distribution:** See above, the material.

**Pholcoidea indet.** (fig. 82) photo 64

**Material:** 1 ?ad. ♀ in Mid Cretaceous Burmite and a separated piece of amber, F2633/BU/CJW.

**Preservation and syninclusions:** The spider's body is strongly deformed, apparently decomposed, the prosoma is depressed laterally, a large gas bubble comes out of the right side of the opisthosoma, the legs are complete.

**Description** (probably adult ♀):

Measurements (in mm): Body length ca. 1.0, prosomal length ca. 0.5, femur I 0.5, tibia I 0.42, tibia II 0.35, tibia III ca. 0.25, tibia IV 0.35.

Prosoma (fig. 82, photo 64) distinctly longer than wide, 6 eyes, clypeus protruding apparently caused by the preservation. Claw of the pedipalpal tarsus absent. Legs (photo) only fairly long, order I/?IV/II/III, femur I as long as the prosoma, patellae quite

short, metatarsi distinctly longer than the tarsi; covered with long hairs, bristles absent. Opisthosoma (fig. 82, photo) almost globular after the deformation but originally apparently oval, bearings partly longer hairs, spinnerets short.

The **relationships** are quite unsure; a male of the taxon is needed. According to the long clypeus, the slender and bristleless legs and the six eyes I regard the spider as a member of the superfamily Pholcoidea. According to the relatively short legs I do not want to exclude that it may be a member of the Ochyroceratidae: Theotiminae. In the Ochyroceratinae, the Psilodercidae and the Eopsilodercidae the legs are distinctly longer.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

**Family EOPSILODERCIDAE** WUNDERLICH 2008 (**stat. restored**) figs. 84-90, photos 51-54, family key no. 27

A recently discovered specimen of this family, the male holotype of *Eopsilodermes serenitas* n. sp., – which is excellently preserved, the mouth parts and the copulatory structures are very well preserved and recognizable (fig. 84, photos 51-52) – lead me to new conclusions on the genus *Eopsilodermes*, and indicate that not the families Ochyroceratidae or Psilodercidae but Sicariidae and Drymusidae may be most related to the family Eopsilodercidae which I again regard as a family of its own (**stat. restored**) but not as a subfamily of the Psilodercidae or Ochyroceratidae. *Furcembolus* WUNDERLICH 2008: 582: See above, unsure Pholcoidea.

Type genus (the only known genus of this family): *Eopsilodermes* WUNDERLICH 2008. The genus *Leclercera* DEELEMANN-REINHOLD 1995 in Burmite – see WUNDERLICH (2012: 178-180) – is not confamiliar with *Eopsilodermes* but is a member of the Psilodercidae, see below. *Furcembolus*: See above (questionable Pholcoidea).

Revised **diagnosis** of the extinct monotypic family Eopsilodercidae (♂; see the description of a probably confamiliar female below):

A medial lamina exists in almost the whole length of the chelicerae which are basally fused together (figs. 84-85), the basal cheliceral articles bear a strong and long retroapical bristle (figs. 84, 89) which may be a „clasping spine“. Pedipalpus (fig. 84): Bulbus simple, almost globular (\*), attached at the tip of the cymbium (tarsus), conductor absent, embolus long and thin.

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(\* ) The right bulbus of the type species *E. loxosceloides* is deformed and lengthened artificially – see WUNDERLICH (2008: 660, fig. 18) in contrast to the almost globular left bulbus of this species and of other congeneric species.

Further characters: Cephalic part abruptly narrowed (fig. 85), low but not flat, clypeus fairly protruding, gnathocoxae long and strongly converging, labium quite large, with a seam to the sternum which is wide as long and widely separating the coxae IV (fig. 86), lateral files absent, fangs small and slender, eyes (figs. 85-86) in three diads in a wide field, clypeus only fairly long, legs long and slender (photo), I longest, position prograde, true spines or bristles absent but bristle-shaped long and straight hairs exist at least in *E. serenitas* (fig. 87), paired tarsal claws toothed (not recognized by me in *E. loxosceloides*), unpaired claw apparently absent, a long hair exists in a similar position (fig. 88), lung covers existing, three pairs of spinnerets, pedipalpal tibia long and thickened.

### **Relationships:**

In 2012: 177 I synonymized the Eopsilodercidae WUNDERLICH 2008 with the elevated Psilodercidae DEELEMANN-REINHOLD 1995 which was upgraded from the subfamily rank of the Ochyroceratidae FAGE 1912 by me (2008: 585).

According to the quite small fangs, the basally fused basal cheliceral articles, the not elongated cymbium, the apical cymbial position of the alveolus and the simple and almost globular shape of the bulbous which lacks a conductor (\*) Eopsilodercidae is a member of the „scytodid hunters branch“, see WUNDERLICH (2004: 645) (\*). According to the strongly reduced or even absent unpaired tarsal claw Eopsilodercidae seems most related to the Sicariidae in which the prosoma is flattened, a long medial cheliceral lamina is absent (only an apical tooth-shaped outgrowth exists), a distinct fovea and cheliceral stridulatory files exist. Furthermore members of the Sicariidae are much larger, their body length is ca. 6-20 mm.

Besides these characters the large labium points to strong relationships to the families Drymusidae (and the Sicariidae as well). In both families – as well as in the Scytodidae in which the cymbium is elongated and the prosoma is domed – a medial lamina along the chelicerae and a cheliceral „clasping spine“ are absent. In the Drymusidae furthermore the labium is almost as long as the sternum and the opisthosoma bears stiff setae. – In the Psilodercidae and the lungless Ochyroceratidae (see below) the basal cheliceral articles are free, a long cheliceral lamina and a cheliceral „clasping spine“ are absent, the clypeus is usually very long and distinctly protruding (less in the Theotiminae of the Ochyroceratidae).

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(\*) These characters are added herewith for the branch of the „scytodid hunters branch“, which – if it really is a branch of its own – needs another name: the „scytodid branch“, because Drymusidae, certain Scytodidae and probably members of the Eopsilodercidae build capture webs. An apomorphic character of this branch may be the loss of the anterior median eyes in contrast to the sister branch – see WUNDERLICH (2004: 645) -, in which basically 8 eyes exist: In the Pholcidae. This branch may be called „pholcid branch“. The inclusion of Ochyroceratidae + Psilodercidae which apomorphically lost their anterior median eyes (Ochyroceratidae lost additionally its lungs) appears unsure to me, and probably the Pholcidae has to transfer to the scytodid branch because of the fused chelicerae. – Leptonetidae and Telemidae were previously included in this branch but are now transferred in the superfamily Leptonetoidea, see below. In the Scytodidae the alveolus possesses a more basal position in contrast to the remaining related families – a plesiomorphic character? – A simplified bulbous – without conductor(s) (and attached in an apical position of the cymbium) – evolved several times within the superfamily Pholcoidea besides the Eopsilodercidae and Sicariidae: In certain members of the families Ochyroceratidae and Psilodercidae.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

Type species: *Eopsilodermes loxosceloides* WUNDERLICH 2008.

Further species: *E. filiformis* (WUNDERLICH 2012) (**n. comb.**) (= ?*Psilodermes f.*) and *E. serenitas* n. sp.

REMARK: According to the recently discovered – previously overlooked – strong retro-lateral cheliceral spine (fig. 89) *filiformis* is a member of the family Eopsilodercidae but not of the Psilodercidae in which it originally has been placed with a question mark (n. comb.).

**Diagnosis:** See the family Eopsilodercidae above.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

***Eopsilodermes serenitas* n. sp.** (figs. 84-88) photos 51-52

Etymology: From serenitas (lat.) = clearing-up; regarding the importance of this male holotype for clearing the relationships of this genus and this family.

**Material:** Holotype ♂ in Mid Cretaceous Burmite, and a separated piece of amber, F2551/BU/CJW.

**Preservation and syninclusions:** The spider is incompletely but partly very well preserved; both legs IV and the left legs I-II are lost beyond the coxa by autotomy, the right leg I is complete, the left leg II is cut off through the metatarsus, the opisthosoma is deformed, translucent, partly empty, bearing inside a dark inclusion, and a bubble on the dorsal surface. – In the separated piece of amber 1 Acari, remains of a tiny insect, insect's excrement, plant stellate hairs and a small spider's peltidium which possesses 6 or 8 eye lenses (the anterior median eyes are not surely recognizable), width 1.25 mm (Pholcoidea?) are preserved. From the same piece of amber I separated the male holotype of *Longissipalpus minor* n. gen. n. sp. (Pholcochyroceridae), F2549/BU/CJW.

**Diagnosis** (♂; ♀ unknown): Tibia I bears a row of 5 retrolateral bristle-shaped hairs (fig. 87); pedipalpus: Fig. 84.

**Description** (♂):

Measurements (in mm): Body length 1.25, prosoma: Length ca. 0.65, width ca. 0.5; tibia I 1.1; opisthosoma: Length ca. 0.6, width ca. 0.45.

Colour light grey brown.

Prosoma (figs. 84-85) crumpled, 1.3 times longer than wide, cephalic part distinctly narrowed, fairly low/convex, hairs partly long, fovea indistinct or even absent, six eyes

of three diads in a wide field, covered with an emulsion, clypeus not long and not protruding, chelicerae robust, in an unnatural deformed diverging position, fused at their base, lateral files absent (I regard widely spaced lateral „files“ in the basal half as artefacts caused by the preservation; a stridulatory pick on the pedipalpal femur is absent), teeth of the fang furrow not recognizable, medial lamina existing almost along the whole cheliceral length, retroapically with a strong and long bristle (apparently a „clasping spine“), fangs at most parts hidden, probably stout, gnathocoxae long, slender, strongly converging, touching in the middle, serrula existing, labium very large, not rebordered, with a seam to the sternum which is as wide as long and widely spacing the coxae IV. – Legs (figs. 87-88, photos) very long and slender, bristles absent but tibia I bears a RETROLateral row of 5 long and straight bristle-shaped hairs, tibiae longer than femora and metatarsi, tarsi quite short, only at most 1/3 the metatarsal length, hairs not dense, of medium length, onychium well developed, paired tarsal claws bearing long teeth, unpaired claw absent or strongly reduced, a long hair-shaped structure exists. – Opisthosoma (photo) strongly deformed, oval, bearing stronger hairs, spinnerets apparently retracted, short, most probably three pairs, lung covers and tracheal fold not surely recognizable. – Pedipalpus (fig. 84): Femur long, patella short, tibia long and fairly thickened, cymbium only fairly long, bearing long retrolateral hairs, position of the alveolus apically, bulbus almost globular, conductor absent, embolus long, thin and bent. In *E. filiformis* the embolus is longer and stronger bent distally.

**Relationships:** In *E. loxosceloides* WUNDERLICH 2008 retrolateral bristle-shaped hairs on tibia I are absent; with a body length of 1.8 mm *loxosceles* is distinctly larger than *serenitas*.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

*Eopsilodermes* sp. indet. photos 53-54

**Material:** 1♂ in Mid Cretaceous Burmite, F2634/BU/CJW.

**Preservation and syninclusions:** The spider is completely and well preserved in a larger clear yellow-orange piece of amber. – 1 Acari, a tiny four-winged insect, numerous stellate plant hairs and tiny bubbles as well as a movable gas bubble in fluid (water?) are also preserved.

#### **Description (♂):**

Measurements (in mm): Body length at least 1.3, tibia I and IV almost 1.0.

Colour medium grey.

Body, legs and pedipalpus quite similar to *E. loxosceloides* WUNDERLICH 2008 but a smaller body exists, and the prosoma bears numerous long and erect hairs.

**Relationships:** I do not want to exclude the conspecificity with *E. loxosceloides*.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

?*Eopsilodermes* sp. indet. (fig. 90)

**Material:** 1♀ in Mid Cretaceous Burmite, F2755/BU/CJW.

**Preservation and syninclusions:** The spider is well and completely preserved in a clear yellow piece of amber. Several air/water bubbles exist on certain leg articles, few fissures within the amber hinder the view mainly on the dorsal part of the body.

**Description:**

Measurements (in mm): Body length 2.7, prosoma: Length 1.2, width 0.85; opisthosoma: Length 1.9, width 1.05; leg I: Femur 1.9, patella 0.3, tibia 1.5, metatarsus 1.3, tarsus 0.5, tibia II 1.5, tibia III 0.9, tibia IV 1.4.

Colour yellow brown.

Prosoma (fig. 90) 2.25 times longer than wide, not raised, cuticula finely corniculate, cephalic part distinctly narrowed, 6 eyes (the eye field is partly hidden), clypeus long, only slightly protruding, basal cheliceral articles long, fused basally, median lamella not observable, gnathocoxae long and strongly converging, labium long and free. – Pedipalpus long, slender and spiny. – Legs only fairly long and slender, bristleless but long and straight bristle-like erect dorsal hair exist on the right femora III and IV; the corresponding hairs on the left femora III and IV are thinner and slightly bent. Unpaired tarsal claw and onychium well developed. – Opisthosoma 1.8 times longer than wide, hairs not numerous, of medium length.

**Relationships:** The characters of body and legs are as in *Eopsilodermes* but a median cheliceral lamella is not observable in the present female because of its preservation.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

**Family PSILODERCIDAE** DEELEMEN-REINHOLD 1995 figs. 91-100, photos. 55-61, family key no. 27

(See the typical characters listed in the key below, and the family Eopsilodercidae above in which certain similar characters exist).

In 2008: 585 I elevated Psilodercinae DEELEMEN-REINHOLD 1995 to family rank from Ochyroceratidae FAGE 1912 in which book lungs are replaced by tracheae. Theotimiinae DEELEMEN-REINHOLD 1995 may be a subfamily of the Ochyroceratidae or a family of its own in my opinion.



Here I describe a second genus besides *Leclercera*: *Propterpsilodermes*, which I regard with some hesitation as a member of the Psilodercidae, too, but which structures of the male pedipalpus are quite different.

Remarks: (1) According to DEELEMEN-REINHOLD (1995: 6) the labium is rounded in the Psilodercinae in contrast to the Ochyroceratinae and Theotiminae sensu DEELEMEN-REINHOLD in which it is incised, but in the Psilodercine *Althepus pum* DEELEMEN-REINHOLD 1995: Fig. 190 the labium appears incised.

(2) The dubious tribe Furcembolusini WUNDERLICH 2008: 582 in Burmite – in which the prosoma is distinctly wrinkled, the clypeus is not protruding and has a vertical position – is regarded as a taxon of the superfamily Pholcoidea with unsure relationships; it is not placed in a specific family.

(3) The three taxa in question may be differentiated by the characters of the **key below**. The absence of lungs in the Ochyroceratidae – in contrast to the Psilodercidae – is usually not recognizable in the fossils. Only members of the Psilodercidae are surely reported from the Mesozoic up to now, but see the remark on a questionable fossil member of the Theotiminae in the key below. The similar extinct family Eopsilodercidae: See above and the family key no. 27.

1 Prosoma about as long as wide, clypeus very long and strongly protruding (figs. 97, 99), legs long, femur I two or more times the length of the prosoma (up to 6 times in extant spiders), promargin of the fang furrow with 0-3 teeth in *Leclercera* (fig. 93). Pedipalpal femur with (pro)ventral spines (figs. 91, 96) or bristles (fig. 100). Cymbium dorsally-apically spiny or horny, in *Leclercera* more basally with a very long bristle which is strongly bent at its end (figs. 92, 98). Bulbus structures very complicated (figs. 95, 98) or simple (fig. 100) in *Propterpsilodermes*. . . . . PSILODERCIDAE

- Similar but promargin of the fang furrow with 6-7 teeth. Bulbus oval, not globular; its structures very variable. . . . . OCHYRO CERATIDAE: OCHYRO CERATINAE

- Prosoma 20-30 % longer than wide, clypeus short, vertical, not distinctly protruding, legs shorter, femur I usually shorter than two times of the prosoma. Tibia III may bear bristles in *Spheocera*, the opisthosoma may be stout. Bulbus globular, attached basal of the end of the cymbium (\*). – A single female in Burmite which relationships are unsure, F2633/BU/CJW. . . . . OCHYRO CERATIDAE: THEOTIMINAE

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(\* ) The ♂-chelicerae may be modified and bear retrolateral stridulatory files like in *Spheocera micrphthalma* sensu BRIGNOLI 1979: Figs. 2, 4. In the male of the Theotiminae *Althepus machadoi* BRIGNOLI 1973: Fig. 4 retrolateral cheliceral files are drawn but not mentioned in the description.

*Leclercera* is the only known fossil genus of this family; see WUNDERLICH (2012: 178-180) with the descriptions of *L. longissipes* and *L. spicula*.

**Diagnosis and relationships:** The genus *Leclercera* is mainly diagnosed by the „double row of teeth“ of the fang furrow (fig. 93; the posterior teeth are quite tiny), and the „retrolateral apophysis on either the tibia or the tarsus“ (= cymbium) by DEELEMEN-REINHOLD (1995: 45). Tiny posterior teeth of the fang furrow exist in the fossils, and a strong retrolateral bristle („apophysis“) of the pedipalpal cymbium exists, too (fig. 98). Male pedipalpal femoral spines – similar to the fossils in Burmite, figs. 91, 96, – exist in *Leclercera spinata* DEELEMEN-REINHOLD 1995: Fig. 133 from Indonesia, in which a long cymbial bristle is absent and the structures of the bulbus are quite different. In the type species of *Leclercera* – *L. khaoyai* DEELEMEN-REINHOLD 1995 from Thailand – a short retrolateral cymbial spoon-shaped outgrowth exists, and the structures of the bulbus are more simple. A tarsal claw of the female pedipalpus is absent.

The fossils of the present species group are characterized mainly by the long retrolateral cymbial bristle and the complicated structures of the bulbus (fig. 98, photo) in contrast to the second genus in Burmite, *Propterpsilodermes* n. gen.

**Habitat of extant spiders:** According to DEELEMEN-REINHOLD (1995: 45) the spiders of *Leclercera* live „under roots of big trees and in riverbanks“ in an „open area in evergreen forest“, „on forest ridge“ and in caves.

**Behaviour of extant spiders:** According to DEELEMEN-REINHOLD (1995) the spiders construct sheet webs. A female of *Leclercera khaoyai* was observed „with egg sac holding between chelicerae, palps and sternum.“.

**Distribution:** Fossil: Mid Cretaceous Burmite; extant: SE-Asia including countries near Myanmar (Burma) like Thailand.

*Leclercera spicula* WUNDERLICH 2012 (figs. 91-92)

Here I add two figs. to the original description of the holotype, the ventral aspect of the right pedipalpal femur which bears four strong spines, and the long bristle of the left cymbium in an almost retrolateral aspect, to show its strongly bent tip.

Derivatio nominis: With pleasure I name this species after SIGHARD ELLENBERGER in Kassel who selected this excellently preserved male for my study (and numerous other spiders as well) from a huge number of pieces of Burmese amber.

**Material**: Holotype ♂ together with a probably conspecific juvenile female (see below, „syninclusions“) in Mid Cretaceous Burmite, F2449/BU/CJW.

**Preservation and syninclusions including a probably conspecific juvenile female**: The holotype is well preserved but partly deformed, enclosed in a larger piece of clear yellowish amber, the right legs II and III are lost beyond the coxa by autotomy, the right anterior leg is stretched forward. – Translucent remains of a probably conspecific juvenile female – body length 1.4 mm, length of tibia I 1.35 mm, position of the metatarsal I trichobothrium in 0.65, claw of the pedipalpal tarsus absent – is preserved near the holotype. Also preserved are spider's threads, 3 spider's legs, 1 Archaeognatha as well as several Acari, Coleoptera, Diptera, Hymenoptera and plant remains.

**Diagnosis** (♂): Pedipalpus: Femur (fig. 94) with three strong prolateral bristles in the distal half, and a weak one more basally, structures of the bulbus as in fig. 95. Anterior leg very long.

**Description** (♂):

Measurements (in mm): Body length 1.5, prosomal length ca. 0.6; leg I: Femur 2.5, patella 0.25, tibia 2.7, metatarsus ca. 2.0, tarsus 0.75; tibia II ca. 2.4, tibia III ca. 1.5, tibia IV 2.3.

Colour: Prosoma dark brown, legs medium brown (not annulated), opisthosoma grey brown.

Prosoma (fig. 93, photos) probably as long as wide like in *L. longissipes* (probably not wider than long as stated in the original description, see WUNDERLICH (2012: 179) (it is distinctly deformed, parts are hidden), 6 eyes in a fairly narrow field, basal cheliceral articles long, free apparently even at their base, diverging, lamina well developed, fangs long and slender, fang „furrow“ with 3 anterior teeth and 3 posterior denticles. – Legs (photos) very long and slender, order I/II/IV/III, III distinctly shortest, tarsi not pseudosegmented, bristleless, two kinds of hairs: Most hairs are short and not distinct, – but e. g. on the metatarsi – long, almost bristle-shaped and more erect hairs exist mainly dorsally and laterally. Position of the metatarsal I trichobothrium in 0.75. Three tarsal claws, paired claws toothed. – Opisthosoma (photos) (it is deformed) oval, bearing few hairs of medium length. Posterior spinnerets long and close together. – Pedipalpus (figs. 94-95, photos): Femur slender, bearing three strong prolateral bristles in the distal half and a weak one more basally, patella short, tibia thick, dorsally-apically bearing an unsclerotized almost globular questionable sensory organ, cymbium large, bearing at least two apical spines (probably additional ventral spines are not observable), bulbus large, bearing complicated structures; I did not identify the embolus besides the conductor(s).

**Relationships:** In *L. longissipes* WUNDERLICH 2012 and *L. spicula* WUNDERLICH 2012 – the only known further fossil species – the legs are shorter and the structures of the bulbus are different; in *spicula* furthermore ventral spines exist on the cymbium.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Birma).

*Leclercera sexaculeata* n. sp. (fig. 96), photo 58

**Etymology:** The name refers to the six proventral spines of the pedipalpal femur, sex (lat.) = six, aculeatus (lat.) = thorny, spiny.

**Material:** Holotype ♂ in Mid Cretaceous Burmite from N-Myanmar, F2711/BU/CJW.

**Preservation and syninclusions:** The spider is well preserved in a clear yellow-orange piece of amber, situated between two narrow flows of amber, and thus flattened; only the right metatarsus and tarsus II and the tip of the right tarsus I are cut off. The body – especially the inclined opisthosoma – are deformed, the sternum bears a white emulsion. – Syninclusions: A probably juvenile questionable member of the spider family Theridiosomatidae, body length 1.1 mm, 1 Hymenoptera, 1 Diptera and plant hairs.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (fig. 96): Femur with 6 proventral spines in a single row, probably exist additional retroventral spines, bulbus with a brush of at least 7 long and strong bristle-shaped hairs.

### **Description** (♂):

Measurements (in mm): Body length 1.5, prosomal length ca. 0.6; leg I: Femur 2.3, patella 0.25, tibia ca. 2.6, metatarsus ca. 2.6, tarsus ca. 0.6, tibia II 1.9, tibia III 1.2, tibia IV ca. 1.9.

Colour yellow brown.

Prosoma (photo) about as wide as long, most parts are deformed or hidden, clypeus long and protruding, basal cheliceral articles fairly large and diverging. – Legs long and slender, III distinctly the shortest, bristles absent but few stronger hairs exist. Position of the metatarsal trichobothria unknown. – Opisthosoma (photo) twice as long as wide, hairs short, anterior spinnerets short and close together at their base. – Pedipalpus (fig. 96): Femur slender, bearing 6 proventral spines in a single row, additional retroventral spines may exist, patella short, tibia thickened, cymbium with a long and strong retro-lateral bristle which stands out, bulbus oval, bearing a long sclerite which is „splitted“ apically, and with a brush of at least 7 long and bristle-shaped hairs.

**Relationships:** A brush of long and bristle-shaped hairs of the bulbus and a row of 6 proventral spines of the pedipalpal femur are absent in the congeneric species which possess spines in an irregular position.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

?*Leclercera* sp. indet. (fig.97) photo 61

**Material:** 1♀ in Burmite, F2631/BU/CJW.

**Preservation and syninclusions:** The spider is fairly well preserved near the surface of a larger clear piece of amber, its body is deformed, the right legs I and II and the left leg I are lost beyond the coxa by autotomy. – 2 tiny Coleoptera, some tiny insects, parts of a Blattodea, 1 Acari, insect's excrement and plant hairs are also preserved.

**Description** (♀):

Measurements (in mm): Body length ca. 1.5; leg II: Femur 1.55, patella 0.18, tibia 1.65, metatarsus 1.9, tarsus 0.7, tibia III 1.05, tibia IV 1.6.

Colour: Prosoma and legs medium brown, opisthosoma light grey.

Prosoma (it is deformed) probably as long as wide, bearing few long hairs, 6 large eyes, clypeus very long and protruding, basal cheliceral articles (fig. 97) long, slender, free and diverging, bearing a prodistal bristle, teeth of the fang furrow and mouth parts hidden. – Pedipalpus long and slender, bearing long hairs, tarsal claw absent. – Legs long and slender, order probably I/IV/II/III, bristleless, most hairs short and indistinct, the right tibia II bears two larger dorsal bristle-shaped hairs. Position of the long metatarsal IV trichobothrium in ca. 0.55. Paired tarsal claws toothed, unpaired claw well developed. – Opisthosoma almost three times longer than high, bearing few long hairs; posterior spinnerets long.

**Relationships:** I am not sure about the existence of a double row of teeth/denticles of the fang furrow; therefore I do not want to exclude that the female may be a member of another genus.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Birma).

*Leclercera* sp. indet. (fig. 98)

**Material:** 1♂ in Burmite, F2632/BU/CJW.

The spider is completely and strongly deformed preserved in a clear piece of amber which also includes several pear-shaped „bubbles“ – probably remains of boring shells – which are connected with the surface of the amber piece.

The body length of the spider is 1.6 mm, the right tibia I is 2 mm long. The structures of the right pedipalpus (fig. 98) are well preserved but partly deformed, similar to *L. longissipes* WUNDERLICH 2012, which may be conspecific.

Leclercera sp. indet.

**Material:** 1♂ near a wasp in Burmite and two separated pieces of amber, F2652/BU/CJW:

The spider is distinctly depressed, the left legs are well preserved, the pedipalpi are difficult to observe.

Measurements (in mm): Body length ca. 1.5; leg I: Femur 2.2, patella 0.2, tibia 2.2, metatarsus 2.0, tarsus 0.55, tibia II 2.1, tibia III 1.3, tibia IV ca. 2.0.

Leclercera sp. indet.

**Material:** 1♂ preserved in the same piece of Burmite as a female Archaeidae, F2709/BU/CJW.

The spider is incompletely preserved and deformed, most leg articles and most parts of the left pedipalpus are cut off.

Body length 1.5 mm, length of leg I (it is completely preserved) ca. 10.5 mm. Ventral spines on the pedipalpal femur: 1 in the middle, a pair near the end, and 1 in the middle between both.

**Propterpsiloderces** n. gen.

**Etymology:** The name refers to the relationships of the new genus to the genus *Psiloderces* FAGE, and propter (lat.) = besides. – The gender of the name is masculine.

**Type species** (by monotypy): *Propterpsiloderces longisetae* n. sp.

**Diagnosis** (♂; ♀ unknown): Prosoma with very long dorsal erect hairs, outgrowths of the clypeus absent (fig. 99), pedipalpus (fig. 100): Cymbium „bifurcate“ apically, bulbus globular, embolus very long, additional sclerites absent.

**Relationships:** According to its characters – e.g. the long clypeus and certain structures of the male pedipalpus – I regard *Propterpsiloderces* with some hesitation as a member of the Psilodercidae. In *Psiloderces* FAGE 1892 the structures of the male pedipalpus are very diverse but a bifurcate cymbium is absent. In my opinion – in

spite of its characters, mainly of the diverse structures of their male pedipalpus – *Psiloderces* has to split up in the future. Today this genus is widely distributed in SE-Asia.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

***Propterpsiloderces longisetae* n. gen. n. sp.** (figs. 99-100)

**Etymology:** The species name refers to the long dorsal erect prosomal hairs, from *longus* (lat.) = long and *setae* (lat.) = hairs.

**Material:** Holotype ♂ in Mid Cretaceous amber from N-Myanmar (Burma), F2710/BU/CJW.

**Preservation and syninclusions:** The spider is incompletely preserved and partly decomposed, partly hidden by a large Auchenorrhyncha, most parts of 6 legs are preserved, most parts of the body are distinctly deformed, the right pedipalpus is lost, ventrally of the left pedipalpal femur is a small rod-shaped particle preserved which I regard as a remain of a plant but not part of the pedipalpus. – Diverse Hymenoptera, several Acari, a small juv. Araneae indet., a larger Auchenorrhyncha, Diptera, Collembola, remains of plants, detritus and particles of earth are also preserved in the piece of amber.

**Diagnosis** (♂; ♀ unknown): See the genus.

**Description** (♂):

Measurements (in mm): Body length 3.0, prosomal length 1.4, opisthosoma: Length 1.6, height 0.8; leg I ca. 11.5, patella 0.4, tibia 3.5, femur III 2.4, leg IV: Femur 3.5, patella 0.4, tibia 3.0, metatarsus 3.0, tarsus ca. 0.6; length of the embolus at least 0.35. Colour mainly grey brown, opisthosoma dark grey.

Prosoma (fig. 99; it is deformed and partly hidden) only fairly high, dorsally with numerous very long and erect hairs, eyes hidden, clypeus long, chelicerae and fangs fairly long. – Legs very long (see above), order probably I/II/IV/III, patellae and tarsi short, bristleless, hairs not long or distinct, position of the metatarsal trichobothria unknown, unpaired tarsal claw existing. – Opisthosoma twice as long as high. – Pedipalpus (fig. 100): Patella short, tibia fairly thickened, paracymbium short, bifurcate apically, bulbus small and globular, attached apically on the cymbium, embolus very long, slightly bent, additional sclerites absent.

**Relationships:** See above. Very long erect dorsal prosomal hairs exist also in the extant species *Psiloderces fredstonei* DEELEMEN-REINHOLD 1995 from Thailand, in which the structures of the male pedipalpus are quite different.



**Ecology:** Most extant Psilodercidae live in leaf litter, see DEELEMEN-REINHOLD 1995. According to the partly decomposed rod of *P. longisetae*, the partly decomposed Auchelorrhyncha, particles of detritus and earth in the same piece of amber the spider most likely lived in leaf litter.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

**Family SCYTODIDAE** BLACKWALL 1854 fig. 101, family key no. 27

Most members of this six-eyed „Spitting Spiders“ are easily recognizable by their domed prosoma (fig. 101); their legs are bristleless. The family has a cosmopolitical distribution, most species live in the tropics. The first mesozoic member, a probably adult female, of this family has been recently described from Jordan as a questionable member of the very diverse genus *Scytodes* LATREILLE 1804, ?*Scytodes hani* WUNDERLICH 2012.

**Family TETRABLEMMIDAE** O. PICKARD-CAMBRIDGE 1873 figs. 102-133, photos 43-50, family key no. 16

Tetrablemmidae are tiny to small strongly armoured spiders in which leg bristles are absent, see WUNDERLICH (2012: 172) and the photos. Besides the Caponiidae, Palpimanidae and Pholcidae – in certain members of these families exist even the basal four pairs of eyes – the Tetrablemmidae is the spider family in which the largest variability of the number of eyes exist (but never 8 eyes), see LEHTINEN (1981): Usually 4 or 6 eyes (apparently the plesiomorphic number of 6 eyes exists in all known spiders in Burmite), occasionally 2; a single eye exists in a species of the genus *Monoblemma*; eyes even may be completely absent in certain species.

### **Relationships:**

In my opinion the family is a member of the pholcoid branch of the Dysderoidea s. l., see fig. F. Pholcidae may be most related, see MICHALIK (2014); in both families leg bristles are absent, tracheae are reduced or even absent, the cheliceral lamella is well developed, the male chelicerae bear usually outgrowths IN THE EXTANT TAXA, a tarsal claw

of the female pedipalpal tarsus is absent, and an egg-carrying behaviour with the help of the chelicerae by females – an important character of the pholcoid branch – has recently been documented within the ancient subfamily Pacullinae by KOH & MING (2013: Fig. p. 251) in a member of the genus *Lamania* LEHTINEN 1981, in contrast to the derived subfamily Tetrablemminae. In the Pholcidae the body is soft (as in the Ochyroceratidae which is related, too), the prosoma is not rugose, the chelicerae are partly (basally) fused, the tarsus IV bears a ventral comb of +/- serrated hairs, certain threads of the capture web bear sticky droplets, and the structures of the copulatory/genital organs are quite different in both sexes. Both families may be regarded as sister taxa if only extant families are taken in consideration but their various important differing characters must be caused by various particular steps during the long evolution of these families and their relatives; therefore a „true“ sister taxon of the Tetrablemmidae should be found within Mesozoic extinct spiders in the future. Furthermore the apparent absence of the Pholcidae in the Mesozoic – the oldest proof comes from Eocene Baltic amber – may indicate a much lower age of the Pholcidae compared with the Tetrablemmidae.

The tropical Tetrablemmidae apparently was a diverse family in the Mid Cretaceous as documented by amber from Myanmar (Burma), and members most probably existed in other tropical or subtropical parts of the former world. The more derived subfamily Tetrablemminae was already known from the Cretaceous; members of the second subfamily – the Pacullinae – are reported here for the first time as fossils.

Three monotypic genera and a male of a gen. indet. have previously been described of the subfamily Tetrablemminae, see WUNDERLICH (2012: 172-176). See below the remarks on the misleading names of the genera *Eascaphiella* and *Eogamasomorpha* which originally have been described erroneously by me as members of the family Oonopidae. Questionable parts of capture webs are preserved with a female of the Tetrablemminae indet., F2695/BU/CJW, and with the male holotype of *Praeterpaculla equester*, see below.

Now I know the following number of Cretaceous taxa of the Tetrablemmidae (all are reported in Burmite):

- (1) Pacullinae: A single genus: *Praeterpaculla* n. gen., 5 species.
- (2) Tetrablemminae: 5 genera, 7 species (one is unnamed).

### **Characters and differences of the subfamilies of the family Tetrablemmidae:**

Partly taken from LEHTINEN (1981: 10-11), modified.

#### **(1) Pacullinae:**

- (a) Body length 3-9.5 mm.
- (b) Position of the metatarsal I-II trichobothrium in 0.5 (e. g. in the fossils) – 0.75.

- (c) Number of the eyes: 6.
- (d) Eye region and clypeus: Unmodified.
- (e) Egg sac carried with the help of the chelicerae (like, e. g., in the Pholcidae).

## (2) Tetrambleminae:

- (a) Body length usually 0.7-2 mm but see *Uniscutosoma* (2.3 mm).
- (b) Position of the metatarsal I-II trichobothrium in 0.33-0.5 (\*).
- (c) Number of the eyes: Most often 4 or 6 (6 in the fossils), rarely 0, 2 or 1.
- (d) Eye region and clypeus usually bearing outgrowths at least in extant taxa.
- (e) Egg sac fixed in the center of the capture web so far known today.

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(\*) In the holotype of *Eogamasomorpha nubila* WUNDERLICH 2008 the position of the metatarsal trichobothrium has been reported as being near the end of the article but now I regard the hair in question as a different kind of sensory hairs.

## (1) Subfamily PACULLINAE

(See the new genus *Uniscutosoma* below which relationships are unsure).

### **Praeterpaculla n. gen.**

**Etymology:** The name refers to the related genus *Paculla* SIMON 1887, from *praeter* (lat.) = besides. – The gender of the name is feminine.

**Type species:** *Praeterpaculla tuberosa* n. sp.

**Diagnosis** (♂; ♀ unknown): No modifications of the prosoma or the basal cheliceral articles; pedipalpus (102-111): Tibia with a ventral-apical apophysis (fig. 106), bulbus small.

**Further characters:** Metatarsal IV trichobothrium existing at least in *P. equester*, its position in 0.5-0.52, cymbium undivided or bilobed (fig. 102), embolus long, it may bear a bristle-shaped apophysis.

**Relationships:** According to the larger body size, the position of the metatarsal trichobothrium and the long leg I *Praeterpaculla* is a member of the Pacullinae, probably of the Pacullini sensu LEHTINEN 1981, in which a divided cymbium exists. In contrast to most other Pacullinae prosoma and basal cheliceral articles are unmodified and the bulbus is smaller. A ventral apophysis of the pedipalpal tibia exists in *Sabahya*

DEELEMEN-REINHOLD 1980 (extant, SE-Asia) but the position of this apophysis is in the middle of the tibia in *Sabahya*.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

Determination of the species: See the shape of bulbi and emboli; deformations are a problem. *P. equester* is the largest species, in *P. tuberosa* the opisthosoma bears small dorsal humps.

***Praeterpaculla armatura* n. gen. n. sp.** (figs. 102-104) photo 46

Etymology: The species name refers to the strongly armoured body of the holotype, from *armatura* (lat.) = scutate.

**Material:** Holotype ♂ in Mid Cretaceous amber, F2697/BU/CJW.

**Preservation and syninclusions:** The spider is completely preserved; the body – including the eyes and the pedipalpi – are strongly deformed, all legs beyond the femora are strongly bent under the body. – 5 Acari of various taxa – including an Erythraeidae – as well as an insect larva are preserved near the spider. A larger particle of soil, plant hairs and several pear-shaped bubbles at the surface of the piece of amber are also preserved.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (figs. 102-104): Cymbium distinctly bilobed, embolus long and bent, s-shaped, bearing a thin and straight (bristle-shaped) apophysis in the distal half.

### **Description** (♂):

Measurements (in mm): Body length 3.2; prosoma: Length 1.7, width 0.9 (the prosoma is compressed laterally!); opisthosoma: Length 1.7, width 1.3, height 0.95; leg I (r./l.): Femur 2.4/2.9, patella 0.4/0.6, tibia 2.4, metatarsus 2.5, tarsus 0.8, femur II 2.2, femur III 1.3, femur IV 1.8.

Colour dark brown.

Prosoma (photo) distinctly longer than wide, dorsally and ventrally strongly wrinkled, without outgrowth, 6 eyes in a wide field, cephalic part distinctly raised, especially the median eyes; basal cheliceral articles fairly large, partly hidden, apparently without outgrowth. The sternum spaces the coxae IV by their diameter. – Legs (photo) long and slender, order I/II/IV/III, bristles absent, position of the trichobothrium on metatarsus II in ca. 0.5. 3 tarsal claws, paired claws well developed, bearing long teeth. – Opisthosoma (photo) strongly deformed, armoured and wrinkled, dorsally, ventrally

and laterally with numerous small scuta, their position more or less in rows. Spinnerets short, surrounded by a short ring. – Pedipalpus (figs. 102-104, photo) (distinctly deformed): Tibia strongly thickened, cymbium distinctly bilobed, bulbus small, embolus long and bent, bearing a thin, straight and bristle-shaped apophysis in the distal half.

**Relationships:** See *P. tuberosa* n. sp. which is closely related. In the extant *Paculla armata* THORELL 1890 from Sumatra a large, wide and bent embolus exists, too, but the prosoma bears an outgrowth, and an apophysis of the embolus is absent.

**Distribution:** Mid Cretaceous amber forest of N-Myanmar (Burma).

***Praeterpaculla biacuta* n. gen. n. sp.** (figs. 105-107) photo 47

**Etymology:** the species name refers to the pointed embolus and the pointed apophysis of the embolus, from lat. bi = two and acutus = pointed.

**Material:** Holotype ♂ in Mid Cretaceous amber, F2727/BU/CJW.

**Preservation and syninclusions:** The spider is excellently preserved in a clear yellow piece of amber, the left patella I and the right leg I beyond the end of the femur and the base of the metatarsus as well as the dorsal-distal part of the left tibia IV are cut off; a thick white emulsion covers parts of the sternum, a fissure exists above the spider. – The larva of an Acari and plant hairs are preserved in the same piece of amber.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (fig. 105-107): Tibia thick, bearing a tiny apical-ventral apophysis, embolus wide, its tip pointed, a pointed apophysis exist in the distal half of the embolus.

### **Description** (♂):

Measurements (in mm): Body length 3.2; prosomal length 1.6; opisthosomal length 1.8; leg II: Patella 0.4, tibia 1.8, metatarsus 1.6, tarsus 0.7, metatarsus IV 1.5; pedipalpal tibia 0.48.

Colour dark brown. Only the left tibia I shows an annulation which may be an artefact. Prosoma (photo) fairly slender, distinctly wrinkled, 6 large eyes (covered with a white emulsion), clypeus long and hairy, basal cheliceral articles only fairly large, labium about as long as wide, gnathocoxae slender and strongly converging. – Legs long and slender, order I/II/IV/III, III distinctly the shortest, fairly hairy, bristles absent. Position of the metatarsal III trichobothrium in 0.55. Paired tarsal claws with long teeth, unpaired claw bent in a right angle. – Opisthosoma (photo) completely strongly armoured, bearing a sclerotized ring around the 3 pairs of spinnerets, the medians small, colulus reduced, anal tubercle fairly small. – Pedipalpus (figs. 105-107, photo) (see also the diagnosis): Tibia with two trichobothria, cymbium small and apparently divided apically, bulbus small and oval.

**Relationships:** See *P. tuberosa* n. sp.

**Distribution:** Mid Cretaceous amber forest of N-Myanmar (Burma).

***Praeterpaculla dissolata* n. gen. n. sp.** (figs. 108-110)

**Etymology:** The species name refers to the decomposed body of the holotype, from *dissolutio* (lat.) = destruction, decomposition.

**Material:** Holotype ♂ in Mid Cretaceous amber, F2698/BU/CJW.

**Preservation and syninclusions:** The spider is preserved in a yellow to orange piece of amber, darkened and partly deformed by heating, the ventral part of the opisthosoma – including the spinnerets – and several leg articles are cut off, the right leg II is completely preserved, the right leg III is broken off beyond the coxa by autotomy and preserved right of the opisthosoma, the tibia of the left leg IV is broken off near its end within the amber, remaining parts are lost. – A large and not well preserved Diptera: Brachycera, body length 7.5 mm, is preserved left above and behind the spider, a small part of an insect's antenna, plant hairs and small grey pear-shaped bubbles (at the surface of the piece of amber) are also preserved.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (fig. 109-110): Tibia with a ventral apophysis, cymbium apically undivided, embolus (deformed) long, wide and bent.

**Description** (♂):

Measurements (in mm): Body length 4.5; prosoma: Length 2.0, width 1.35; opisthosoma: Length 3.5, width 2.1; Leg I: Femur 2.6, patella 1.15, femur II 2.4.

Colour dark brown.

Prosoma (fig. 108) 1.5 times longer than wide, without outgrowth, cephalic part distinctly raised and strongly wrinkled, hairs short, eyes hidden/deformed, basal cheliceral articles, without outgrowth, fairly stout, carina well developed, fang furrow with two teeth, labium free, slightly longer than wide, gnathocoxae long and converging, sternum strongly wrinkled, 1.7 times longer than wide, spacing the coxae IV by less than their diameter. – Legs (photo) long and slender, order I/II/IV/III, without bristles, hairs not distinct, position of the questionable metatarsal II trichobothrium in 0.5. – Opisthosoma (photo) oval, 1.7 times longer than wide, incompletely preserved, spinnerets cut off, strongly armoured, hairs short. – Pedipalpus (figs. 109-110) (See the diagnosis): Tibia distinctly thickened.

**Relationships:** See *P. equester* n. sp.

**Distribution:** Mid Cretaceous amber forest of N-Myanmar (Burma).

***Praeterpaculla equester* n. gen. n. sp.** (figs. 111-112) photos 48-49

**Etymology:** The species name refers to the strongly armoured body of the holotype, from equester (lat.) = knight.

**Material:** Holotype ♂ in Mid Cretaceous amber, F2699/BU/CJW.

**Preservation and syninclusions:** The spider is completely and fairly well preserved in an orange piece of amber, deformed and strongly darkened by natural heating and pressure during the preservation, a thin emulsion covers parts of the opisthosoma. – A branched thin spider's thread is preserved below the spider in a longitudinal direction, partly in contact with the legs; it may be part of the capture web of the male. – An Acari, remains of an insect's exuvia, the larva of a Blattaria, cerci of a Dermaptera and remains of plants are also preserved in the piece of amber.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (figs. 111-112): Tibia strongly thickened, cymbium probably not divided apically, embolus without an apophysis. Compare the left and the strongly deformed right embolus which is strongly lengthened by the preservation.!

**Description** (♂):

Measurements (in mm): Body length 3.5; prosomal length 2.1, opisthosomal length 2.1; leg I: Femur 1.9, patella 0.4, tibia 2.1, metatarsus 1.8, tarsus 0.7, tibia II 1.3, tibia III 0.8, tibia IV 1.15.

Colour dark brown.

Prosoma (it is strongly deformed, parts like the eyes are hidden) distinctly longer than wide, strongly wrinkled, outgrowth absent, cephalic part raised, 6 eyes, clypeus long, basal cheliceral articles without outgrowth, fangs stout, labium slightly longer than wide, gnathocoxae long and converging, sternum distinctly wrinkled. – Legs (photo) long and slender, order I/II/IV/III, I distinctly the longest, III distinctly the shortest, bristleless, position of the metatarsal IV trichobothrium in 0.5, the paired tarsal claws bear large teeth. – Opisthosoma (photo) oval, strongly deformed. – Pedipalpus (figs. 111-112): See above. The tibia bears a small ventral-apical apophysis.

**Relationships:** In *P. dissolata* n. sp. an apophysis of the embolus is absent, too, but the shape of the embolus is different.

**Distribution:** Mid Cretaceous amber forest of N-Myanmar (Burma).

***Praeterpaculla tuberosa* n. gen. n. sp.** (figs. 113-116)

**Etymology:** The species name refers to the small opisthosomal humps, from tuberosus (lat.) = humpy.



**Material:** Holotype ♂ in Mid Cretaceous amber, F2700/BU/CJW.

**Preservation and syninclusions:** The spider is fairly well and strongly darkened preserved in a clear yellow piece of amber; parts of the eyes, of the left pedipalpus and the right legs I and II are cut off. – Two juv. Araneae indet. (not confamiliar; at least the larger one is eight-eyed), 4 Acari, 1/2 Hymenoptera and some plant hairs are also preserved.

**Diagnosis** (♂; ♀ unknown): The armoured opisthosoma (fig. 114) bears low humps; pedipalpus (figs. 115-116): Tibia with a distinct ventral-apical hump, the deformed long embolus bears a pointed apophysis in the distal half.

**Description** (♂):

Measurements (in mm): Body length 3.0; prosoma: Length 1.5, width 1.0; opisthosoma: Length 1.9, width 1.4, height 0.5; leg I: Femur probably 2.8, patella ca. 0.5, tibia ca. 3.8, metatarsus 2.75, tarsus 0.85; femur II ca. 2.9, femur III 1.5; leg IV: Femur 1.5, patella 1.3, tibia 1.65, metatarsus 1.5, tarsus 0.6.

Colour dark brown.

Prosoma (fig. 113) 1.5 times longer than wide, distinctly wrinkled, cephalic part not strongly raised, with distinct furrows to the thoracic part, fovea indistinct, 6 large eyes in a wide field, clypeus long and vertically sloping, basal cheliceral articles well developed, few teeth on the fang furrows, fangs stout. – Legs (photo) long and slender, order I/II/IV/III, I distinctly the longest, bristleless, hairs fairly long and rather dense, position of the metatarsal I trichobothrium in 0.5, paired tarsal claws with long teeth, unpaired claw well developed, strongly bent. – Opisthosoma (fig. 114) 1.36 times longer than wide, flattened, completely strongly armoured, dorsally bearing more than 30 low humps and posterior furrows, spinnerets stout, surrounded by a sclerotized ring. – Pedipalpus (figs. 115-116): See the diagnosis. The apical margin of the cymbium is hidden.

**Relationships:** In the remaining congeneric species opisthosomal humps are absent.

**Distribution:** Mid Cretaceous amber forest of N-Myanmar (Burma).

## (2) Subfamily TETRABLEMMINAE

Key to the genera in Burmite (♂): See WUNDERLICH (2012: 172-173). Two genera are added in this paper: (1) *Bicornoculus* n. gen. is the only described fossil genus in which the anterior lateral eyes are placed on „horns“ (fig. 117), and the bulbus is unusually large/long (fig. 120); see also below: ?Gen. sp. indet., ♂. (2) In *Uniscutosoma* n. gen. the clypeus bears TWO pairs of „horns“ (fig. 131), the ventral opisthosoma is seemingly entire and a sclerotized ring around the spinnerets is absent.

## ***Bicornoculus* n. gen.**

**Etymology:** The name refers to the anterior lateral eyes which are placed on „horns“, corn = part of cornutus (lat. = horned) and bi (lat. = double). – The gender of the name is masculine.

**Type species** (by monotypy): *Bicornoculus levis* n. sp.

**Diagnostic characters** (♂; ♀ unknown): Prosoma only finely rugose, 6 eyes, anterior lateral eyes placed on „horns“ and directed anteriorly-laterally (fig. 117), prosoma not raised, clypeus and chelicerae without outgrowth, sternum almost smooth, bulbus (figs. 120-121) strongly elongated (resembling certain members of the Oonopidae, Gamasomorphinae).

The **relationships** are unsure: Shape and structures of the bulbus of the genus are quite unusual within the Tetrablemminae, the body size and the position of the metatarsal trichobothrium are between the characters of the Pacullinae and the Tetrablemminae. Therefore I do not want to exclude that *Bicornoculus* is a member of a third and undescribed – „primitive“? – subfamily of the Tetrablemmidae in which the prosoma is only weakly rugose. According to the prosoma which is not raised it may be a member of the Eoscapheellini WUNDERLICH 2012. In the remaining related taxa in Burmite the prosoma (peltidium and sternum) is distinctly wrinkled and the structures of the bulbus are quite different.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

***Bicornoculus levis* n. gen. n. sp.** (figs. 117-121) photos 43-44

**Etymology** of the species name refers to its smooth sternum: *Levis* (lat.) = smooth.

**Material:** Holotype ♂ in Burmite from N-Myanmar (Burma) and a separated piece of amber, F2692/BU/CJW.

**Preservation and syninclusions:** The species is excellently and completely preserved in a clear yellow piece of amber, ventrally are some gas bubbles preserved. – A thin thread in contact with the right metatarsus IV may have been part of the capture web of the spider. Detritus, insect's excrement and plant hairs are preserved in the same piece of amber. In the separated piece of amber ½ Diptera is preserved.

**Diagnosis** (♂; ♀ unknown): See above. Pedipalpus (figs. 120-121) with a long and large bulbus.

**Description** (♂):

Measurements (in mm): Body length 1.9; prosoma: Length 0.9, height 0.4; opistho-

soma: Length 1.05, height 0.6; leg I: Femur 0.7, patella 0.25, tibia 0.55, metatarsus 0.37, tibia II 0.45, tibia III 0.35, tibia IV 0.52.

Colour: Prosoma and legs redbrown, opisthosoma dorsally light grey, ventral scuta red brown.

Prosoma (figs. 117-118) distinctly longer than wide or high, profile convex and fairly raised as in ?*B. sp.* (fig. 122), finely rugose and bearing few long hairs, fovea absent, six large eyes in a „segestriid position“, median eyes close together, anterior lateral eyes placed on „horns“, its lenses small and directed anteriorly-laterally, clypeus long and without outgrowth, basal cheliceral articles without outgrowth, fangs fairly stout, partly hidden, labium free, gnathocoxae long and strongly converging, sternum almost smooth (finely wrinkled), coxae IV spaced by about half of their diameter. – Legs (photo) only fairly long, order I/IV/II/III, III distinctly the shortest, bristleless, hairs fairly long, position of the metatarsal I trichobothrium in 0.4, onychium well developed, paired tarsal claws large and with long teeth, unpaired claw quite thin, best observable on the right leg I. – Opisthosoma (fig. 119, photo) oval, hairs short, dorsally completely covered with a wrinkled scutum, ventrally with three large scuta, laterally with rows of small and hair-bearing scuta which are not distinctly bordered, the short spinnerets are surrounded by a large scutum. – Pedipalpus (figs. 120-121) with stout articles, tibia quite thick, bulbus large and strongly elongated, embolus unknown, probably small.

**Relationships and distribution:** See above.

?*Bicornoculus* sp. (fig. 122)

**Material:** 1♂ (adult?) and a separated piece of amber in Mid Cretaceous Burmite, F2693/BU/CJW.

The male is completely and fairly well preserved, parts are hidden by bubbles and layers of the amber, the dorsal side is well preserved. Its body length is 1.8 mm, its prosomal length 0.85 mm, its tibial I length 0.6 mm. Shape of the prosoma as in fig. 122, as in *B. levis* n. sp. The pedipalpus is quite different from *B. levis*: The tibia is more slender, the tarsus is „crumbled“, almost as wide as long. Therefore I do not want to exclude that the male is subadult and probably conspecific with *B. levis*.

A Diptera: Nematocera and a tiny Acari larva (above the right leg I) are preserved in the same piece of amber.

***Eogamasomorpha*** WUNDERLICH 2008

**Revised diagnosis** (♂; ♀ unknown): Prosoma relatively low, peltidium and basal cheliceral articles apparently without modifications, prosoma almost smooth (the type spe-

cies *E. nubila* WUNDERLICH 2008) or distinctly wrinkled (fig. 124), eyes (fig. 124): Most probably 6 in diads of a wide field, pedipalpus (figs. 127-130): Cymbium very long, bulbus subglobular, embolus long and thin, conductor absent.

**Relationships:** *Eogamasomorpha* has originally erroneously been described by me as a member of the Oonopidae: Gamsomorphinae mainly because of the absence of modifications of peltidium and chelicerae, a cheliceral lamina (fig. 124) and lateral opisthosomal scuta have not been observed. According to the small body and the thin embolus *Eogamasomorpha* is a member of the subfamily Tetrablemmiinae sensu LEHTINEN 1980 and strongly related to *Eoscapheia* WUNDERLICH 2008. Brignoliellini sensu LEHTINEN 1981 may be related; bulbus and embolus are similar in certain SE-Asian species of the genera *Pahanga* SHEAR 1979 and *Brignoliella* SHEAR 1979, but in these genera the cymbium is short. – I do not want to exclude that the tetrablemmid taxa in Burmite may be members of an ancient extinct subfamily, a sister group to all extant taxa including the Pacullinae which probably is not the most basal taxon of the Tetrablemmidae.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

?*Eogamasomorpha clara* n. sp. (figs. 124-130) photo 145

**Etymology** of the species name: From clarus (lat.) = clear, based on the clear amber which encloses the holotype.

**Material:** Holotype ♂ in Mid Cretaceous amber from Northern Myanmar (Burma), and two separated pieces of amber, F2465/BU/CJW.

**Preservation and syninclusions:** The spider is completely and excellently preserved in a clear yellow-orange piece of amber. For a closer study the piece has been cut by me once in front of the spider and after this a second time; a tiny worm-shaped larva and a mite are lost now by the cutting. The anterior median part of the spiders peltidium including the eye region and the anterior lateral parts of the opisthosoma are covered with bubbles, some leg articles are covered with small bubbles or emulsions. – Syninclusions are 4 Acari, remains of a Diptera, a tiny insect at tiny bubbles, remains of plants including „stellate hairs“, and long questionable hyphae.

**Diagnosis** (♂; ♀ unknown): Peltidium and chelicerae apparently without modifications/outgrowths, peltidium and sternum distinctly wrinkled (figs. 124-125), position of the metatarsal I trichobothrium in 0.38, opisthosomal scuta: fig. 126, photo, pedipalpus (figs. 127-130, photo): Bulbus subglobular, embolus thin and long, bent dorsally.

**Description** (♂):

Measurements (in mm): Body length 1.1, prosomal length 0.5, opisthosoma: Length 0.65, width 0.5, height 0.3; leg I: Femur 0.4, patella 0.1, tibia 0.3, metatarsus 0.2, tarsus

0.2, metatarsus II 0.19, metatarsus III 0.16, leg IV: Tibia 0.35, metatarsus 0.23, tarsus 0.2, diameter of a medium eye 0.05.

Colour (photo) redbrown, the dorsal opisthosomal scutum dark redbrown.

Prosoma (figs. 124-125) distinctly wrinkled, not raised, not modified, no outgrowth of the peltidium and of the basal cheliceral articles. Eyes (they are hidden dorsally by a bubble): Most probably six in a wide field of diads, clypeus long, basal cheliceral articles large/robust and diverging, laterally bearing widely spaced furrows (not stridulatory files), apically with hair-bearing humps, medium lamella well developed. Labium triangular, gnathocoxae strongly converging, sternum wide anteriorly and posteriorly, prominent, and deeply inclined at the margin (apparently a family character). – Legs (photos) slender, sequence IV/I/II/III, III not much shorter than II, bristle-less, I without modifications, tarsi about as long as metatarsi, position of the metatarsus I trichobothrium in 0.38. – Opisthosoma (fig. 126, photo) 1.3 times longer than wide, dorsally completely covered with a scutum which bears short hairs, laterally with three longitudinal scuta, the ventral one apparently tripartite, ventrally bearing probably three scuta, large lung covers strongly sclerotized, spinnerets retracted within a large sclerotized ring. – Pedipalpus (figs. 127-130, photo): Femur and patella slender, tibia fairly thickened, cymbium very long, bulbus subglobular, no conductor, embolus long, slender and bent dorsally in the distal half.

**Relationships:** According to the apparently unmodified peltidium and chelicerae (probably like in other taxa in Burmite), the not raised prosoma, and the very long cymbium *clara* may be congeneric with the type species of *Eogamasomorpha*, *E. nubila* WUNDERLICH 2008, but in *nubila* the prosoma is almost smooth, the position of the metatarsal trichobothrium is near the end of the article, the embolus is relatively to the bulbus longer, and is thicker in the basal half. Unfortunately the exact position of the eyes is unknown in both species.

**Distribution:** Mid Cretaceous amber from Myanmar (Burma).

### **Uniscutosoma n. gen.**

**Derivatio nominis:** The name refers to the seemingly entire ventral opisthosomal scutum (lat.). – The gender of the name is feminine.

**Type species** (by monotypy): *Uniscutosoma aberrans* n. sp.

**Diagnosis** (♂; ♀ unknown): Opisthosoma ventrally bearing a seemingly entire scutum (see below), prosoma anteriorly-dorsally bearing two pairs of „horns“ (fig. 131).

**Further character:** Opisthosoma bearing numerous small plates (fig. 133), scutate ring around spinnerets probably absent, position of the metatarsal trichobothrium in less than 0.4 body length 2.3 mm, articles of the pedipalpus fairly slender, structures of the bulbus unknown.

The **relationships** are unsure, the structures of the bulbus are still unknown, the shape of the ventral opisthosomal scutum is quite unusual. The position of the metatarsal trichobothrium indicates relationships to the Tetrablemmineae but *aberrans* is larger than all other known members of this subfamily (and smaller than the known members of the Pacullinae).

**Distribution:** Mid Cretaceous amber forest of N-Myanmar (Burma).

***Uniscutosoma aberrans* n. gen. n. sp.** (figs. 131-133) photo 50

**Etymology:** The name refers to the seemingly entire/undivided (latin) ventral opisthosomal scutum. – The gender of the name is feminine.

**Material:** Holotype ♂ and 4 separated pieces of amber in Mid Cretaceous Burmite from N-Myanmar (Burma), F2714/ BU/CJW:

**Preservation and syninclusions:** The spider is not well preserved, was apparently dried out, decomposed and is deformed, the chelicerae are loose and are placed anteriorly above the prosoma, the right femur II is lost from the base to the patella, most femora are depressed laterally, most eyes, the mouth parts and the spinnerets are hidden.- **Syninclusions:** Thin spider's threads, 1 Acari and few particles of detritus are preserved with the spider. In the remaining 4 pieces numerous Acari, some Diptera, remains of an Auchenorrhyncha, 1 Psocoptera, plant hairs and particles of detritus are preserved.

**Diagnosis:** See above.

### **Description (♂):**

Measurements (in mm): Body length 2.3, prosomal length 1.2; opisthosoma: Length 1.3, width 1.05, height (the opisthosoma is strongly flattened) ca. 0.3; leg I: Femur ca. 0.9, patella 0.3, tibia 1.1, metatarsus 1.1, tarsus 0.5, tibia II 1.0, tibia III 0.8, tibia IV 1.25. Colour redbrown, legs not annulated.

Prosoma (figs. 131-132, photo) (deformed, parts are hidden or lost) finely punctuated, apparently 6 small eyes, anteriorly bearing two pairs of erect „horns“, basal cheliceral articles fairly long, probably fused basally, lamella well developed, anterior margin of the fang furrow with two large teeth, fangs long and slender. Coxae IV separated by almost their diameter. – Legs (photo) slender and rather long, order IV/II/III, bristleless, hairs not distinct and of medium length, position of the metatarsal trichobothrium in less than 0.4, unpaired tarsal claw long and slender. – Opisthosoma (fig. 133, photo) deformed, 1.24 times longer than wide, strongly armoured, dorsally with numerous small and hair-bearing plates, laterally bearing few (mainly hidden) small longitudinal scutate furrows, ventrally with a large scutum which is seemingly entire/fused, and bears a transverse rim behind the middle, spinnerets hidden, ring around spinnerets not recognizable, probably absent. – Pedipalpus: Articles fairly slender, both bulbi are lost.

**Relationships and distribution:** See above.

**Material indet.** (Tetrablemminae):

F2694/BU/CJW: 1♀, body length 1.1 mm. The spider is well and completely preserved, dorsal parts are hidden. The pedipalpi are small and quite slender.

F2695/BU/CJW: 1♀, body length 1.2 mm. The spider is fairly well and completely preserved, parts of the eyes are hidden. The right leg II and the left leg IV are broken through an article within the amber. Few spider's threads – probably part of the capture web of the spider – are preserved mainly in front of the spider and partly in contact with the spider. Some long-branched plant hairs are preserved in the same piece of amber.

F2696/BU/CJW: 1♀, body length 1.35 mm. The spider is not well but almost completely preserved in a clear yellow piece of amber, only the left tarsus I is cut off. It is strongly darkened and distinctly depressed/inclined dorso-ventrally. The eyes are large, the pedipalpi are of normal size, a tarsal claw is absent. Badly preserved remains of an Acari are also preserved.

F2702/BU/CJW: 1♀, body length 1.3 mm. The spider is well and completely preserved. A larger decomposed Araneae indet and numerous insects are preserved in the same piece of amber.

F2703/BU/CJW: 1♀, body length 1.05 mm. The spider is well and completely preserved.

F2723/BU/CJW: 1♀, body length 1.1 mm. Two Opiliones are preserved in the same piece of amber.

?**Gen. sp. indet.** (fig. 123)

**Material:** 1♂ in Mid Cretaceous amber from Myanmar (Burma), coll. HUANG 0909.

Body length 1.5 mm, tibia I 0.5 mm long, six eyes (partly hidden) in three diads, clypeus with 2 pairs of dorsal outgrowth which are distinctly deformed (similar to *Biconoculus levis* in which the structures of the bulbus are quite different, position of the metatarsal I trichobothrium in 0.48, cymbium excavated apically, bulbus large and globular, embolus – apparently deformed – wide basally (fig. 123), an additional sclerite exists. The relationships of this taxon remain unclear.



## SUPERFAMILY LEPTONETOIDEA

To my recent knowledge Leptonetoidea is one of the most diverse Mesozoic superfamilies of araneomorph spiders. In amber from Myanmar (Burma) and Jordan I suppose the existence of 4 families: (1) Leptonetidae (a single species of the extinct ecribellate subfamily Palaeoleptonetinae), (2) the ecribellate Praeterleptonetidae (probably five tribes; the relationships of the Autotomianini and the Palaeohygropodini are unsure), (3) the cribellate Pholcochyroceridae, and (4) the Jurassic – Cretaceous cribellate family Mongolarachnidae. A fifth leptonetoid family – Telemidae (extant and Eocene Baltic amber) – was unknown from the Cretaceous (and the whole Mesozoic as well) see the family key no. 27.

Previously the family Leptonetidae – as well the family Praeterleptonetidae by me – were regarded as members of the superfamily Dysderoidea, see WUNDERLICH (2008). This relationship were questioned e. g. by LEDFORD & GRISWOLD (2010) and WUNDERLICH (2011: 586). The two families were regarded as members of the superfamily Leptonetoidea by me, and as the sister group of the Pholcoidea, see WUNDERLICH (2012: 190) but are now placed away from the Pholcoidea, see fig. F, note (13).

The taxonomy of members of this haplogyne superfamily is still quite provisional, and probably it is not monophyletic.

**Diagnosis:** Slender articles (\*) of the ♂-pedipalpus (apparently an apomorphy), tendency to spiny articles (\*) – including the cymbium – of the ♂-pedipalpus, well expandable bulbus/basal haematodocha (in all taxa?) (\*\*).

Selected further characters, see WUNDERLICH (2012: 182-183, 191, tab. 1):

Lungs existing, a single pair.

Feathery hairs absent.

Cheliceral teeth and teeth of the tarsal claws usually tiny or even absent, basal cheliceral articles not fused, medial lamella absent. Retrolateral stridulatory files exist in some taxa of the Leptonetidae, see LEDFORD et al. (2010: 8).

Teeth of the tarsal claws usually tiny or even absent.

Apparently – at least in some taxa – existence of cylindrical gland spigots.

Cribellate or ecribellate (\*\*): Telemidae (Cretaceous to extant), Praeterleptonetidae (Cretaceous) as well as certain extant taxa of the Leptonetidae – Leptonetinae and the genus *Darkoneta* LEDFORD & GRISWOLD 2010 of the Archoleptonetinae – are ecribellate; the remaining taxa – the Jurassic/Cretaceous Mongolarachnidae (its relationships are unsure, see below), the Cretaceous Pholcochyroceridae as well as the extant genus *Archoleptoneta* GERTSCH 1974 of the Leptonetidae: Archoleptonetinae – are cribellate but see *Palaeoleptoneta* below. The cribellum is probably undivided; it may be indistinct in the male sex.

Number of the eyes: The basic number of 8 eyes exists in the extinct praeterleptonetoid branch (Mongolarachnidae, Pholcochyroceridae and Praeterleptonetidae). 6 eyes exist in the leptonetoid branch sensu WUNDERLICH (2012: 190) (the families Leptonetidae and Telemidae). The only known six-eyed Cretaceous taxon of the superfamily Leptonetoidea is *Palaeoleptoneta* WUNDERLICH 2012 of the Leptonetidae: Palaeoleptonetinae.

Leg III distinctly the shortest. Leg I frequently strongly elongated.

Leg autotomy: Probably basically no leg autotomy (questionable plesiomorphy), with the exception of the advanced subfamilies Archoleptonetinae and Leptonetinae of the Leptonetidae (both are unknown from the Cretaceous) and the new Cretaceous tribe Autotomianini of the Praeterleptonetidae which evolved a patella-tibia autotomy convergently in my opinion. This kind of autotomy is unknown – absent? – in the Cretaceous subfamily Palaeoleptonetinae. See also below, the paragraph „distribution“.

Cymbium: Wide and (usually) ventrally distinctly excavated/concave, spiny in some taxa..

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(\*) Convergently evolved, e. g., in several members of the Ochyroceratidae and Psilodercidae (Pholcoidea).

(\*\*) The complicated structures of the bulbus of certain taxa reminds on the structures of members of the entelegyne Araneoidea s. l.

(\*\*\*) In most cribellate spiders the anterior spinnerets are widely spaced at their base and – usually strongly – converging distally (fig. 134b), in most ecribellate taxa exist a large colulus (which is largest in the Telemidae) or a small colulus see below: *Biapophyses beate* n. sp. (Praeterleptonetidae). – In certain taxa it may be quite difficult to distinguish between a very large colulus („pseudocribellum“) and a – really functionless? – cribellum, e. g. in the extinct subfamily Mizaliinae of the Oecobiidae, see WUNDERLICH (2004: 845, fig. 11, in which the colulus erroneously is called calamistrum).

**Relationships**: See fig. F (see note (13)) and fig. G. I do not want to exclude that Leptonetoidea is a close descendent of the ancient Hypochilomorpha and not closely related to (other) „Haplogynae“ but may include the root(s) to entelegyne „Orbiculariae“ like Uloboridae and Araneidae. The Praeterleptonetidae share some characters with the Theridiosomatidae, see below.

**Distribution**: Extant: Cosmopolitical; fossil: JURASSIC: Mongolia (Mongolarachnidae); CRETACEOUS: Only Myanmar (Burma) and Jordan up to now.

**Note**: Perhaps still not discovered or overlooked taxa exist in other Cretaceous amber deposits: Probably an unnamed taxon – published under Linyphiidae – in Cretaceous Ethiopian amber may be a member of this superfamily. This ecribellate eight-eyed taxon possesses a patella-tibia autotomy like the genus *Autotomiana* of the Praeterleptonetidae.

List of the Cretaceous higher taxa of the superfamily Leptonetoidea:  
(Mongolarachninae is Jurassic)

Leptonetidae: Palaeoleptonetinae: *Palaeoleptoneta* (apparently ecribellate, six-eyed),  
Praeterleptonetidae (ecribellate, eight-eyed): Five tribes: Autotomianini (probably),  
Biapophysini, Praeterleptonetini, Zarqaraneini, and probably Palaeohygropodini,  
Pholcochyroceridae (cribellate, eight-eyed): *Pholcochyrocer*, *Spinicreber*,  
Mongolarachnidae (cribellate, probably all eight-eyed): Three subfamilies:  
Longissipalpiniae, Mongolarachninae and Pedipalparaneinae.

**Key to the Mesozoic families of the Leptonetoidea:**

All the described fossil taxa are extinct. Most Cretaceous Leptonetoidea are eight-eyed, the six-eyed genus *Palaeoleptoneta* is an exception, the number of the eyes (probably eight) is unknown in the Jurassic Mongolarachninae.

Note on the family Leptonetidae: Two subfamilies are known from today: the partly/basically cribellate Archoleptonetinae and the ecribellate Leptonetinae; the third subfamily – the Palaeoleptonetinae – is extinct, and a cribellum is apparently absent.

1 Six eyes (fig. 134a), cribellum (fig. 134b) probably existing (see below), bulbus large, embolus very long (fig. 134c). Only *Palaeoleptoneta calcar* WUNDERLICH 2012 (Palaeoleptonetinae) in Burmite. . . . . Leptonetidae

- Eight eyes (figs. 135, 160) (unsure number in the Mongolarachninae), cribellate or ecribellate. . . . . 2

2(1) Ecribellate. (probably including the genera *Autotomiana* and *Palaeohydropoda*). (Note: Body shape and leg bristles are similar in the family Theridiosomatidae). . . . . Praeterleptonetidae

- Cribellate (figs. 185). . . . . 3

3(2) Pedipalpal articles extremely long (figs. 184, 186, 196), bulbi very small; spiny except in the Longissipalpinae. In stone, Mongolia, *Mongolarachne jurassica* (the Jurassic Mongolarachninae) and in Mid Cretaceous Burmese amber (Longissipalpinae and Pedipalparaneinae). . . . . Mongolarachnidae

- Pedipalpal articles not extremely long, see WUNDERLICH (2012: 226, fig. 34), pedipalpal articles not spiny, bulbi not very small. Cretaceous amber: Burmite. . . . . Pholcochyroceridae

**Family LEPTONETIDAE SIMON 1890 figs. 134a-c, family key no. 23**

Spiders of this family are six-eyed and either ecribellate (the extant and Eocene taxa of the subfamily Leptonetinae and the extant genus *Darkoneta* LEDFORD & GRISWOLD 2010 of the subfamily Archoleptonetinae) or cribellate (*Archoleptoneta* GERTSCH 1974 of the extant subfamily Archoleptonetinae and the single Cretaceous species of the

subfamily Palaeoleptonetinae, see below). An important apomorphic character of the Leptonetidae is the patella-tibia autotomy (\*) which is not frequent in spiders.

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(\*) The kind of autotomy is unknown from the Cretaceous Palaeoleptonetinae from which only a single specimen is known, see below.

Patella-tibia autotomy is known from members of four superfamilies, of the families (a) Filistatoidea: Filistatidae;

(b) Leptonetoidea: Leptonetidae as well as *Autotomiana* of the Praeterleptonetidae; (c) Oecobioidea: Hersiliidae and several taxa of the Oecobiidae;

(d) Araneoidea: Linyphiidae and Pimoidae.

### **Subfamily PALAEOLEPTONETINAE WUNDERLICH 2012: 187**

**Diagnostic characters** (♂; ♀ unknown): Questionable cribellum fig. 134b (\*), unpaired tarsal claw small (reduced), most probably six eyes in an almost circular position (fig. 134a), kind of autotomy unknown (absent in the single known specimen), ♂-pedipalpus (fig. 134c): Cymbium with a large spur, embolus very long.

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(\*) In contrast to my suggestion in 2012 I am now not sure about the kind of the structure in front of the spinnerets of the single known and heated specimen of this taxon: it may be a large/wide colulus or a cribellum (apparently undivided) without function. A calamistrum is clearly absent.

**Relationships:** See WUNDERLICH (2012: 188) and above. I regard the Archoleptonetinae (extant, North America) – which is cribellate and possesses eyes in a contiguous position – as probably most related.

**Distribution:** Mid Cretaceous amber from Myanmar (Burma). (Only the type species *Palaeoleptoneta calcar* WUNDERLICH 2012 is known).

### **Family PRAETERLEPTONETIDAE WUNDERLICH 2008 figs. 135-174, photos 74-91, family key no. 35**

See WUNDERLICH (2008: 588f) under Praeterleptonetinae: Praeterleptonetini.

11 extinct genera; one of the most diverse spider families in Burmite if all genera are confamiliar, see below.

**Diagnostic characters** (\*): Ecribellate, 8 eyes in two rows (figs. 135, 160, photos), ventral tibial bristles usually not paired; pedipalpus (figs. 141f) quite variable, articles spiny and/or bearing apophyses, tibial (e. g. *Biapophyses*, *Crassitibia*) or patellar (e. g. *Autotomiana*, *Curvitibia*) apophyses may exist (\*\*), the embolus may be long.

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(\*) The original diagnosis was only based on a single species – *spinipes* – of *Praeterleptoneta*; see WUNDERLICH (2008: 588).

(\*\*) Depending on the position of the pedipalpus the apophyses of the articles are not observable in all taxa and may exist in more genera than known today, see the key.

**Further – including plesiomorphic – characters** (see also above, the superfamily Leptonetoidea; the key to the genera below shows certain diverse characters of the family): A single pair of lungs, femoral bristles existing, three tarsal claws, a single metatarsal trichobothrium, no tarsal trichobothria, the male leg I may be modified, colulus apparently large (see *Biapophyses*), cymbium large/wide, frequently spiny, well covering parts of the large bulbus which may possess complicated structures, leg autotomy usually absent but existing between patella and tibia in the Autotomianini.

Note: I did not observe sticky droplets at threads in the pieces of amber with the spiders.

**Genera:** *Autotomiana* n. gen. (relationships unsure), *Biapophyses* n. gen., *Crassitibia* n. gen., *Curvitibia* n. gen., *Groehnianus* n. gen., *Hypotheridiosoma* WUNDERLICH 2012, *Parvispina* n. gen., *Praeterleptoneta* WUNDERLICH 2008, *Palaeohygropoda* PENNEY 2004 (relationships unsure), *Spinipalpitibia* n. gen. and *Zarqaraneus* WUNDERLICH 2008.

**Relationships and intrafamilial subdivision:** The relationships of the extinct Cretaceous ecribellate family Praeterleptonetidae are unsure like several other Cretaceous spider families, and I am not sure about its monophyly. The extinct Cretaceous cribellate families Mongolarachnidae and Pholcochyroceridae may be most related. Because of the known differences – see above, e. g. the characters of the Palaeoleptonetinae – it appears unlikely to me that Leptonetidae is nothing else than the „crown taxon“ of Praeterleptonetidae + Pholcochyroceridae/Mongolarachnidae, but more likely it is its sister group, see the possible cladogram given by WUNDERLICH (2012: 190).

Previously I regarded three genera with some hesitation as taxa of the family Praeterleptonetidae and of the Cretaceous Leptonetoidea, see WUNDERLICH (2008: 586ff): *Praeterleptoneta*, *Palaeohygropoda* and *Pholcochyrocer*, each in a tribe of its own. Four years later I argued not to include Praeterleptonetidae in the superfamily Araneoidea – see WUNDERLICH (2012: 190-191, 197) –, although certain similarities (now considered as convergences) exist –, and I regarded Pholcochyroceridae as a family of its own. The relationships of *Autotomiana* and *Palaeohygropoda* appear still unsure to me. *Hypotheridiosoma* WUNDERLICH 2012 was erroneously described as a member of the family Theridiosomatidae (superfamily Araneoidea) but is now – after the study of new material – regarded as a member of the Praeterleptonetidae.

In 2008: 641f, 645 I regarded the *Zarqaraneini* WUNDERLICH 2008 – based on *Zarqaraneus hudei* – with some doubt as a member of the extinct Eocene family Protheridiidae WUNDERLICH 2004 of the superfamily Araneoidea. Based on the find of a second male of *Praeterleptoneta tibialis* WUNDERLICH 2011 (now *Parvispina*, see

below) and related species I revise my previous opinion: According to the chaetotaxy, the trichobothriotaxy and the structures of the male pedipalpus I regard *hudei* and *tibialis* as members of related genera. The type species of *Praeterleptoneta* is *P. spinipes* WUNDERLICH 2008), and I transfer here *tibialis* from *Praeterleptoneta* to *Parvispina* n. gen. (**n. comb.**). The outgrowth of the cymbium („paracymbium“) of *tibialis* and *hudei* has probably not the retroBASAL position as in the Araneoidea but its position seems to be more distally. Furthermore the (almost?) toothless basal cheliceral articles and tarsal claws are typical as in other members of the Leptonetoidea in contrast to most members of the superfamily Araneoidea. – Although there are several similarities shared by members of the Praeterleptonetidae and the Theridiosomatidae I noted a striking difference: In *Zarqaraneus hudei* a sternal pit of the sternal organ is surely absent. (The sternum of other members of the Praeterleptonetidae is usually not well observable, and the characteristic long tibial trichobothria of the Theridiosomatidae may be rubbed off). I do not want to exclude that the family Praeterleptonetidae is polyphyletic and has to be split up, and that the tribe Zarqareini has to be regarded as a family of its own, PROBABLY as a member of the superfamily Araneoidea, related to the Theridiosomatidae.

**Distribution:** Most taxa: Mid Cretaceous Burmese/Myanmar amber forest but *Zarqaraneus hudei*: Early Cretaceous amber forest of Jordan.

# Key to the higher taxa of the family Praeterleptonetidae:

In a former key – see WUNDERLICH (2008: 587) – the tribe Pholcochyrocerini has turned out to be cribellate, and I gave the taxon the rank of a family, see above.

Most taxa are only known from Mid Cretaceous amber of Myanmar (Burma); only Zarqaraneini is known from Burmese amber (5 genera) AND Jordanian amber (*Zarqaranaus hudei*).

1 Legs very long and slender, tarsi and metatarsi spiny, flexible and pseudoarticulate, III not much shorter than I and II, patella of the ♂-pedipalpus (fig. 163) with a strong out-standing spur. *Palaeohygropoda myanmarensis* PENNEY 2004. . . . Palaeohygropodini

- Legs QUITE SETOSE (fig. 136) and long, PATELLA-TIBIA AUTOTOMY (fig. 137), ♂-pedipalpus (figs. 138-139) with a dorsal patellar outgrowth and a long embolus which stands out. *Autotomiana hirsutipes* n. gen. n. sp. . . . . Autotomianini

- Legs not very setose and long, male pedipalpal patella without an outgrowth. . . . 2

2(1) Prosomal cuticula finely but distinctly wrinkled (photo), metatarsi with several bristles (fig. 140), ♂-pedipalpus (figs. 141-142): Tibia apically with a pair of erect DORSAL apophyses. *Biapophyses beate* n. gen. n. sp. . . . . Biapophysini

- Prosomal cuticula smooth, metatarsal and ventral tibial bristles absent or extremely rare, ♂-pedipalpus different, apical erect dorsal tibial apophyses absent. . . . . 3
- 3(2) Clypeus quite long and protruding ventrally (fig. 169). Short leg bristles. Cymbium (fig. 170) spiny, with a distinctly sclerotized retrolateral spur. *Praeterleptoneta spinipes* WUNDERLICH 2008. . . . . Praeterleptonetini
- Clypeus usually rather short, not protruding. Leg bristle usually long (fig. 146) but short in *Parvispina* (fig. 164). Cymbium (e. g. figs. 145, 152) without a sclerotized retrolateral spur but with a pointed, frequently horn-shaped and sclerotized retrolateral „paracymbium“. . . . . Zarqaraneini 4
- 4(3) ♂: Pedipalpus as in fig. 174. Tibia I relatively stout, not thickened in the basal half. Jordanian amber. Only *Z. hudei*. . . . . Zarqaraneus
- ♂: Pedipalpus as in fig. 156. Tibia I usually more slender, except *Crassitibia* (photos), not thickened in the basal half. Opisthosoma (fig. 155, photo 87) DORSALLY LEATHERY, bearing 3 pairs of sigillae. Burmite. Only *G. burmensis*. . . . . Groehnianus
- ♂: Pedipalpus different. Tibia I thickened in the basal half (fig. 143) or not. Burmit. . . 5
- 5(4) ♂: Tibia I not thickened, its bristles relatively short (fig. 171). Pedipalpus (fig. 172): Tibia very long, ventrally with a transverse rim and a pair of long bristles. Only *S. maior*. . . . . Spinipalpitibia
- ♂: Tibia I not thickened, its bristles quite long (fig. 161). Pedipalpus (fig. 157, 162): Tibia probably without a ventral bristle, cymbium with two long bristles. Body length 0.9-1.1 mm. 2 species. . . . . Hypotheridiosoma
- ♂: Tibia I usually thickened (fig. 164). Pedipalpus (figs. 166-168): Tibia without a ventral bristle but apophyses may exist. . . . . 6
- 6(5) ♂: Tibia I thickened dorsally AND ventrally, proapical bristle of tibia I rather short (figs. 164-165). Ventral pedipalpal tibial bristle and apophyses apparently absent (figs. 166-168). Only *P. tibialis*. . . . . Parvispina
- ♂: Tibia I thickened only ventrally (but not in *Crassitibia tenuimanus*), proapical bristle of tibia I very long (fig. 143). Certain pedipalpal articles with apophyses (figs. 147-152). . . . . 7
- 7(6) ♂: Bristles of leg I more numerous, metatarsus I dorsally-basally compressed (fig. 149). Pedipalpus (figs. 152-154): Patella with a large dorsal apophysis, paracymbium standing out with a long branch. Only *C. curima*. . . . . Curvitibia
- ♂: Bristles of tibia I less numerous, metatarsus I straight and longer than in the related genera (fig. 143). Pedipalpus (figs. 144, 147): Patellar bulging but apophysis absent, ventral tibial apophyses may exist, paracymbium wide and widely fused to the cymbium. 2 species. . . . . Crassitibia



## Tribe AUTOTOMIANINI n. trib.

Etymology: See the type genus.

Type genus (by monotypy): *Autotomiana* n. gen.

**Diagnosis** (♂; ♀ unknown): Leg autotomy between patella and tibia (\*) (fig. 137, photo), distal leg articles covered densely with long setae (fig. 136, photo), in the holotype femora III-IV bear long sensory setae (fig. 136) similar to trichobothria (or true trichobothria?) (\*\*) (see below), in a ventral position on IV (in the juvenile and probably related specimens they are absent on all femora). ♂-pedipalpus (holotype, figs. 138-139): Patella with a blunt short dorsal spine on an outgrowth, embolus standing widely out. Body length (adult male) 7 mm (largest member of the family Praeterleptonetidae).

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(\*) This kind of autotomy is frequent in this genus: One case exists in the holotype, one resp. two cases in the two most probably congeneric specimens.

(\*\*) Similar setae – but only few – exist in the cribellate genus *Pedipalparaneus* (family Mongolarachnidae).

Further characters: Two rows of eyes, posterior row procurved to recurved (in the holotype, the only adult male), posterior lateral eyes widely separated from the anterior lateral eyes (fig. 135), prosomal cuticula finely corniculate. Legs annulated, long in the holotype, distinctly shorter in the two juvenile spiders which are probably con-familiar.

Remark: The spinnerets and both metatarsi IV are lost in the holotype. The finely corniculate prosomal cuticula – which is not furrowed as in most cribellate spiders may indicate that the holotype is ecribellate.

The **relationships** (see the key and the tab. above) are doubtful. I do not know a strongly related extinct or extant genus. The kind of patella-tibia leg autotomy is not unique within the Leptonetoidea, see above and may be a hint to the relationships of *Autotomiana*; the ventral position of the femoral III-IV trichobothria-like setae is quite unusual. – In some respect – e. g. the kind of leg autotomy – the new taxon is similar to members of the family Linyphiidae in which the clypeus is long, retrolateral cheliceral fangs and a paracymbium exist.

**Distribution**: Mid Cretaceous amber forest of Myanmar (Burma).

*Autotomiana* n. gen.

Etymology: The name refers to the special kind of autotomy of the type species.

The gender of the name is feminine.

**Type species** (by monotypy): *Autotomiana hirsutipes* n. sp.

**Relationships and distribution:** See above.

***Autotomiana hirsutipes* n. gen. n. sp.** (figs. 135-139) photos 74-78

Etymology: The species name refers to the distal leg articles which bear long and dense setae.

**Material**: Holotype ♂ in Mid Cretaceous amber from Myanmar (Burma), F2766/BU/CJW. – See also the description of the two specimens below which I regard as probably congeneric.

**Preservation and syninclusions**: The spider is incompletely preserved in a fairly muddy piece of amber, most leg articles are cut off, the right leg IV is lost beyond the patella (the stump has apparently healed) by autotomy, both legs III are complete, the body is covered with an emulsion probably caused by the preservation the opisthosoma is strongly depressed dorsoventrally, injured and cut off posteriorly. – A tiny Hymenoptera and few Acari exist also in this piece of amber, one Acari is preserved between the left coxae III and IV of the spider.

**Diagnosis, relationships and distribution**: See above.

**Description** (♂):

Measurements (in mm): Body length ca. 7.0; prosoma: Length 3.5, width 3.0; most parts of the legs and of the opisthosoma are not preserved, length of tibia III 1.5, length of femur IV ca. 4.5, diameters of femora I/IV: 0.6 and ca. 0.4.

Colour grey brown, legs annulated.

Prosoma (fig. 135, photos) 1.17 times longer than wide, covered with an emulsion, flat, „thoracal shoulders“ absent, eye field wide, anterior median eyes not enlarged, posterior row strongly recurved, posterior lateral eyes on humps and distinctly separated from the anterior lateral eyes, clypeus short, basal cheliceral articles relatively long, retrolateral files apparently absent. – Legs (fig. 136, photos) (only parts are preserved, see above, both metatarsi IV are not preserved) long, bristles numerous and partly long, existing on femora, patella and tibia and metatarsi, quite setose, especially the metatarsi are densely covered with partly longer hairs. Long sensory setae – similar to trichobothria – are apparently absent on I and II, frequent retroventrally in the basal half on III and ventrally on IV (a quite unusual position of trichobothria). The large paired tarsal claws bear long teeth. – Opisthosoma strongly injured and deformed, apparently distinctly longer than wide, spinnerets cut off. – Pedipalpus (figs. 138-139) with slender articles, prolateral stridulatory pick absent, patella with a short blunt spine on a dorsal-

distal hump, cymbium large/wide, bearing several long bristles, paracymbium absent, embolus (I am not quite sure about the identity of this structure) long and standing out basally from the bulbus; other sclerites are difficult to identify and partly hidden.

?*Autotomiana* sp. 1 (photo 77)

**Material:** 1 ?juv. ♀ in Mid Cretaceous Burmite, F2768/BU/CJW.

**Preservation and syninclusions:** The spider is well and almost completely preserved, the opisthosoma is twisted by 180° (upside down) and injured anteriorly on the left side, the right leg IV is lost at its base near the opisthosomal injury apparently not by autotomy, both anterior legs are lost beyond the patella by autotomy. – A fissure in the amber runs dorsally longitudinally along the prosoma. A hairy Acari larva is preserved below the tip of the opisthosoma. A second Acari larva, a small larva of Coleoptera, few particles of insects excrement and numerous particles of detritus exist in the same piece of amber.

**Diagnosis** (?juv. ♀): Femoral trichobothria absent, opisthosoma widened in the anterior half (photo), legs relatively short, patella-tibia autotomy (photo) existing, metatarsus IV straight and not compressed.

**Description** (?juv. ♀):

Measurements (in mm): Body length 3.75, prosoma: Length 1.75, width 1.2; opisthosoma: Length 2.0, width 1.5; legs: Femur I: Left 1.9, right 1.0, II: Femur 1.8, tibia 1.45, tibia III ca. 1.0; leg IV: Femur 1.65, patella 0.6, tibia 1.25, metatarsus 1.9, tarsus ca. 0.8.

Colour medium grey brown, legs distinctly annulated.

Prosoma 1.46 times longer than wide, hairs short, feathery hairs absent, cephalic part distinctly narrowed anteriorly, eyes small, field wide, similar to *V. hirsutipes* but posterior row only slightly recurved and posterior lateral eyes not on humps. Clypeus short, mouth parts hidden. – Legs only fairly long, III distinctly the shortest, femur I not thicker than the remaining femora, a patella-tibia autotomy exists on both legs I, the right femur I is distinctly shorter than the left one, caused probably by a regeneration. Hairs indistinct, bristles numerous, fairly short, calamistrum absent, metatarsus IV straight and not compressed, femoral trichobothria absent. – Opisthosoma (photo) widened in the anterior half, spinnerets hidden.

The **relationships** are unsure: A patella-tibia autotomy exists in *Autotomiana hirsutipes*, too, and the eye position is similar but in *hirsutipes* exist femoral setae similar to trichobothria on III-IV, the legs are longer, the leg bristles are longer, and dense leg setae exist.

**Distribution:** Med Cretaceous amber forest of Myanmar (Burma).

?*Autotomiana* sp. 2 (photo 78)

**Material:** 1 ?juv. ♀ in Mid Cretaceous Burmite and 5 small separated pieces on amber, F2769/BU/CJW.

**Preservation and syninclusions:** The spider is almost completely preserved but some parts like the cribellum and the calamistrum are hidden, the opisthosoma is strongly deformed. The left leg II articles beyond the patella are lost by autotomy, parts of the left patella and tibia I (basally) are cut off, the opisthosoma is deformed. – Some thin spider's threads without droplets – partly cribellate? – are preserved below and right of the spider. A small Diptera: Nematocera and few plant hairs.

**Diagnosis** (?juv. ♀): Femoral trichobothria absent, legs relatively short, a patella-tibia autotomy exists.

**Description** (?juv. ♀):

Measurements (in mm): Body length ca. 4.7; prosoma: Length ca. 2.5, width 1.8; leg I: Femur 2.7, patella 1.1, tibia ca. 3.2.

Colour medium grey brown, opisthosoma lighter, legs indistinctly annulated.

Prosoma 1.4 times longer than wide, hairs short, foves deep and narrow, eyes in a wide field, small, in two rows, similar to *V. hisutipes* but posterior row procurved, posterior lateral eyes not on tubercles, and anterior and posterior lateral eyes less spaced. Clypeus short, mouth parts hidden. Basal cheliceral articles large, bearing each two large bristles. Legs setose, similar to *V. hirsutipes*. – Legs setose and relatively short, metatarsus IV hidden, a pair of ventral-apical bristle is observable on the left tarsus I, tibia I-II bear 3 pairs of ventral bristles besides laterals, feathery hairs absent, position of the metatarsal trichobothria unknown. – Pedipalpus large, the claw long. – Opisthosoma strongly deformed, hairs short, spinnerets hidden.

**Relationships:** According to its characters the spider may be a member of the genus *Autotomiana*.

**Distribution:** Med Cretaceous amber forest of Myanmar (Burma).

**Tribe BIAPOPHYSINI n. trib.**

Etymology: See below.

Type genus (by monotypy): *Biapophyses* n. gen.

**Diagnostic characters:** Prosomal cuticula finely but distinctly wrinkled (photo), tibiae and metatarsi with several bristles (fig. 140), ♂-pedipalpus (figs. 141-142): Tibia apically with a pair of erect dorsal apophyses, embolus long and in an almost circular position.

**Relationships:** See the key above.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

***Biapophyses* n. gen.**

Etymology: The name refers to the two tibial apophyses of the male pedipalpus, from bi (lat.) = two, and apophysis (gr.) = apophysis. The gender of the name is masculine.

Type species (by monotypy): *Biapophyses beate* n. sp.

**Diagnosis** (♂; ♀ unknown), **relationships and distribution:** See the new tribe.

***Biapophyses beate* n. gen. n. sp.** (figs. 140-142) photo 79

Derivatio nominis: The species is dedicated to BEATE STOLZ in Bremen, our German guide of a trip in Myanmar in I-II 2013, who was very kind and helpful, e. g., in getting fossil spiders from dealers for my scientific work.

**Material:** Holotype ♂ in Mid Cretaceous amber from N-Myanmar (Burma), F2548/BU/CJW.

**Preservation:** The spider is excellently and completely preserved in a clear yellow piece of amber; parts of body and legs are fairly deformed, few emulsions cover the mouth parts and other ventral parts of the spider.

**Diagnosis** (♂; ♀ unknown): See above; pedipalpus as in figs. 141-142.

**Description** (♂):

Measurements (in mm): Body length 2.0, prosoma: Length 0.9, width 0.55; opisthosoma: Length 1.0, width 0.5; leg I: Femur 0.9, patella 0.25, tibia 0.8, metatarsus 0.7, tarsus 0.42, tibia II 0.75, tibia II 0.6, tibia IV 0.65.

Colour: Prosoma and legs medium to dark brown (legs not annulated), opisthosoma light grey.

Prosoma (photo) 1.6 times longer than wide, anteriorly abruptly and distinctly smaller, cuticula finely but distinctly wrinkled, hairs absent, fovea deep. 8 larger eyes, anterior

medians smallest, posterior row straight, posterior medians spaced by their diameter, lateral eyes close together, clypeus long and strongly concave, basal cheliceral articles long and slender, distally bearing long and probably plumose hairs, lateral files absent, teeth of the anterior margin of the fang furrow tiny or probably absent, posterior margin with about 3 denticles, fangs fairly long, gnathocoxae long, slender and not converging, labium partly hidden, large and probably free, sternum wrinkled, spacing the coxae IV by almost their diameter. – Legs (fig. 140, photo) long and slender, hairs indistinct, order I/II/IV/III, bristles numerous and fairly long, existing on all femora, patellae, tibiae and metatarsi, all femora bear a dorsal one, I additionally a prolateral one in the distal half, patellae and tibiae bear 2 dorsal bristles, tibia I additionally 1 ventral, 1 retrolateral and 2 prolateral bristles, metatarsus I with two pairs of ventral

bristles and a crumple of 3 apicals, metatarsus IV bears a dorsal bristle near the middle besides the apical crumple; bristle of the remaining articles were not studied. Tibia IV bears 4 trichobothria which partly are very long, all metatarsal with a single trichobothrium, its position on IV in 0.62, tarsal trichobothria absent. Tarsal claws large, the paired ones apparently smooth, unpaired claw strongly bent, onychium existing. – Opisthosoma soft, twice as long as wide, hairs short and indistinct; it bears a pair of lung covers and 3 pairs of spinnerets, the medians bear several small spigots. Colulus (it bears an emulsion) probably large. – Pedipalpus (figs. 141-142, photo) with slender articles, femur slightly bent, patella and tibia fairly short, tibia with a pair of slender erect apical outgrowths, the dorsal one a bit longer, the retrodorsal one wider in its distal part, cymbium large, paracymbium absent, bulbus standing out, bearing a divided apophysis and a long and slender embolus in an almost circular position.

**Relationships and distribution:** See above.

**Tribe PALAEOHYGROPODINI** WUNDERLICH 2008: 590

**Diagnostic characters** (♂; ♀ unknown): Legs very long and slender, tarsi and metatarsi spiny, flexible and pseudoarticulate, III not much shorter than the remaining legs, patella of the ♂-pedipalpus (fig. 163) with a strong outstanding spur. Body length 4 mm.

Only *Palaeohygropona myanmarensis* PENNEY 2004.

The **relationships** are quite dubious, see WUNDERLICH (2008: 590) and the key above. I do not want to exclude relationships to the Hypochilomorpha. Originally the taxon was described erroneously as a member of the family Pisauridae (Lycosoidea) of the RTA-clade.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

## Tribe PRAETERLEPTONETINI WUNDERLICH 2008: 587

Type genus (by monotypy): *Praeterleptoneta* WUNDERLICH 2008.

**Diagnostic characters** (♂; ♀ unknown) (See the key above): Clypeus long and protruding ventrally (fig. 169). Pedipalpus (figs. 144f): Cymbium with a distinctly sclerotized retrolateral spur/outgrowth. I am not sure about the identity of the sclerites of the bulbus. I do not want to exclude that the sclerite named embolus in the holotype of *P. spinipes* WUNDERLICH 2008 is really a tegular apophysis. Body length only 1.0 mm (smallest known member of the Praeterleptonetidae besides *Hypotheridiosoma spinipes*).

**Relationships:** See the key above.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

### *Praeterleptoneta* WUNDERLICH 2008

Two species of this genus have been described under *Praeterleptoneta*: *P. spinipes* WUNDERLICH 2008 (the type species, figs. 169-170), and *P. tibialis* WUNDERLICH 2011; *tibialis* is here transferred to *Parvispina* n. gen.: see below.

**Diagnosis, relationships and distribution:** See the tribe.

## Tribe ZARQARANEINI WUNDERLICH 2008: 642

Type genus (by monotypy): *Zarqaraneus* WUNDERLICH 2008.

Further genera: *Crassitibia* n. gen., *Curvitibia* n. gen., *Hypotheridiosoma* WUNDERLICH 2012 (n. relat.), *Parvispina* n. gen. and *Zarqaraneus* WUNDERLICH 2008.

**Diagnosis** (♂; ♀ unknown): Metatarsal bristles absent. Pedipalpus: Cymbium (figs. 144f) retrobasally with a pointed, usually horn-shaped and more or less sclerotized „paracymbium“.



**Relationships:** The tribe is transferred here from the Araneoidea: Protheridiidae to the family Praeterleptonetidae (see above). See also the key to the taxa of this family above.

**Distribution:** Mid Cretaceous Burmese amber forest and Early Cretaceous amber forest of Jordan: *Zarqaraneus hudei*.

### **Crassitibia n. gen.**

Etymology: The name refers to the thick tibia I of the taxon, from crassus (lat.) thick.

The gender of the name is feminine.

Type species: *Crassitibia longispina* n. sp. – Further species: *C. tenuimana* n. sp.

**Diagnosis:** (♂; ♀ unknown): Tibia I (fig. 143) thickened ventrally in the basal half or not thickened (in *tenuimanus*), relatively stout and bearing a very long proapical bristle. Metatarsus I unusually long. Pedipalpus (figs. 144, 147): Tibia with at least a single apophysis (*tenuimanus*) or (in *longispina*) a ventral, a retroapical and a proapical apophysis, paracymbium compact and wide (not sickle-shaped), widely fused to the cymbium, strongly sclerotized.

**Relationships:** See the key to the genera; the genera *Curvitibia* and *Parvispina* are most related. Probably less leg bristles than in the related genera; metatarsus I is longer than in the related taxa.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

### ***Crassitibia longispina* n. gen. n. sp. (figs. 143-145) photo 84**

Etymology: The species name refers to the long leg bristles; from longus (lat.) = long and spina (lat.) = spine, bristle.

**Material:** Holotype ♂ in Mid Cretaceous Burmite, F2779/BU/CJW.

**Preservation and syninclusions:** The spider is well and completely preserved in a small and clear yellow piece of amber. The opisthosoma is fairly compressed dorso-ventrally, some bubbles exist under the pedipalpi, on the legs and ventrally on the prosoma.

**Diagnosis:** See above.

**Description** (♂; ♀ unknown):

Measurements (in mm): Body length 1.3, prosomal length 0.8, opisthosomal length (it is deformed) 0.8; leg I: Femur 0.85, patella 0.32, tibia 0.6, metatarsus 0.9, tarsus 0.32, tibia II 0.4, tibia III 0.22, tibia IV 0.36.

Colour: Prosoma and legs medium brown, legs probably not annulated, opisthosoma light brown.

Prosoma (photo) distinctly longer than wide, off, probably short and indistinct (most hairs are rubbed off), fovea hidden, apparently 8 eyes which are strongly deformed clypeus not protruding, sternum and most mouth parts deformed or hidden, basal cheliceral articles probably small, fangs thin. – Legs (fig. 143, photo) only fairly long but metatarsus I quite long, I longest, III distinctly shortest, tarsi short, tibia I thickened basally-ventrally, hairs indistinct, bristles long, especially the distal patellar one (the basal one is weak), and the proapical tibial one on leg I, femur I bears 3, tibia I 5 bristles, metatarsal trichobothria and tarsal organs unknown, unpaired tarsal claws apparently smooth (as observable in a magnification of 150x), unpaired claw not bent upwards. – Opisthosoma deformed, hairs not numerous, partly long, most spinnerets are hidden. – Pedipalpus (figs. 144-145) (see also the diagnosis): Structures of the bulbus partly hidden, bearing at least two tegular apophyses, embolus unknown.

**Relationships:** See *C. tenuimana* n. sp.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

***Crassitibia tenuimana* n. gen. n. sp.** (figs. 146-148)

**Etymology:** The species name refers to the tarsi and metatarsi of the holotype which are thinned by the preservation; from *tenuis* (lat.) = thin and *manus* (lat.) = hand/tarsus.

**Material:** Holotype ♂ and 2 separated pieces of amber in Mid Cretaceous Burmite, F2784/BU/CJW.

**Preservation and syninclusions:** The spider is completely and fairly well preserved in a yellow piece of amber; mainly tarsi and metatarsi are thinned by the preservation parts of body and legs are covered with an emulsion, the prosoma is compressed dorso-ventrally, particles of detritus are preserved near the spider. – Remains of few arthropods like a Diptera: Nematocera and two insect larvae are preserved in the separated pieces of amber.

**Diagnosis** (♂; ♀ unknown): Tibia I not thickened, pedipalpus (figs. 147-148): Patella bulgind dorsally-apically, paracymbium long, widely fused with the cymbium, questionable embolus strongly bent (shape quite different in a different position!).

**Description (♂):**

Measurements (in mm): Body length 1.6; prosoma (it is distinctly deformed): Length 0.75, width 0.65; opisthosoma (deformed): Length ca. 1.2, width and height 0.9; leg I: Femur 1.1, patella 0.3, tibia 0.6, metatarsus 0.75, tarsus 0.3.

Colour: Prosoma and legs medium brown, opisthosoma light brown.

Prosoma (badly preserved and deformed) with 8 strongly deformed eyes, clypeus relatively long, not protruding. – Legs (deformed) (fig. 146): Order I/II/IV/III, IV relatively small, bristles long, existing on femora, patellae and tibiae, femora 1 dorsally, at least I additionally 1 prolaterally in the distal half, patella I dorsally a weak basal and a long apical one, tibia I with 2 dorsals, 1 prolateral and 3 near its end. Only few trichobothria on tibia III and IV, metatarsal trichobothria unknown. Three large and smooth tarsal claws, the unpaired claw bent in a right angle and almost straight in the distal half. – Opisthosoma deformed, not high, hairs short, spinnerets stout. – Pedipalpus (see above) only fairly large; a retroventral tibial apophysis may exist.

**Relationships:** In *C. longispina* n. sp. the shape of the paracymbium and of the questionable embolus are quite different, its questionable embolus is s-shaped.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

**Curvitibia n. gen.**

**Etymology:** The name refers to the swollen and bent tibiae I-II, from *curvus* (lat.) = bent.

The gender of the name is feminine.

**Type species** (by monotypy): *Curvitibia curima* n. sp.

**Diagnosis:** (♂; ♀ unknown): Legs I-II (fig. 149): Tibia thickened basally ventrally, metatarsus basally dorsally compressed. Pedipalpus (figs. 151-154): Patella with a long and protruding dorsal apophysis, tibia short, probably bearing a pointed prolateral apophysis (\*), cymbium with a long and pointed retrolateral „paracymbium“, bulbus with a large tegular apophysis and a long and bent embolus.

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(\* ) I am not quite sure about the origin of this apophysis which may be a tegular apophysis.

**Relationships:** See the key to the genera. The genera *Crassitibia* and *Parvispina* are most related.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

***Curvitibia curima* n. gen. n. sp.** (figs. 149-154) photos 85-86

**Etymology:** The species name refers to the dorsally incomplete prosoma of the holotype which is cut off within the amber, from *curimus* (lat.) = cut off.

**Material:** Holotype ♂ in Mid Cretaceous Burmite and a separated piece of amber, F2778/BU/CJW.

**Preservation and syninclusions:** The spider is preserved in a small and clear yellow piece of amber, a dorsal part of the prosoma including the eyes is rubbed off on a layer within the amber, both pedipalpi are excellently preserved, the opisthosoma is compressed dorsally. – A thin spider's thread without droplets is running cross just in front of the spider's anterior legs. A short thread and tiny remains of plants exist in the separated piece of amber.

**Diagnosis:** See above.

**Description** (♂; ♀ unknown):

Measurements (in mm): Body length 1.2, prosoma: Length 0.6, width (it is compressed) 0.65; opisthosoma : Length 0.8, width (compressed) 0.85; leg I: Femur 0.8, patella 0.22, tibia 0.55, metatarsus 0.55, tarsus 0.38, tibia II 0.45, tibia III 0.22, tibia IV 0.34. Colour light brown, legs not annulated.

Prosoma (photo) probably (see above) as wide as long, eye region cut off, clypeus relatively long and slightly protruding, basal cheliceral articles slender, fangs thin, anterior margin of the fang furrow with 3 short and wide teeth, gnathocoxae large and converging, labium distinctly wider than long, sternum elongated between the coxae IV. – Legs (figs. 149-150, photos) fairly long, order I/II/IV/III, I distinctly longest, III distinctly shortest, hairs indistinct, tibia I-II bulging ventrally basally, metatarsi I-II compressed dorsally basally, tarsi relatively long, bristles very long, existing on femora, patellae and tibiae; I: Femur at least 6, patella dorsally a weakly developed basally and a very long apically, tibia at least 6 (observable in prolateral aspect). Tibia III-IV without a larger number of long trichobothria, metatarsal trichobothria and tarsal organs unknown, three tarsal claws which apparently are smooth, the unpaired one not bent upwards. – Opisthosoma (photos) (it is deformed) about as wide as long, hairs numerous and short, colulus and anal tubercle well developed, three pairs of spinnerets, the anteriors fairly widely spaced. – Pedipalpus (figs. 151-154, photos) (see also above: Femur slender, „paracymbium“ with a pointed hook near its base, embolus in contact with a wide conductor.

**Relationships and distribution:** See above.

## **Groehnianus n. gen.**

**Etymology:** It is a pleasure to me to dedicate this genus to CARSTEN GRÖHN in Glinde, the owner of the generotype.

**Type species** (by monotypy): *Groehnianus burmensis* n. sp.

**Diagnosis** (♂; ♀ unknown): Opisthosoma leathery, bearing at least three pairs of sigillae (fig. 155), tibia I not thickened, bearing long bristles; pedipalpus (fig. 156): Questionable paracymbium (or tegular apophysis?) bent in a right angle, with a point near the middle and weakly divided apically, bulbus wide, basally with a flattened apophysis.

**Relationships:** According to its characters (e. g. eyes, chaetotaxy, clypeus, paracymbium) *Groehnianus* is a member of the Praeterleptonetidae: Zarqaraneini). In the related genera – see the key – the opisthosoma is soft and the shape of the paracymbium is different.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

## ***Groehnianus burmensis* n. gen. n. sp. (figs. 155-156) photo 87**

**Etymology:** The species name refers to the type area (within the northern part of) Myanmar (Burma).

**Material:** Holotype ♂ in Mid Cretaceous Burmite, coll. C. GRÖHN no. 11039; later most probably Geol.-Palaeontol. Inst. Univ. Hamburg.

**Preservation and syninclusions:** The spider is completely and well preserved in an oval yellow piece of amber which is 2 cm long. Small (?gas) bubbles cover parts of body, legs and ventral parts of the pedipalpi. – Syninclusions: A line of questionable insect's excrement, 11 mm long, plant hairs and a large leaf of a fern – as long as the piece of amber – are preserved in the same piece of amber.

**Diagnosis** (♂; ♀ unknown): See above.

### **Description** (♂):

Measurements (in mm): Body length 1.25; prosoma: Length 0.7, width 0.5; opisthosoma: Length 0.85, width 0.5; leg I: Femur 0.65, patella 0.17, tibia ca. 0.38, metatarsus 0.4, tarsus 0.3, tibia II ca. 0.35.

Colour: Prosoma and legs medium brown, opisthosoms light grey brown.

Prosoma (photo) 1.4 times longer than wide, anteriorly distinctly narrowed, bearing few long hairs (others most probably rubbed off), fovea absent, 8 eyes in a wide field,

posterior row slightly recurved, posterior median eyes spaced by less than their diameter, lateral eyes close together, anterior median eyes fairly protruding. Clypeus not protruding, mouth parts partly hidden, gnathocoxae in a parallel position, labium wide, not rebordered, with a seam to the sternum which is distinctly elongated between the coxae IV. – Legs (photo) only fairly long, order I/II/IV/III, tibia I not thickened, hairs indistinct, metatarsal trichobothria and position of the tarsal organ unknown, bristles numerous and quite long, the distal one on patella I about as long as the article, existing on femora, patellae and tibiae, femora: I, II and IV 2 dorsals, III only a single one, I additionally 2 prolaterals in the distal half, patellae dorsally with a weak basal and a long distal one, tibia I 2 very long dorsals and a long prolateral one in the middle of the article, II apparently similar, III and IV without a prolateral bristle. Three smooth tarsal sc claws, the unpaired one long and strongly bent. – Opisthosoma (fig. 155, photo) 1.7 times longer than wide, dorsally leathery and bearing at least three pairs of sigillae hairs short and indistinct, anterior spinnerets stout and fairly spaced, colulus probably absent. – Pedipalpus (fig. 156) (see above; the ventral part is hidden) with slender articles, patella longer than wide, bulbus relatively large; I am not quite sure about the identity of the paracymbium.

**Relationships and distribution:** See above.

***Hypotheridiosoma*** WUNDERLICH 2012: 215 (figs. 157-162) (**n. relat.**)

Type species (by monotypy): *Hypotheridiosoma paracymbium* WUNDERLICH 2012.

**Diagnosis:** (♂; ♀ unknown): Tibia I not thickened (fig. 161). Pedipalpus (fig. 162): Cymbium with two dorsal bristle-shaped hairs and a long, pointed and bent retrobasal „paracymbium“. Smallest spiders of the Praeterleptonetidae besides *Praeterleptoneta spinipes*, body length 0.9-1.1 mm.

**Relationships:** Originally this taxon was regarded by me as a member of the family Theridiosomatidae with some hesitation („I do not know a closely related genus“.). In the single previously known male of this taxon the area of theridiosomatid sternal pits is hidden but in *falcata* n. sp. this area is well observable, and sternal pits are absent. . Long tibial III-IV trichobothria are absent (they frequently are rubbed off in fossil spider). In contrast to the Theridiosomatidae the unpaired tarsal claw is bent downwards, the cymbium bears bristle-shaped hairs, and the paracymbium is quite long. Therefore I transfer the genus from the Theridiosomatidae to the Praeterleptonetidae (**n. relat.**). *Spinipalpitibia* n. gen. may be most related.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

***Hyportheridiosoma falcata* n. sp.** (fig. 157) photos 88-89

**Etymology:** The species name refers to the sickle-shaped paracymbium, from *falcatus* (lat.) = sickle-shaped. (A similar paracymbium exist in some related taxa, too).

**Material:** Holotype ♂ in Mid Cretaceous Burmite, F2783/BU/CJW.

**Preservation and syninclusions:** The spider is very well and almost completely preserved in a small and clear yellow piece of amber, only parts of the right leg I (tarsus, parts of metatarsus and Tibia) are cut off, prosoma and opisthosoma are slightly deformed. – Organic remains are preserved near the right patella II, an incomplete Diptera: Nematocera is preserved in the same piece of amber.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (fig. 157): Cymbium slender and elongated apically, paracymbium long, sickle-shaped, pointed and standing widely out, embolus bent, in a distal position.

**Description** (♂):

Measurements (in mm): Body length 1.1; prosoma: Length 0.6, width 0.45; opisthosoma: Length 0.7, width 0.6, height 0.45; leg I: Femur 0.85, metatarsus 0.68, tarsus 0.33, femur II 0.68, femur III 0.45, femur IV 0.63, basal bristle of tibia I 0.28.

Colour: Prosoma and legs medium brown, legs not annulated, opisthosoma light brown. Prosoma (photo) 1.33 times longer than wide, not raised, hairs and fovea indistinct, 8 eyes (they are partly covered with an emulsion) in a wide field, posterior row strongly recurved, anterior eyes fairly protruding, clypeus fairly long, concave, not protruding, basal cheliceral articles only fairly large, labium large, sternum wide, the coxae IV widely spacing. – Legs fairly long (see above), most bristles very long, existing on femora, patellae and tibiae, femora bearing a dorsal one, I with an additional prolateral one in the distal half, patella I with a weak basal and a long apical one, tibia I 2 dorsally, a long prolateral one in the basal half and 3 distal/apical bristles. Position of the metatarsal trichobothrium unknown, tibia III and IV bear very few long trichobothria. 3 long and smooth basal claws, the unpaired claw bent in a right angle. – Opisthosoma 1.33 times longer than wide, oval, not high, bearing shorter and longer hairs, sigillae may exist, lung covers large, 3 pairs of spinnerets, the anteriors stout, colulus probably absent. – Pedipalpus (fig. 157) (see above) with slender articles, the distal cymbial bristle is longer than the basal one, bulbus flat.

**Relationships:** In *H. paracymbium* WUNDERLICH 2012 (figs. 159, 162) – the only further congeneric species – exist also two long cymbium bristles in a similar position but the paracymbium is fairly s-shaped bent (its embolus is unknown).

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).



## ***Parvispina* n. gen.**

**Etymology:** The name refers to the relatively small/weak leg bristles of the taxon, from parvus (lat.) = small and spina (lat.) = spine, bristle.

**Type species** (by monotypy): *Praeterleptoneta tibialis* WUNDERLICH 2011.

The gender of the name is feminine.

**Diagnosis** (♂; ♀ unknown) (see also the characters of the tribe Zarqaraneini): Tibia I (figs. 164-165) thickened in the basal half dorsally AND ventrally, pedipalpus: Figs. 166-168.

**Relationships:** See the key to the genera above. According to the existence of a thickened male tibia I the genera *Crassitibia* and *Curvitibia* are most related; tibia I is thickened only ventrally in these genera and the structures of the bulbus sclerites are different.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

***Parvispina tibialis*** (WUNDERLICH 2011) (under *Praeterleptoneta*) (**n. comb.**)  
(figs. 164-168)

I tried to find a tarsal organ in the holotype of this spider, and I found a questionable one in a position 0.5 on the left tarsus I. (These organs are very difficult to recognise in fossils with the help of a light microscope).

**New material:** 1♂ in Mid Cretaceous amber from Burma (Myanmar), F2453/BU/CJW.

**Description and discussion:** The spider F2453 is completely and fairly well preserved, a larger gas bubble covers the left anterior part of the prosoma. Its body length is 1.8 mm, its prosomal length 0.9 mm, the dorsally AND ventrally thickened tibia I is a typical character of this species. An additional dorsal bristle exists on all femora but has not been drawn in the holotype in which it exists, too. In contrast to the holotype the bulbi of the present male are not deformed by the preservation – see the figs. 167-168 – and allow further conclusions on the sclerites of the tegulum and probably even on the relationships of the family Praeterleptonetidae although I am still not sure about the identity of some tegular sclerites of this taxon, especially I doubt the correct identity of the embolus described in the holotype of *tibialis*: I do not want to exclude that the sclerite named embolus in the holotype is really a tegular apophysis, and the „sperm duct“ of this male – see WUNDERLICH (2011: fig. 5) – may really be the embolus. Sclerites 1 and 2 (probably including „Q“) of F2453 are tegular apophyses (see the figs.), and sclerite 3 may

be a „median apophysis“ which probably is homologous to the median apophysis in the superfamily Araneoidea. The cymbial „horn“ („paracymbium“) originates probably in a more distal position than the retrobasal paracymbium in the superfamily Araneoidea.

### **Spinipalpitibia n. gen.**

Etymology: The name refers to the ventral bristles – from spina (lat.) = bristle, spine – of the male pedipalpal tibia.

The gender of the name is feminine.

Type speciess (by monotypy): *Spinipalpitibia maior* n. sp.

**Diagnosis** (♂; ♀ unknown): Tibia I not thickened. Pedipalpus (fig. 172): Articles without apophyses, tibia long, with a transverse ventral rim and with a pair of long ventral bristles, the cymbium bears a long bristle, the existence of a „paracymbium“ is unknown.

**Relationships** (see the key above): *Hypotheridiosoma* may be most related.

**Distribution**: Mid Cretaceous amber forest of Myanmar (Burma).

### ***Spinipalpitibia maior* n. gen. n. sp. (figs. 171-172) photo 90**

Etymology: The species name refers to the body which is larger than in most other members of this family.

**Material**: Holotype ♂ in Mid Cretaceous Burmite from N-Myanmar (Burma), F2713/BU/CJW.

**Preservation and syninclusions**: The spider is strongly deformed – prosoma and opisthosoma are inclined dorsally – and almost completely preserved (only the right leg IV is probably lost) in a clear yellow-orange piece of amber which is full of inclusions. The spiders pedipalpi are well preserved but partly hidden, ventrally the spider is hidden by a larger Diptera which is ca. 3 mm long, is partly in contact with the spider, and has probably been the prey of the spider. – Further syninclusions: A tiny insect larva above the spider, numerous Hymenoptera and Diptera, several Acari, one – the larva of the family Erythraeidae – is parasitising a Nematocera dorsally, 1 ?Grylloidea larva, numerous particles of soil and detritus. Two grey and pear-shaped „bubbles“ – produced by boring bivalves? – are preserved at the surface of the piece of amber and

are connected with each other by a remain of a plant between their openings. Another bubble is connected by a soft grey „outflow“ of the bubble with remains of a Diptera which is partly cut off at the surface of the piece of amber. More than half of a fourth „bubble“ has been cut off and is filled with tiny particles of questionable pebble.

**Diagnosis** (♂; ♀ unknown) (see the new genus): Pedipalpus: Fig. 172 (see below); body length ca. 1.8 mm.

**Description** (♂):

Measurements (in mm): Body length ca. 1.8, prosomal length 0.9; leg I: Femur 0.9, patella 0.3, tibia 0.75, metatarsus 0.8, tarsus 0.37, tibia II more than 0.65, tibia III ca. 0.45, tibia IV ca. 0.6.

Colour: Prosoma dark brown, legs medium brown, not annulated, opisthosoma dark grey.

Prosoma (it is strongly deformed): 8 larger eyes in two rows similar to *Praeterleptoneta spinipes*, see WUNDERLICH (2008: 661, fig. 23). – Legs (fig. 171, photo) only fairly long, I not distinctly the longest, hairs indistinct, bristles fairly long and numerous, existing on femora to metatarsi; leg I: Femur at least 6, patella 2 dorsally, tibia at least 9, metatarsus at least 5. Position of the long metatarsus I trichobothrium in 0.93, unpaired tarsal claws existing. – Opisthosoma (photo) (it is strongly deformed, the spinnerets are hidden) oval, bearing short hairs. – Pedipalpus (fig. 172) (the distal part is hidden, spiny, tibia long, ventrally with a distinct transverse rim and a pair of long bristles, cymbium with a strong – apparently straight – retrolateral bristle, bulbous large, bearing a thin sclerotized retrodistal sclerite which stands out – the distal part of the embolus?).

**Relationships and distribution:** See above.

***Zarqaraneus*** WUNDERLICH 2008 (figs. 173-174)

Type species (by monotypy): *Zarqaraneus hudei* WUNDERLICH 2008.

**Diagnosis** (♂; ♀ unknown): Clypeus rather short and not protruding. Tibia I not thickened. Pedipalpus as in fig. 174.

Notes on the holotype: (1) The sternum of the single known specimen, is well preserved and well observable; sternal pits – like in the family Theridiosomatidae – are surely absent. (2) The unpaired tarsal claws are not bent upwards like in the Theridiosomatidae. (3) At some thin spider's threads near the holotype sticky droplets are absent.

**Relationships:** See the key above.

**Distribution:** Early Cretaceous amber forest of Jordan.

**?*Praeterleptonetidae* indet., female with two clutches of eggs** (figs. A–B, photo 91)

**Material:** 1♀ and two clutches of eggs (A and B) in the same piece of Mid Cretaceous amber from Myanmar (Burma), F2735/BU/CJW.

**Preservation and syninclusions:**

The flat yellow-orange piece of amber consists of about half a dozen layers. Some layers are partly darkened brown apparently by the preservation, the pressure of the resin. The female spider is fairly well and almost completely preserved, only the tip of the left tarsus I is cut off; its body and legs are partly deformed – the prosoma is laterally inclined – and darkened by the preservation. The spider has been captured by the resin alive: The legs I and II are stretched forward but not bent under the body as is typical in dead spiders. – **Syninclusions:** Small – ca. 0.1 mm long – deformed and translucent remains of an arthropod indet. are preserved just right of the right tibia III; I do not want to exclude that it has been a PREY of the spider. Two CLUTCHES OF EGGS are preserved near the spider; one of these clutches is almost in contact with three legs of the spider (fig. B, photo), the other is preserved 5 mm left of the spider's body. Both clutches are distinctly deformed and partly cut off and broken off at the surface of the amber, four eggs of clutch B are preserved away from the remaining eggs and one egg is preserved on the other side of the plant remains (fig. B). The eggs were translocated within the resin. Clutch (A) is attached to a thick thread, clutch (B) is preserved on questionable – apparently decomposed – remains of a plant (a leaf?). Few spider threads without droplets, particles of detritus and pyrite are also preserved in this piece of amber.

**Descriptions:**

(a) The female spider (photos)

Measurements (in mm): Body length 2.5, prosomal length 1.3; leg I: Femur ca. 1.15, patella 0.25, tibia 1.55, metatarsus 1.5, tarsus 0.9.

Colour medium grey brown.

Prosoma distinctly longer than wide, hairs short, most of the (eight?) eyes hidden, clypeus relatively short, not protruding, basal cheliceral articles slender, not protruding, largely free (basally hidden), fangs long, teeth of the fang furrow partly hidden, at least one larger tooth is observable on the anterior margin, coxae IV spaced by less than their diameter. – Pedipalpus long and slender, not spiny, tarsal claw apparently absent. – Legs long, order I/II/IV/III, III distinctly the shortest, hairs short, bristles fairly short, few and thin, absent on femora, tibiae and tarsi, tibia IV bears a dorsal-basal and a retroapical one, metatarsi with an apical garland of several bristles, position of the metatarsal I trichobothrium in ca. 0.88, paired tarsal claws with long teeth, unpaired claw long and bent in a right angle. – Opisthosoma oval, hairs short, spinnerets short, the anteriors thick and close together, colulus tiny or absent.

(b) The clutches of eggs (figs. A-B, photos):

Measurements: The diameter of the deformed clutches was originally probably about 2.5 mm, the diameter of the eggs in average is ca. 0.3 mm. – Both clutches are deformed and partly cut and broken off at the surface of the amber. Threads on/between the eggs are apparently absent (not observable); a sticky (?) emulsion – a glue? – or a secretion exists at least on the surface which may have originated from the female or from the eggs. The larger clutch (A) is connected with a thick divided thread which may have fixed it to plants, clutch (B) is attached to questionable remains of a plant, partly hidden (figs. A and B) and almost in contact with the tips of three legs of the female. I did not find distinct structures within the eggs which are partly cut. The surface of some eggs bears tiny white „cornicules“ which may be Bacteria. Ca. 9 eggs exist at the „equator“ of a clutch, and so I estimate that each clutch may have contained about 150 eggs.

### **Discussion:**

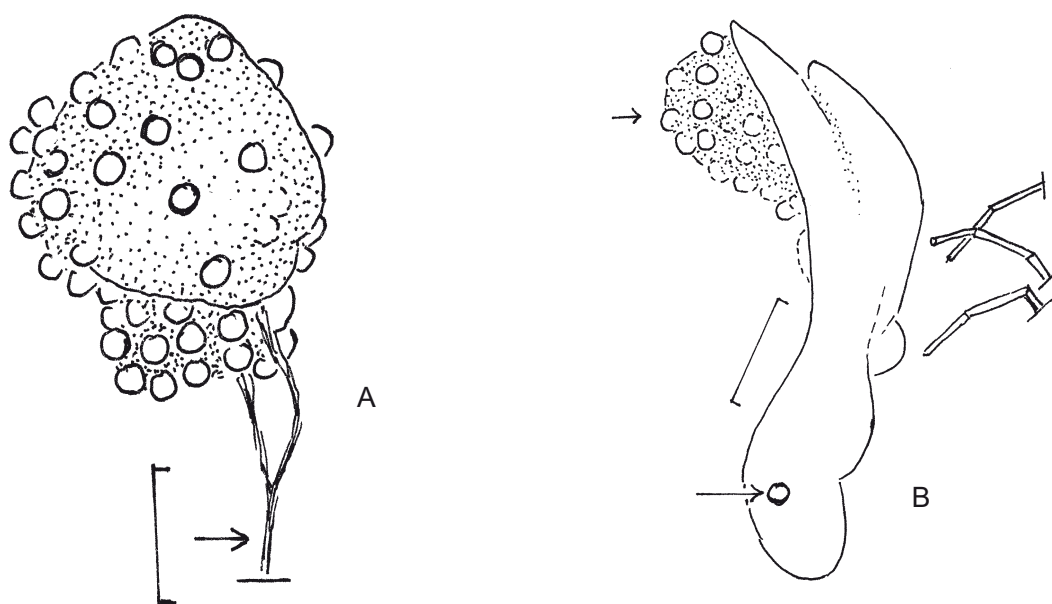
The eggs: Fossil eggsacs/cocoons/clutches are reported from fossil spiders in Eocene Baltic amber, see WUNDERLICH (2004: 79-87, photos 494-523) but up to now they have not been reported from older fossils to my knowledge. The existence of a spider female together with its eggs is a lucky coincidence. (\*)

Most entelegyne spiders build true cocoons (egg cases); these are surrounded by loose mash of threads in most Trionycha or tough and thin-walled in most Dionycha. In Haplogynae the eggs are usually not thickly covered with threads but hold together with only few and indistinct threads like in the present clutches. The construction of more than a single egg sac or clutch of eggs by the same female is not very rare in spiders. The number of eggs in spiders varies from one or two to more than a thousand but usually a case or clutch contains some few hundred eggs. I regard the remains of the two clutches of eggs as produced by the present female spider.

Relationships of the present female: The almost „naked“ kind of the present clutches of eggs corresponds to the type of most haplogyne spiders. In contrast to members of the haplogyne superfamily Pholcoidea – in which females carry their eggs with the help of their chelicerae – the eggs are attached on a substrate in the present female, similar e. g. to extant members of the family Leptonetidae. Unfortunately the number of eyes is unknown in the present female; if it possesses eight eyes I would not exclude with certainty that it may be the member of the superfamily Leptonetoidea. In contrast to the present female in the extinct family Praeterleptonetidae (Leptonetoidea) – which is ecribellate, too – a larger number of leg bristles (including femoral bristles) exists in the described Praeterleptonetidae as well as (in all taxa?) a larger colulus, and no or tiny teeth of the paired tarsal claws.

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(\*) A questionable true cocoon of a spider is preserved in the same piece of amber as are two Acari and remains of a female of the family Oecobiidae indet. and spider threads, F2377/BU/CJW. It is still not described.



Figs. A-B: Two clutches of eggs in the same piece of Burmese amber as a female of a questionable member of the extinct family *Praeterleptonetidae* indet.

An „emulsion“ on the surface of the clutches hides several eggs. Scale 1 mm.

A) Clutch of eggs connected to thick threads (arrow). The clutch has been crumbled and deformed, and originally contained about 150 eggs according to my estimation.

B) Clutch of eggs (short arrow) and a loose egg (long arrow) attached to a larger and apparently decomposed piece of plant. Few articles of three legs of the „mother female“ are shown on the right.

**Family PHOLCOCHYROCERIDAE** WUNDERLICH 2008 figs. 175-182, photos 70-73, family key no. 29

Originally this family – under *Pholcochyrocerini* WUNDERLICH 2008 – was based solely on the type genus *Pholcochyrocer* WUNDERLICH 2008 in Cretaceous Burmese amber. In this paper I add the new genus *Spinicreber*. In 2012: 192-193 I elevated the tribe *Pholcochyrocerini* to family rank.

Members of this family are **characterized** within the Leptonetoidea by the existence of a cribellum (plesiomorphy) (probably undivided), usually spiny pedipalpal articles, and at least two large slender and pointed tegular apophyses (figs. 177f ) (an apomorphy?), one, apparently, is connected with the embolus.

Further characters: 8 eyes in a wide field, a pair of lungs, basal cheliceral articles not fused, probably basically a long unpaired tarsal claw and existence of „auxiliary hairs“ of tarsus IV, bulbus attached ventrally on the cymbium.

The **relationships** are unsure; see the families Mongolarachnidae (cribellate, too) and Praeterleptonetidae (ecribellate), fig. G.

Type genus: *Pholcochyrocer* WUNDERLICH 2008.  
Further genera: *Spinicreber* n. gen. and *Spinipalpus* n. gen.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

**Key to the genera of the family Pholcochyroceridae (♂):**

- 1 Pedipalpal femur with a dorsal-distal comb of teeth-shaped structures (fig. 175), bulbus with long, furcate and strongly sclerotized tegular apophyses, one of these bears the embolus. . . . . *Pholcochyrocer*
- No such comb nor TWO long tegular apophyses. . . . . 2
- 2(1) Bulbus with a long, strongly sclerotized and sickle-shaped apophysis and with a large u-shaped apophysis (figs. 177-178). . . . . *Spinicreber*
- Bulbus with two short and strongly sclerotized apophyses, without an u-shaped apophysis (figs. 181-182). . . . . *Spinipalpus*

***Pholcochyrocer*** WUNDERLICH 2008

Type species: *Phocochyrocer guttulaeque* WUNDERLICH 2008.  
Further species: *P. pecten* WUNDERLICH 2012 and ?*P. baculum* WUNDERLICH 2012.



**Diagnosis** (♂; ♀ unknown): Pedipalpal femur with a dorsal-distal comb of teeth-shaped structures (fig. 175), bulbus with long, furcate and strongly sclerotized tegular apophyses, one of these bears the embolus.

**Further characters:** See the family.

**Relationships:** In *Spinicreber* n. gen. exists a weakly sclerotized u-shaped apophysis of the bulbus and a single strongly sclerotized tegular apophysis.

**Distribution:** Mid Cretaceous amber forest of N-Myanmar (Burma).

**Spinicreber n. gen.**

Type species (by monotypy): *Spinicreber antiquus* n. sp.

**Diagnosis** (♂; ♀ unknown): pedipalpus (figs. 177-178): Bulbus large, bearing an u-shaped weakly sclerotized tegular apophysis which is widened apically, and a slender, pointed and strongly sclerotized tegular apophysis; the questionable embolus may be long.

**Further characters:** Legs with numerous long bristles including few ventral tibial and metatarsal ones (fig. 176).

**Relationships:** According to the existence of 8 eyes and a cribellum as well as the structures of the pedipalpus I regard *Spinicreber* as a member of the Pholcochyroceridae. In *Pholcochyrocer* a pedipalpal femoral comb exists, an u-shaped, widened and weakly sclerotized tegular apophysis is absent.

**Distribution:** Mid Cretaceous amber forest of N-Myanmar (Burma).

*Spinicreber antiquus* n. gen. n. sp. (figs. 176-178) photo 70

Etymology of the species name: From antiquus (lat.) = old, existing in former times.

**Material:** Holotypus ♂ in Mid Cretaceous amber from N-Myanmar (Burma), F2552/ BU/ CJW.

**Preservation and syninclusions:** The spider is incompletely preserved in a clear piece of amber; the opisthosoma and several leg articles are cut off, the right legs and most articles of the left legs III and IV are preserved, the structures of the bulbus are well observable. – Few questionable spider's threads and two Diptera are preserved in the same piece of amber.

**Diagnosis** (♂; ♀ unknown): Bristles of leg I as in fig. 176, pedipalpus as in figs. 177-178.

**Description (♂):**

Measurements (in mm): Body length ca. 2.5, prosoma: Length 1.35, width 1.3; leg I: Femur 2.0, patella 0.6, tibia 1.5, metatarsus 1.65, tarsus 0.75, tibia II 1.0, tibia III 0.5, tibia IV 0.7.

Colour dark brown, legs not annulated.

Prosoma about as long as wide, smooth, hairs and fovea indistinct, 8 large deformed eyes in two rows, posterior row distinctly recurved, lateral eyes distinctly spaced from each other, basal cheliceral articles long, mouth parts hidden. – Legs (fig. 176): Order I/II/IV/III, I and II fairly long, I clearly the longest, III distinctly the shortest, hairs short, numerous long bristles on femora, patellae, tibiae and metatarsi; leg I: Femur 7, patella 2 dorsally and a single retrolateral one, tibia 10 including a ventral pair in the basal half, metatarsus 10 including a ventral pair near the middle, metatarsus IV ca. 8. Metatarsus IV straight, calamistrum consisting of short bent hairs in the basal 40% of the length. Position of a questionable trichobothrium on metatarsus III in ca. 0.3, paired tarsal claws probably toothless, unpaired claw not smaller. – Opisthosoma cut off. – Pedipalpus (figs. 177-178) (see also above) with slender articles, patella spiny, most parts of the questionable embolus are hidden.

**Relationships and distribution:** See above.

**Spinipalpus n. gen.**

Etymology: The name refers to the spiny articles of the male pedipalpus, from spinosus (lat.) = spiny, and (pedi)palpus. – The gender of the name is masculine.

**Type genus** (by monotypy): *Spinipalpus vetus* n. sp.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (figs. 181-182): The bulbus bears two tegular apophyses which are close together and originate on a sciny membrane; the questionable embolus is long, describes more than a single circle, its distal part stands out from the tip of the cymbium.

**Relationships:** *Spinicreber* is most related, see the key to the genera above.

**Distribution:** Mid Cretaceous amber forest of N-Myanmar (Burma).

***Spinipalpus vetus* n. gen. n. sp.** (figs. 179-182) photos 71-73

Etymology of the species name: From *vetus* (lat.) = old, former.

**Material:** Holotype ♂ in Mid Cretaceous amber from N-Myanmar (Burma) and a separated piece of amber, F2712/BU/CJW.

**Preservation and syninclusions:** The spider is completely preserved in a thin clear yellow piece of amber between narrow layers of the fossil resin, therefore body and legs are flattened and the legs are spread sideways; it is injured and decomposed: The body is distinctly deformed, the prosoma is deeply inclined dorsally; eyes, clypeus, the base of the right femur I and the skinny parts between the right femur and patella I and II are covered with hyphae which probably have grown within the fossil resin; the strongly inclined/deformed opisthosoma has been separated from the prosoma. – **Syninclusions:** 1 Auchenorrhyncha, 1 Coleoptera, few Collembola, 1 Diptera, 1 deformed insect and plant hairs. The Diptera, body length 1.2 mm, is of special interest: It is placed directly in front of the spider's chelicerae, is covered with hyphae and has a very slender abdomen which probably has been sucked out by the spider. Therefore I regards this midge as a probable prey of the spider.

**Diagnosis** (♂; ♀ unknown): See above. Bristles of leg I: Fig. 179, pedipalpus: Figs. 181-182.

**Description** (♂):

Measurements (in mm): Body length ca. 2.5, prosomal length ca. 1.3; leg I: Femur 2.9, patella 0.7, tibia 2.9, metatarsus 3.1, tarsus 1.4; tibia II 1.7, tibia III 1.2, tibia IV 1.7.

Colour light grey brown.

Prosoma (photo) (it is strongly deformed): 8 eyes, basal cheliceral articles fairly slender, gnathocoxae distinctly longer than wide, coxae IV distinctly spaced by the sternum.

– Legs (fig. 179, photos) slender and spiny, order I/II/IV/III, I distinctly the longest, III distinctly the shortest; long bristles exist on femora to metatarsi, tibia and metatarsus I bear more than a dozen each, calamistrum absent, position of the metatarsal III trichobothrium in 0.4, paired tarsal claws toothed, unpaired claw existing. – Opisthosoma (fig. 180, photos) longer than wide, spinnerets strongly deformed, anteriors widely spaced basally, converging, cribellum apparently large and not divided. – Pedipalpus (figs. 181-182, photos) (see the diagnosis): Femur slender, patella and tibia short and spiny, cymbium large.

**Relationships and distribution:** See the genus.

**Family MONGOLARACHNIDAE** SELDEN et al. 2013 (figs. 183-197) photos 65-69

Three extinct monotypic subfamilies in Burmite are united here with some hesitation: Mongolarachninae SELDEN et al. 2013, Longissipalpinæ n. subfam. and Pedipalparachninae n. subfam.

Provisional (\*) **diagnosis**: Male pedipalpus (figs. 184f): Articles extremely long and slender, leg-shaped (similar to the relatively short leg III), usually spiny, cymbium and bulbus quite/relatively small, bulbus with a thin embolus and probably two tegular apophyses.

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(\*) After the knowledge of more taxa – see the dubious Jurassic genus *Zhizhu* SELDEN 2015 (which may be haplogyne but not entelegyne) (#), the dubious genera *Argyrarachne*, *Juraneus* and *Triasaneus* as well as the questionable Pholcoidea (see above, figs. 80-81) – the family diagnosis has probably distinctly to modify. Especially the leg and pedipalpal articles may be shorter/more stout in certain taxa of an enlarged family, and the structures of the bulbus may be quite variable.

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(#) *Zhizhu* has been regarded by SELDEN as a member of the Entelegyne by its „complex male pedipalpus“ but the bulbus structures of numerous Haplogynae are quite complex, see DEELEMEN-REINHOLD (1995) and this paper! In my opinion *Zhizhu* is more likely a member of the Haplogynae, see above.

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Further characters: Cibellum existing, undivided (fig. 185) (\*), 8 eyes (their number is unknown in the Mongolarachninae), most probably a single pair of lungs, long legs (at least I very long) (photos), order of the legs I/II/IV/III (in contrast to the Uloboridae in which IV is usually longer than II), numerous leg bristles (figs. 184, 186), usually existence of ventral tarsal IV bristles (except in the Longissipalpinae), metatarsus IV straight in the three treated subfamilies, feathery hairs absent.

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(\*) It is well observable as undivided e. g. in the holotype and the paratype of *Longissipalpus minor* n. sp.

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The **relationships** are quite unsure; Pholcochyroceridae may be most related: A cribellum exists, too, and spiny articles of the male pedipalpus may also exist, but the articles of the male pedipalpus are not extremely long/thin (leg-like) and bulbus/ cymbium are larger. See also above, the superfamily Leptonetoidea and the subfamilies below.

I do not want to exclude with certainty that the differences may be too weak to separate two different families (Pholcochyroceridae and Mongolarachnidae).

I also do not want to exclude with certainty that the peculiar size/shape of the male pedipalpi evolved convergently in the three genera in question. Besides the shape of the male pedipalpus only plesiomorphic characters unite the three genera and subfamilies: The existence of a cribellum, 8 eyes, probably a single pair of lungs, and usually ventral tarsal III-IV bristles (absent in the Longissipalpinae) as well as the absence of feathery hairs. Furthermore close relationships of the Pedipalparaneinae to the Deinopidae/ Uloboridae, and of the remaining subfamilies to the Hypochilomorpha may exist. The discovery of more fossils – including well preserved spinnerets and respiratory system – may help to answer these questions.

**Distribution**: Jurassic of Mongolia (Mongolarachninae) and Mid Cretaceous, the amber forest of Myanmar (Burma) (Longissipalpinae and Pedipalparaneinae).

### Key to the subfamilies:

1 Large spiders, the body length may be about 16 mm. Tibiae with clusters of many trichobothria in the basal half, and with „gaiters“ (numerous short hairs), female with peculiar leg tufts (fig. 183), male pedipalpal patella short (fig. 184). Jurassic, in stone, Mongolia. *Mongolarachne*. . . . . Mongolarachninae

- Body length 2-4 mm. Tibiae without clusters of many trichobothria, „gaiters“ absent, pedipalpal patella long (figs. 186, 196). Mid Cretaceous (Burmite). ♀ unknown . . . . . 2

2(1) Posterior eye row strongly recurved (fig. 191), opisthosoma with hair-bearing humps (fig. 192), femora III-IV with strong ventral bristles (fig. 194), pedipalpal patella distinctly shorter than the tibia (fig. 196), bulbus attached ventrally at the cymbium (fig. 197), body length 4 mm. *Pedipalparaneus*. . . . . Pedipalparaneinae

- Posterior eye row most probably not strongly recurved, opisthosoma without hairy humps, femora III-IV without strong ventral bristles, pedipalpal patella almost as long as the tibia (fig. 186), bulbus attached at the end of the cymbium (fig. 187). Body length 2-2.7 mm. *Longissipalpus*. . . . . Longissipalpinae

### **Subfamily MONGOLARACHNINAE SELDEN et al. 2013 (figs 183-184)**

Type genus (by monotypy): *Mongolarachne* SELDEN et al. 2013.

Type species (by monotypy): *Nephila jurassica* SELDEN et al. 2011, (♀) (preserved in stone from the Middle Jurassic of China).

**Diagnosis** (♂♀): Tibiae with clusters of many trichobothria in the basal half, and with „gaiters“ (numerous short hairs), male pedipalpus see SELDEN et al. (2013: Fig. 2f) with a short patella (fig. 184), female with peculiar leg tufts (fig. 183), genital area with a nose-shaped outgrowth which is not sclerotized.

Further characters (see the family characters): Lungs unknown, feathery hairs and femoral trichobothria absent, leg I very long, numerous strong leg bristles standing out from their article, tarsi and metatarsi IV with short ventral bristles, metatarsus IV straight, calamistrum uniserrate, probably 8 eyes, largest (questionable) member of the superfamily Leptonetoidea, body length probably ca. 16 mm.

**Relationships:** According to SELDEN et al. (2013) the position of this ancient extinct taxon may be near the origin of the Araneoidea s.l. (= „Orbiculariae“). In the derived Deinopidae and Uloboridae (fossil and extant) a cribellum exists, too, and leg I is quite long but feathery hairs usually (!) exist, a peculiar eye position exists in the Deinopidae; and in the Uloboridae the eye field is usually very wide and long, femoral trichobothria usually exist, metatarsus IV is usually distinctly concave and laterally depressed. In the derived taxa of the Uloboridae femoral trichobothria exist but such sensory hairs are still absent in basal extinct Uloboridae, see this family below. – Extremely long/large articles of the male pedipalpus (and frequently very small bulbi and spiny pedipalpal articles, too) are not rare in ancient spiders like Mygalomorpha, Hypochilidae, Filistatidae and (other) haplogyne spiders, but they are extremely rare in entelegyne spiders like “Orbiculariae”. Therefore the Mongolarachninae may be not strongly related to the ENTELEGYNE family Uloboridae in my opinion, but more likely to the “Haplogynae” although a prominent genital area – similar an epigyne – is rather rare in haplogyne spiders (outgrowth of the female genital area may exist e. g. in certain Uloboridae). The superfamily Leptonetoidea may well include the Mongolarachninae (**n. quest. relat.**) or even the Mongolarachnidae, which may be related to the Pholcochyroceridae, see the family key no. 29 and above, the superfamily Leptonetoidea and the mongolarachnid subfamilies. – The cribellate Jurassic family Juraraneidae ESKOV 1984 may be related, too.

Certain similar characters of the Mongolarachnidae exist (with) in the Hypochilomorpha – see above and SELDEN et al. (2013) – in which large basal cheliceral articles exist, the position of the fangs is „mediograde“, and two pairs of lungs exist basically and usually.

**Distribution:** Jurassic of Mongolia.

### Subfamily LONGISSIPALPINAE n. subfam.

Etymology: See the type genus.

Type genus (by monotypy): *Longissipalpus* n. gen.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (figs. 186-188): Bulbus relatively short, wide, bulbus attached at the end of the cymbium (\*).

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 (\*) A similar attachment in araneomorph spiders exists e. g. in members of the Sicariidae, in certain extant members of the Ochyroceratidae like *Psilodermes howarthi* DEELEMANN-REINHOLD 1995, and in the family Hypochilidae of the Hypochilomorpha.

Further characters: Fangs in a labidognath position, gnathocoxal serrula in a single row, legs very long and slender (fig. 186, photos), prograde, bristles numerous, long

and thin, absent on all tarsi. Calamistrum untypical/indistinct, see below. Pedipalpus (figs. 186-188): Articles not spiny, very slender and extremely long (leg-shaped) (\*): Femur I as long as the body, patella + tibia as long as the femur, embolus long and slender. Body length 2 – 4 mm.

**Relationships:** The chaetotaxy is like in other Mongolarachnidae and Pholcochyroceridae but the pedipalpi are quite different. Extremely long articles of the ♂-pedipalpi with small bulbi (fig. 186) exist, e. g., also in the monotypic Jurassic subfamily Mongolarachninae, preserved in stone of Mongolia. On the tibiae of *Mongolarachne jurassica* (SELDEN et al. 2011) (= *Nephila j.*) exist „gaiters“ (dense short hairs) as well as clusters of many trichobothria in the basal half, metatarsus and tarsus IV bear a row of short ventral bristles, and the pedipalpal patella is quite short in contrast to the Longissipalpiinae. – In the Pedipalaraneinae the pedipalpal articles are extremely long too, and the bulbi are quite small, but the opisthosoma bears hairy humps, femora III-IV bear strong ventral bristles, the posterior eye row is strongly recurved, and the structures of the male pedipalpus – e. g. of the bulbus – are quite different, the male pedipalpal patella is not much shorter than the tibia.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

### **Longissipalpus n. gen.**

**Etymology:** From longissimus (lat.) = very long, and palpus for the very long male pedipalpus of the new species. – The gender is masculine.

**Type species:** *Longissipalpus minor* n. sp.

**Diagnosis, relationships and distribution:** See above.

### **Longissipalpus minor n. gen. n. sp.** (figs. 185-188) photos 65-66

**Etymology:** From minor (lat.) = small, concerning the body smaller than of *L. maior* and *magnus*.

**Material:** Holotype ♂ in Mid Cretaceous amber (Burmite) from N-Myanmar (Burma), F2549/BU/ CJW. The male was separated from a piece of amber which included also a member of the Sicariidae: Loxoscelinae, F2551/BU/CJW, see above. – Paratype ♂ in Burmite, F2707/BU/CJW.



**Preservation and syninclusions:** Holotype: The spider is very well and almost completely preserved (only the tip of the left tibia I is cut off) in a muddy yellow piece of amber. Most parts of the opisthosoma are translucent/hollow. – Remains of a tiny questionable insect are preserved right below the spider's prosoma, small parts of detritus and tiny brown droplets are also preserved. – The paratype is almost completely preserved in a clear yellow piece of amber, it is partly decomposed and injured and apparently has dried out; some femora are depressed/inclined ventrally, the prosoma is deformed anteriorly, the chelicerae are lost.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (figs. 186-188): Cymbium not strongly elongated, embolus longer than the cymbium, standing out anteriorly.

### **Description** (♂):

Measurements (holotype, in mm): Body length 2.0, prosomal length 0.9, opisthosoma: Length 1.3, width 0.85, height 0.8; leg I: Femur 1.9, patella 0.45, tibia 1.8, metatarsus 2.3, tarsus 1.0, tibia II 1.1, tibia III 0.4, tibia IV 0.75; pedipalpus: Femur 1.9, patella 0.95, tibia 0.85; height of femur I 0.2. – Paratype: Body length 2.2, prosomal length 0.9, femur I (r./l.) 2.2/2.4, tibia I 1.9.

Colour yellow grey brown, legs not annulated.

Prosoma (photo) (parts are hidden by legs) distinctly longer than wide, low, hairs short, 8 eyes in two wide rows, clypeus long and fairly concave, ventral margin not protruding, chelicerae apparently labidognath, basal articles only fairly large, most mouth parts and sternum hidden, gnathocoxal serrula in a single row. – Legs (fig. 186, photos) long and slender, order I/II/IV/III, III distinctly smallest, I distinctly longest, hairs longer but indistinct, trichobothria unknown, bristles numerous, well observable in the paratype, long and thin, absent on tarsi, femora with a dorsal bristle in the basal half which probably is absent on IV as well as with lateral and distal/apical ones, all patellae and tibiae bear 2 dorsal ones (they are hair-shaped on the patellae), tibia I additionally with 3 pairs of lateral bristles, metatarsus I with at least 8 bristles including a dorsal-basal pair, tibiae III and IV bear a prolateral-basal bristle besides the dorsals, metatarsus III and IV bear apical bristles. Metatarsus IV straight, calamistrum indistinct or quite untypical: Long retrodorsal hairs exist in almost two basal thirds of the article in a regular position (well preserved in the paratype), only slightly bent, similar to hair on other legs; 2 large and toothed paired tarsal claws, unpaired claw smaller. – Opisthosoma (fig. 185, photos) 1.5 times longer than wide, hairs short, I did not recognize lung covers or tracheal spiracles, 3 pairs of spinnerets, anterior ones widely spaced, slender and converging behind the wide cribellum which is fairly observable in both specimens; it may be undivided. – Pedipalpus (figs. 186-188): Femur, patella and tibia extremely long (see above), patella slightly longer than the tibia, tibial apophysis absent, cymbium wide, fairly protruding dorsally, bearing long hairs especially apically, bulbus attached apically to the cymbium, bearing a short and divided tegular apophysis and a long, bent and pointed second tegular apophysis (probably a functional conductor), embolus very long, thin, bent and directed forward. The structures of the pedipalpus of the paratype are as in the holotype.

**Relationships:** According to the structures of the pedipalpus *L. magnus* is strongly related, see below.

**Distribution:** Mid Cretaceous amber forest of N-Myanmar (Burma).

*Longissipalpus maior* n. gen. n. sp. (fig. 189)

Etymology: From maior (lat.) = large, concerning the body larger than of *L. minor*.

**Material**: Holotype ♂ in Mid Cretaceous amber from N-Myanmar (Burma), F2550/BU/CJW.

**Preservation and syninclusions**: The spider is fairly well and completely preserved in an orange piece of amber. Body and legs are covered with tiny bubbles similar to an emulsion. Larger ?gas bubbles are attached to the left side of the opisthosoma. Long and apparently hairy leg-shaped particles are preserved between the anterior legs. – Few spider's threads exist just below the spider's legs and in front of the spider, a thin thread is running forward from the tip of the right tarsus IV. Numerous Acari (most are larvae), remains of different arthropods including a questionable Collembola, excrements of insects and remains of plants are also preserved.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (fig. 189): Cymbium distinctly protruding dorsally, embolus in a transverse position.

**Description** (♂):

Measurements (in mm): Body length 2.7, prosomal length 1.3, opisthosoma: Length 1.6, height 0.7; leg I: Femur 3.6, patella 0.9, tibia 3.4, metatarsus 4.1, tarsus 1.75, tibia II 2.2, tibia III ca. 1.1, tibia IV 1.5; height of femur I 0.4 pedipalpus: Femur and patella + tibia almost 2.5 each.

Colour: Prosoma and legs dark brown, opisthosoma light grey brown.

Prosoma (parts are hidden by legs) apparently quite similar to *L. minor* n. sp. – Legs and opisthosoma (parts are hidden by droplets) probably quite similar to *L. minor*. – Pedipalpus (fig. 189): Femur, patella and tibia extremely long and slender, similar to *L. minor*. Cymbium wide, protruding dorsally, bulbous apically attached to the cymbium, most tegular apophyses are hidden, embolus long, thin and in a transverse position.

**Relationships**: See *L. minor* n. sp. which is smaller and *L. magnus* which is larger.

**Distribution**: Mid Cretaceous amber forest of N-Myanmar (Burma).

*Longissipalpus magnus* n. gen. n. sp. (fig. 190)

Etymology: From magnus (lat.) = large; *magnus* is the largest known species of the genus.

**Material**: Holotype ♂ in Mid Cretaceous Burmite from N-Myanmar (Burma), F2708/BU/CJW.

**Preservation and syninclusions:** The spider is only fairly well preserved in a muddy orange-brown piece of amber which has been rolled, its legs are bent in different directions, the apical part of the opisthosoma and several leg articles are cut off, the left legs III and IV are completely preserved, the right legs II and III are almost completely preserved. – Few spider's threads, 1 Thysanoptera, 1 questionable Acari and numerous plant hairs are preserved in the same piece of amber.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (fig. 190): Questionable embolus long and bent in the basal half, straight in the distal half, the prolateral tegular apophysis 1 is not much shorter.

**Description** (♂):

Measurements (in mm): Body length at least 4.0, prosomal length 2.0, tibia II 2.3, height of femur I 0.5.

Colour dark grey brown (apparently darkened by the preservation).

Prosoma (it is not well preserved and partly hidden): Chelicerae with long fangs. – Legs (partly cut off, hard to observe): Order I/II/IV/III, I distinctly the longest and thickest, III distinctly the shortest, bristles numerous, absent on the tarsi, position of the metatarsal trichobothria unknown, calamistrum indistinct. – Opisthosoma long oval, hairs short, spinnerets cut off. – Pedipalpus (fig. 190): Articles extremely long and slender, as in the related species, structures of the bulbus not well observable, see above.

**Relationships:** In *L. minor* n. sp. embolus and tegular apophysis 1 are fairly similar but the embolus is bent in the distal half and the body length is only 2 – 2.2 mm. In *magnus* femur I is thicker (0.5 mm high) than in *minor* (0.2 mm) and *maior* (0.4 mm); furthermore the latter is smaller, body length 2.7 mm, and its bulbus structures are quite different.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

Subfamily **PEDIPALPARANEINAE** n. subfam.

Etymology: See the type genus.

**Type genus** (by monotypy): *Pedipalparaneus* n. gen.

**Diagnosis** (♂; ♀ unknown): Opisthosoma with paired hairy humps (fig. 192), eye field very wide, posterior eye row distinctly recurved (fig. 191), femora III-IV with strong ventral bristles (fig. 194), femora with few long ventral trichobothria-shaped sensory hairs (fig. 193), pedipalpus (figs. 196-197) with spiny articles, patella distinctly shorter than the tibia, bulbus with two tegular apophyses, attached ventrally at the cymbium..

**Relationships:** The extremely long and slender articles of the pedipalpus and the small cymbium and bulbus are like in other members of the Mongolarachnidae. Differences: See the key above as well as the Longissipalpinae and the Mongolarachninae. – See also below, the superfamily family Uloboridae and related taxa, which are similar in some respect.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

**Pedipalparaneus n. gen.**

Etymology: Pointing to the long articles of the pedipalpus and the genus name *Araneus* in which the position of the eyes is a bit similar.

The gender of the name is masculine.

**Type species** (by monotypy): *Pedipalparaneus seldeni* n. sp.

**Diagnosis, relationships and distribution:** See the new subfamily.

**Pedipalparaneus seldeni n. gen. n. sp.** (figs. 191-197) photos 67-69

Derivatio nominis: The spiders' name is dedicated to PAUL A. SELDEN, who described excellently numerous fossil arachnid taxa (mainly spiders) which are preserved in stone.

**Material:** Holotype ♂ in Mid Cretaceous amber from Myanmar (Burma), F2674/BU/CJW.

**Preservation and syninclusions:** The spider is completely and very well preserved, the opisthosoma is injured (dorsally inclined), its tip and the legs are bent ventrally. – Thin spider's threads without droplets – probably remains of a two-dimensional capture web of a spider – exist near the spider. Plant hairs and grey pear-shaped structures at the margin of the piece of amber are also preserved.

**Diagnosis** (♂; ♀ unknown) (see also the family diagnosis): Pedipalpus (figs. 196-197): Bulbus with two tegular apophyses and a thin embolus in a distal position.

**Description (♂):**

Measurements (in mm): Body length 4.0, prosoma: Length 1.9, width 1.6; opisthosoma (it is deformed): Length ca. 2.6, width ca. 1.3; leg I: Femur 3.7, patella 1.2, tibia 3.0, metatarsus 3.15, tarsus ca. 1.35, tibia II 2.2, tibia III 1.1, tibia IV 1.4; pedipalpus: Femur 2.9, patella 1.0, tibia 1.9.

Colour light brown, legs indistinctly annulated.

Prosoma (fig. 191, photos) 1.2 times longer than wide, slightly inclined artificially in front of the long and deep fovea, covered densely with plumose (?) hairs, thoracic part elevated and with a pair of „shoulders“, 8 eyes in a wide field, lateral eyes deformed, posterior row distinctly recurved, length of the clypeus ca. 2 diameters of the anterior median eyes, basal cheliceral articles slender and fairly long, lateral files and condylus absent, fangs long, (teeth of the) fang furrow hidden, labium probably as long as wide, gnathocoxae distinctly longer than wide, coxae IV widely spaced, – Legs (figs. 191-195, photos) long and slender, order I/II/IV/III, I distinctly longest, III distinctly shortest, covered densely with – apparently not feathery – hairs, bristles numerous and long, existing on femora, patellae, tibiae, metatarsi and at least ventrally on tarsus IV. Femora III-IV bear strong ventral bristles besides thinner ones, tibia I bears ca. 10 bristles, metatarsi III and IV bear a garland of apical bristles. Sensory hairs/ trichobothria: Femora without dorsal or lateral trichobothria but with few long ventral sensory hairs which are similar to trichobothria (fig. 193) (\*). The right metatarsus I bears 3 long retrodorsal sensory hairs in the basal half whose shape is quite similar to trichobothria. Calamistrum indistinct or even absent; short bent retrodorsal hairs exist in the basal half of metatarsus IV which is free of bristles in this part. Metatarsal trichobothria unknown, tarsal trichobothria absent. Three small tarsal claws, „auxiliary hairs“ apparently existing. – Opisthosoma twice as long as wide, densely covered with – plumose? – hairs, and with few small hairy paired (and apparently few additional dorsal) humps. Spinnerets partly deformed and hidden, apparently 3 pairs, anterior pair thick and widely spaced, cribellum most probably existing. – Pedipalpus (figs. 196-197) with very long and slender articles, leg-like, femur without a ventral-basal outgrowth (existing in Uloboridae), bearing at least 6 bristles, tibia almost as long as the femur, bearing a pair of long dorsal-distal bristles, cymbium and bulbus small, cymbium covering most parts of the bulbus, paracymbium absent, tegulum with two apophyses, embolus thin, observable in a distal position.

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(\*). Similar – but numerous – hairs exist in the genus *Vetuloborus* (Uloboridae).

**Relationships:** See above. Opisthosomal humps exist also in certain members of the Uloboridae in which they evolved convergently in my opinion.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

## SUPERFAMILY ARCHAEOIDEA

(= PALPIMANOIDEA, see the remark directly below)

Remarkably numerous authors ignore – or are not firm with – certain Rules of the Zoological Nomenclature: The older name for this superfamily – and well in use for a longer time not only by the present author – is Archaeoidea, based on Archaeidae KOCH & BERENDT 1854 but not Palpimanoidea, based on the younger family name Palpimanidae THORELL 1870. See the inconsequent note by FORSTER & PLATNICK (1984: 104).

### NOTES on two dubious Jurassic taxa:

(1) *Seppo koponensis* SELDEN & DUNLOP 2014 – based on a probably adult female in calcit – has been regarded as a member of the superfamily Archaeoidea (under Palpimanoidea), and not assigned to family level. I consider this genus more likely to be a member of the superfamily Araneoidea, of the families Araneidae or Zygiellidae, see above, the chapter on erroneous determinations, and below, the superfamily Araneoidea s. l.: The araneoid branch.

(2) *Sinaranea metaxyostraca* SELDEN et al. 2008, preserved in Jurassic stone from China, based on a probably adult male and juveniles (I am unsure that the male is really adult), is regarded as a taxon of uncertain family relationships within this superfamily. – Note: The taxon has been published as a member of the Entelegynae but Archaeoidea (= Palpimanoidea) is apparently a „splitted“ taxon, partly entelegyne and partly secondary haplogyne.

FORSTER & PLATNICK (1984) published a review of the archaeid spiders and their relatives including a cladogram (fig. 394) of the superfamily Archaeoidea (under Palpimanoidea). These authors did not include the fossil family Spatiatoridae in their cladogram, but they included erroneously the families Holarchaeidae, Micropholcommatidae, Mimetidae, Pararchaeidae and Textricellidae which all are taxa of the entelegyne superfamily Araneoidea.

The present author – see WUNDERLICH (2004: 761) – published a „possible cladogram“ (under Eresoidea), including the fossil families Lagonomegopidae and Spatiatoridae as well as the extant family Eresidae which I later and now exclude(d) from the haplogyne Archaeoidea mainly because of its entelegyne and cribellate status as well as the absence of cheliceral „peg teeth“. The relationships of the family Lagonomegopidae was stated as unsure in this cladogram. The Mecysmaucheniidae was (and still is by me) included in the Archaeidae (s. l.) as a subfamily but this assignment may be not justified, see WOOD et al. (2013). The Huttoniidae was regarded as sister family to the Spatiatoridae.

A further fossil family of the Archaeoidea – the Micropalpimanidae WUNDERLICH 2008 –, is placed here in the lagonomegopid subbranch, see figs. D and F.

The recent discovery of Cretaceous fossils of the Archaeidae, Lagonomegopidae and Micropalpimanidae lead me to new conclusions on the diagnoses and relationships of these families as well as of the superfamily Archaeoidea.

Recently WOOD et al. (2012) presented a „Phylogenetic placement of pelican spiders (Archaeidae, Araneae)....“, see the discussion below. Most fossil Archaeidae are included; not included in that paper are, e. g., the fossil families Lagonomegopidae, Micropalpimanidae and Spatiatoridae. *Lacunauchenius* WUNDERLICH 2008 of the Archaeidae: Lacunaucheniinae (extinct, Cretaceous) is regarded (p. 29) as a possible new palpimanoid family or a new genus of the family Mecysmaucheniidae, but see below: Archaeidae s. l. See WOOD et al. (2013).

**Diagnostic/apomorphic characters of the Archaeoidea:** See fig. D below (and the family Caponiidae of the Dysderoidea). But see fig. G p. 287!

Selected basic (plesiomorphic) characters of the Archaeoidea: entelegyne and haplogyne stage (\*) (see above), existence of lungs, 3 pairs of spinnerets (median and posterior spinnerets are reduced or absent, e. g., in the Huttoniidae, Mecysmaucheniinae, Palpimanidae and Stenochilidae), an unpaired tarsal claw (lost in the Stenochilidae), not enlarged anterior legs, and 8 eyes (6 eyes in Lagonomegopidae (probably 4 in few genera), certain Palpimanidae, as well as most Mecysmaucheniidae, except *Aotearoa*). – Furthermore plesiomorphic characters are: The ABSENCE OF A CRIBELLUM AS WELL AS OF A COLULUS (!) (\*\*) tarsal trichobothria (existing in the lagonomegopid subbranch as a regain, see fig. D below), feathery hairs, a HUGE diastema and foramen, a tibial apophysis of the male pedipalpus (except in certain Lagonomegopidae and Mecysmaucheniidae), and a „paracymbium“ (except in certain Mecysmaucheniidae like *Mecysmauchenus*).

NOTE: I do not want to exclude that the existence of cheliceral stridulatory files (see fig. D) may be a further phylogenetically old, plesiomorphic (or apomorphic?) character of the Archaeoidea, which is known in haplogyne spiders also e. g. in the Plectreuridae and Pholcoidea (= Scytodoidea), see below.

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(\*) FORSTER & PLATNICK (1984) mixed erroneously haplogyne and entelegyne families in their paper on the superfamily Archaeoidea, see above.

(\*\*) I did not find a colulus in the fossil spiders. The – real? – absence of a colulus may indicate that archaeoid ancestors never had a cribellum and that its branching is older than the branching of the cribellate Hypochilomorpha!

**Ecology, prey and behaviour:** See Archaeidae and mainly Lagonomegopidae.



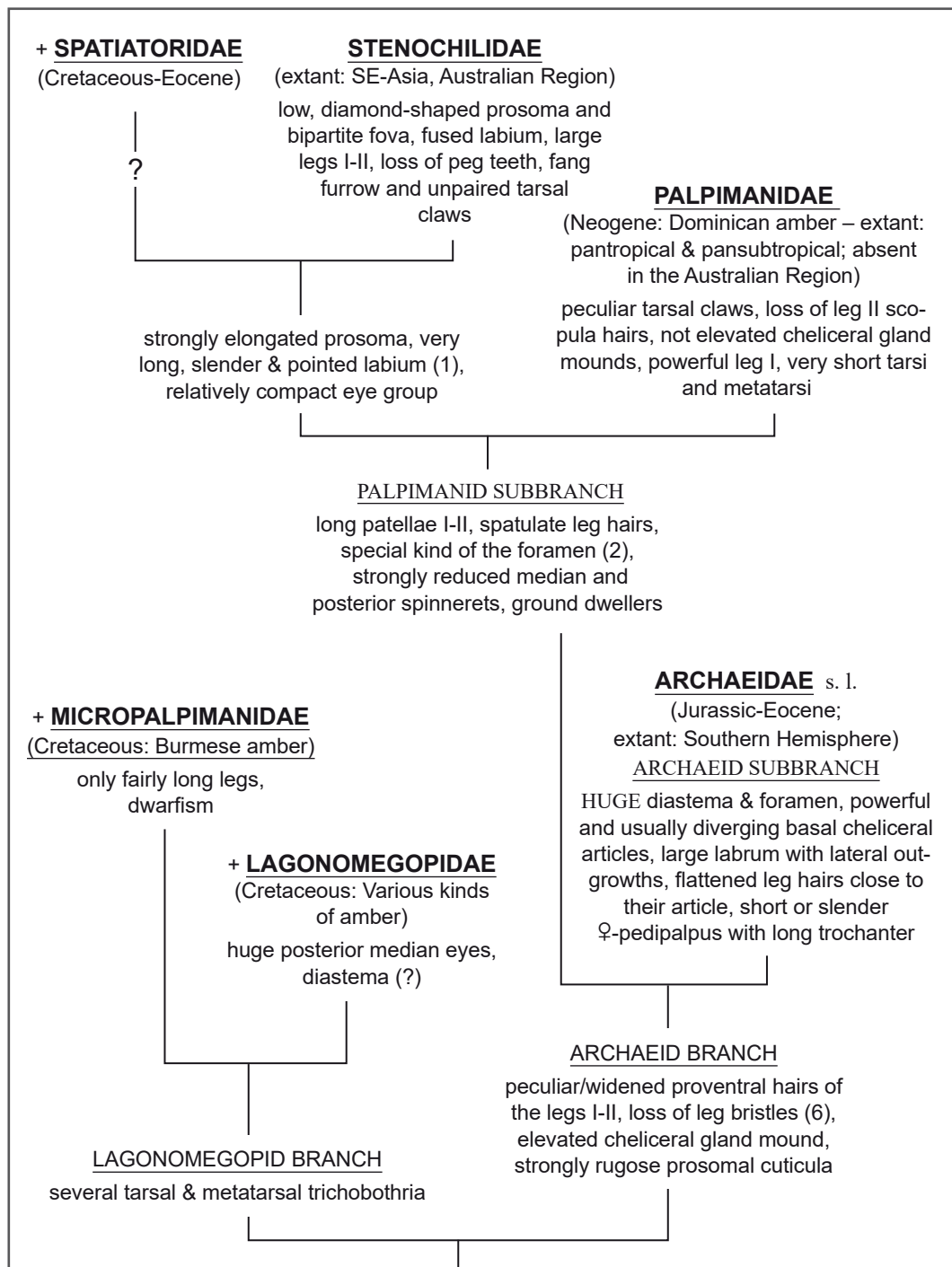


Fig. D. Possible cladogram of extant and fossil families of the superfamily **Archaeoidea** (= Palpimanoidea), based on selected relevant characters. See fig. G!

The enigmatic family Huttoniidae – New Zealand and allegedly in Cretaceous New Jersey amber preserved – is not included.

Apomorphies: Chelicerae bearing: „peg teeth“ (more exactly: „peg bristles“) (\*) (figs. 203, 245, 277, photos), retrolateral stridulatory files? (3) and an elevated gland mound (fig. 257); probably existence of a diastema (fig. 207, photos); a raised cephalic part with a very huge (very wide and long) eye field with the tendency to one huge pair of eyes (figs. 201f, photos) (4), a rugose prosoma (photos), metatarsal III-IV preening hairs/comb (figs 210, 225) (5), frequently a basal modification/constriction of the tarsi, a complete loss of leg bristles (6), probably short patellae I (II) (\*\*), tendency to the reduction of median and/or posterior spinnerets (7), a strongly reduced/absent female pedipalpal claw, long and dense hairs on the cymbium and the tarsus of the female pedipalpus (figs. 221, 227, 256), basically relative large cymbium and deep alveolus, araneophagy (8), basically probably nocturnal life style as sit-and wait-predators of higher strata of the vegetation, but this supposition is unsure. Grund dwellers are Archaeidae s. l.: Mecysmaucheniinae, extant Huttoniidae (not the alleged Cretaceous fossils), Palpimanidae and Stenochilidae. – See also the note above on cheliceral stridulatory files.

(\*) „Peg teeth are absent in the Stenochilidae. – Interestingly araneophagous spiders of different superfamilies convergently evolved cheliceral „peg teeth“: Members of the Archaeoidea (as a synapomorphy), Mimetidae and few Theridiidae of the Araneoidea, as well as few Thomisidae of the RTA-clade. Is the kind of prey capturing connected with the existence of „peg teeth“?

(\*\*) Short patellae existing mainly in LONG-legged members of dwellers of higher strata: Archaeidae and Lagonomegopidae (as well as in the fairly short-legged Micropalpimanidae).

(1) Similar e. g. in the Lagonomegopidae.

(2) See WOOD et al. (2012: 15).

(3) In my opinion the existence of cheliceral files is more likely a plesiomorphic character, see below, fig. E. The diastema is lost in the Huttoniidae, probably lost in the Micropalpimanidae and certain Lagonomegopidae; cheliceral files are absent/lost in certain Lagonomegopidae, and reduced (or absent?) in the Micropalpimanidae and Huttoniidae; see also *Burmesarchaea*. The retromargin of the fang furrow may bear true teeth e.g. in (all?) Archaeidae s.l.

(4) A flat resp. not step-like cephalic part exists e. g. in the Huttoniidae as well in certain Archaeidae s.l. (*Eoarchaea*, *Planarchaea*, and *Saxonarchaea*, see WUNDERLICH (2004: 805: Fig. 42; 2008, and figs. below). A compact eye group exists e. g. in the Stenochilidae; both as reversals in my opinion.

(5) Frequently exist no regular hairs/bristles of a true preening comb (e. g. in the Lagunaucheniinae) but often strong hairs exist in an irregular position, see, e.g., PENNEY (2006: Fig. 1G, questionable Huttoniidae), WUNDERLICH (2004: 790, 804: Fig. 36, *Saxonarchaea*, Archaeidae).

(6) Bristles exist in the Huttoniidae which have bristles at least on legs III-IV, as well as in the Micropalpimanidae and in certain Lagonomegopidae of the lagonomegopid branch (?mainly in juveniles).

(7) These spinnerets are reduced/absent in the families Huttoniidae, Palpimanidae, Stenochilidae, and in subfamilies of the of the Archaeidae: Mecysmaucheniinae (both pairs) as well as (reduction or loss of the median pair) in some Archaeidae like *Archaeomecys* (Archaeinae) and *Lacunauchenius* (Lacunaucheniinae).

(8) Extant spiders: Lost in the Archaeidae s. l.: Mecysmaucheniinae, basically absent/lost in the Huttoniidae; unknown in most fossils, but araneophagy is known (a) in Palaeogene (Eocene) Archaeidae, see below and WUNDERLICH (2004: 98, fig. 5, 567, photo 628), as well as (b) in an Eocene member of the extinct family Spatiatoridae: *Spatiator* sp. indet. in Baltic amber, a juvenile spider with a captured female member of the family Synotaxidae, *Acrometa* sp. indet., F2566/BB/CJW, see the paper on the spiders in this volume. (c) Probably members of the Cretaceous Lagonomegopidae did not (only) feed on spiders: A juvenile of *Archaealagonops* sp. indet. is preserved in Burmite with two Diptera: Nematocera as its prey, see below.

## Discussion (see also the notes directly below)

Remark: In my opinion characters of the life style are not less important than molecular results. But such characters are frequently not treated in cladograms.

The cladogram (fig. D) may appear logical in most respect but does it reflect the real relationships? There are numerous open questions, see FUENTE et al (2013) and WOOD et al. (2012). See also the – real? – „reversals“ and „losses“, which are listed in the remarks nos. 3-4 and 6-7 above, but there are more reversals like the small diastema, e. g., in the genus *Baltarchaea* of the family Archaeidae and in most members of the Lagonomegopidae.

Recently WOOD et al. (2012) presented a „Phylogenetic placement of pelican spiders (Archaeidae, Araneidae) ....“, including „phylogeny“ (similar to cladograms) on related extant families, based on molecular data combined with morphological data (fig. 2 in that paper), concentrated on molecular data (fig. 3) and based on morphological data (fig. 4) (not included the fossil taxa: See above). Entelegynae regarded as sister group to the Archaeoidea is not a new idea, see, e. g., WUNDERLICH (2011: 575) but it seems quite unsure to me.

There exist remarkable differences between the results by molecular and morphological data concerning the relationships of the families of the Archaeoidea, e. g., Huttoniidae is the most basal family in fig. 4, and Archaeidae is the sister group to the Mecysmaucheniidae while in fig. 3 Mecysmaucheniidae is the most basal taxon (not strongly related to the Archaeidae), and Huttoniidae is regarded as sister to Palpimanidae. (Note that the entelegyne Pararchaeidae is shown as „sister“ of the haplogyne Archaeidae + Stenochilidae!).

My conclusions on the relationships of the archaeoid families are more similar to the morphological data (fig. 4) with certain exceptions, e. g., of the Huttoniidae which I regard as more derived, and the Mecysmaucheniidae which I regard as a subfamily of the Archaeidae (at least as strongly related), see below and fig. D.

## Notes on the possible relationships of few selected families and of certain characters:

Length of the patellae and life style: To my hypothesis the basic Archaeoidea possessed quite long patellae I(II) which frequently are longer than the short tarsi – in my opinion an apomorphic character of the Archaeoidea, still existing in most short-legged members of the Palpimanid subbranch, see fig. D (\*). I suppose – with some hesitation – that the basic Archaeoidea where ground-living spiders like the Palpimanidae, and the preference of higher strata is an advanced character, evolved three times convergently, (a) in the lagonomegopid branch (Lagonomegopidae + Micropalpimanidae), (b) in the Archaeidae: At least in the Archaeinae, (c) in the Spatiatoridae. Micropalpimanidae have relatively short but slender legs, Spatiatorinae have relatively stout legs.

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(\*) Quite long patellae (and short tarsi) exist also in the members of the family Dysderidae, which are ground-living spiders, too.

Archaeidae s. l.: In my opinion this old family – the only member of the „archaeid sub-branch“ – is the sister group to the „palpimanid subbranch“, see fig. D. Archaeidae is regarded by me as a basal family of the „archaeid branch“ which may be the sister group to the „lagonomegopid branch“ or to all remaining Archaeoidea.

The oldest reports of the superfamily Archaeoidea are Jurassic members of the family Archaeidae (if the determination is really correct!): *Jurarchaea* ESKOV 1987 (Jurarchaeinae) and *Patarchaea* SELDEN et al. 2008 (unknown subfamily), as well as a genus of an unplaced family: *Sinaranea* SELDEN et al. 2008. Members of the Lagonomegopidae, Micropalpimanidae, Archaeidae: Lacunaucheniinae and questionable members of the Huttoniidae (e. g.) are not reported before the Cretaceous but they may well have existed already at that time in my opinion.

The relationships of the quite remarkable and very diverse extinct family Lagonomegopidae is still debated: „If lagonomegopids are considered palpimanoids <!>, the lineage is most likely basal or sister to other palpimanoid lineages.“ (FUENTE et al. (2013: 21)). According to many apomorphic characters of the Archaeoidea (= Palpimanoidea) I regard Lagonomegopidae doubtless as a member of the Archaeoidea, and a member of the (most?) basal – lagonomegopid – branch, related to the Micropalpimanidae, see fig. D and below.

Relationships of the families Huttoniidae (extant and probably Cretaceous: See below), Micropalpimanidae (extinct, Cretaceous), and Spatiatoridae (extinct, Cretaceous to Eocene): According to the combined data given by WOOD et al. (2012: Fig. 2) Palpimanidae is most related to the Huttoniidae but in my opinion both families are not very strongly related, see the characters listed in fig. D. Huttoniidae and Micropalpimanidae are SIMILAR in some respect, see also below. According to PENNEY & SELDEN (2011: 60, 69) as well as DUNLOP & PENNEY (2012: 124) (\*) Micropalpimanidae and Spatiatoridae are „not valid“ (!), and will be synonymized with the Huttoniidae „in the near future“. Alleged validity and synonymy: The authors did not explain why these family names are not valid since they have never been explicitly synonymized. Close relationships of the Spatiatoridae are unclear; see the enlarged diagnosis of this family below. Huttoniidae and the dwarf Micropalpimanidae share the strongly reduced or even absent fovea, the stout fangs (a plesiomorphy of the Archaeoidea), the existence of few leg bristles, and probably the absence of a foramen (unsure in the Micropalpimanidae). BOTH FAMILIES DIFFER CLEARLY IN SEVERAL IMPORTANT CHARACTERS: (1) The cephalic part is distinctly raised in the Micropalpimanidae in both sexes (photos) (\*\*), but not raised in the Huttoniidae; (2) the prosomal cuticula is distinctly wrinkled in the Micropalpimanidae but almost smooth in the Huttoniidae (finely scaly only); (3) the basal cheliceral articles are stout in the Micropalpimanidae but long in the Huttoniidae; (4) **the tarsi bear trichobothria** in the Micropalpimanidae (fig. 267) in contrast to the Huttoniidae (and the Spatiatoridae) (but as in the Lagonomegopidae as well as in the Caponiidae of the Dysderoidea); (5) the median and the posterior spinnerets are strongly reduced/absent in the Huttoniidae but at least the posterior spinnerets are well developed in the Micropalpimanidae; (6) the shape of the cymbium – long and slender in the Micropalpimanidae – and the structures of the bulbous are clearly different in both families, e. g., regarding the position of the embolus. Therefore I place the Micropalpimanidae and the Huttoniidae in different branches of the Archaeoidea, see fig. D.

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(\*) Without a personal investigation of micropalpimanid material (!).

(\*\*) In a previously described – probably conspecific female; see WUNDERLICH (2012: 228, fig. 51) – the prosoma is less strongly raised compared with the male holotype, but the body is deformed in the female, and apparently the prosoma is somewhat depressed dorso-ventrally.

## DESCRIPTIONS OF THE MESOZOIC FAMILIES OF THE ARCHAEOIDEA

Mecysmaucheniidae: See Archaeidae: Mecysmaucheniinae; no fossil record.  
See *Archaeomecys* below.

**Family ARCHAEIDAE s. l.** figs. 198-219, photos 118-130, family key no. 13

**Subfamilies:** I regard Archaeidae in a wide sense, including Jurarchaeinae, Lacunaucheniinae) and (with hesitation) Mecysmaucheniinae (= Mecysmaucheniidae auct.) besides Archaeinae, see below and fig. E.

**Notes:** (1): The rank as subfamilies or families may be a matter of opinion.

(2): The quite unusual genus *Patarchaea* SELDEN et al. 2008 (fig. 217) – preserved in stone from China and published under „Archaeidae“ sensu SELDEN et al. – is not placed here in a subfamily; it may be a member of a subfamily of its own. The preservation of these fossils in stone is much worse than of fossils in amber. The spinnerets are laterally surrounded by a sclerotization but not by a ring like in the Archaeinae. Its male pedipalpus is very different from other fossil or extant taxa. The anterior patella is called as „conspicuously long“ in the original description but it is not shown as unusually in the figs. 7-8. Spatulate hairs/setae on the anterior tibia and metatarsus are mentioned although figs. 11-12 show only flattened adpressed but NO SPATULATE hairs. Such not-spatulate pointed hairs are typical for several taxa of the family Archaeidae while true spatulate hairs exist in the remaining archaeiod families except in the Lagonomegopidae. Retrolateral cheliceral stridulatory files exist. The cymbium bears a strong bristle and a large questionable paracymbium.

**Fossils and relationships of selected subfamilies** (see the possible cladogram below): Archaeidae is – in the geological sense – one of the oldest families of the Archaeoidea, reported already from the Jurassic: *Jurarchaea* ESKOV 1987 and *Patarchaea* SELDEN et al. 2008 (see above) besides the unplaced genus *Sinaranea* SELDEN et al. 2008 (see above). During the Cretaceous Archaeidae has been the most diverse family of this superfamily besides the extinct family Lagonomegopidae. Jurassic fos-

sils of this family are extremely rare. Cretaceous members in Burmese amber were treated only six years ago, see WUNDERLICH (2008: 752-792); in this paper few more fossils are described. (Palaeogene Archaeidae in Baltic amber were revised ten years ago, see WUNDERLICH (2004)). – JURARCHAEINAE: The relationships of the extinct, only weakly diagnosed and oldest subfamily are unsure; it is not supported by special characters. (See also the notes on *Patarchaea* above!). – MECYSMAUCHENIINAE: The smooth body, the loss of median and posterior spinnerets and the loss of spider eating are advanced characters of this subfamily in my opinion which may be relative young; it is not known before the Tertiary in contrast to the remaining subfamilies; a sure report of mysmaucheniine fossils is absent.

**Distribution:** Today the family is restricted to the Southern Hemisphere of South America, South Africa, Madagascar, and the Australian Region. Fossils have only been reported from the Northern Hemisphere up to now from where large amber deposits are known in contrast to the Southern Hemisphere.

**Prey:** Today members of the Archaeinae feed on spiders, and the same prey is known from a member in Palaeogene Baltic amber, but the prey is unknown from the Cretaceous and Jurassic Archaeinae and Jurarchaeinae up to now; Lacunarchaeinae: see below. Members of the Mecysmaucheniinae are known as generalists.

An Eocene juvenile Archaeidae (*Archaea* or *Eoarchaea* sp. indet.) with a juvenile Theridiidae indet. – was published by WUNDERLICH (2004: 98, fig. 5, 567, photo 626). Both animals are not in direct contact but the position of the juvenile Theridiidae is very close to the chelicerae/mouth parts of the spider, and the folds of the shrunk opisthosoma indicate in my opinion that the Theridiidae has really been a prey of the archaeid spider. Also preserved in Eocene Baltic amber is a juvenile member of the extinct archaeoid spider family Spatiatoridae capturing a member of the family Theridiidae, see the paper on this matter in this volume.

Cretaceous: It is remarkable that near the male holotypes of two new described Cretaceous species of *Lacunauchenius* (Lacunaucheniinae) not less than five juvenile spiders are preserved which partly may have been potentiell prey of the archaeid males, see below.

### **Diagnostic characters of the Archaeidae s. l.:**

See FORSTER & PLATNICK (1984), WOOD et al. (2012: 28)

- Large labrum with lateral outgrowth, see FORSTER & PLATNICK (1984: Figs.90-92), (unknown in the fossils);
- huge gap between chelicerae and gnathocoxae (diastema, fig.207, photos);
- powerful/long chelicerae originating from a sclerotized surrounding (foramen, photos);
- unsclerotized dorsal modification of tarsus I, see WOOD et al. (2012: Fig. 8f, but see fig. 8c); probably absent in fossil Jurarchaeinae and Lacunaucheniinae; it may be ring-shaped;
- ♀-pedipalpus small (short and/or slender, fig. 202., photos), with elongated trochanter;
- probably basically spider eaters (unknown in the Jurarchaeinae and Lacunaucheniinae but see directly above); loss of this character in the Mecysmaucheniinae.

Further characters: See fig. D: Apomorphies of the Archaeoidea, and fig. G. Addressed flattened and pointed (not spatulate!) and plumose leg hairs are characteristic – mainly in Archaeinae (except *Eoarchaea* and probably *Burmesarchaea*) as well as Mecysmaucheniinae, see fig. D –, and exist frequently on the body, too (as also in other taxa).

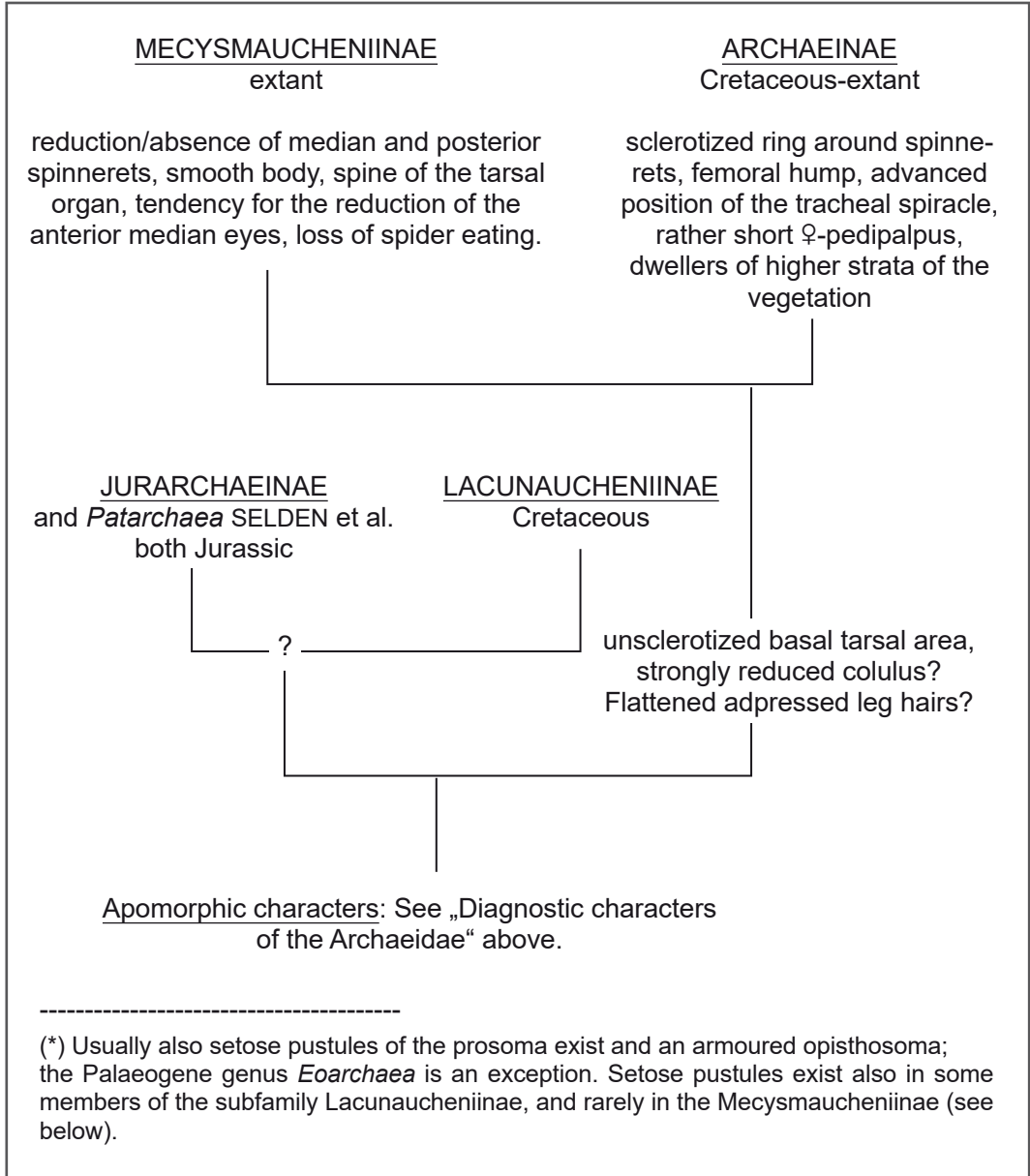


Fig. E. Possible **relationships** of the subfamilies of the Archaeidae s. l. and *Patarchaea* SELDEN et al. 2008. See WOOD et al. (2013). The left branch is surely not monophyletic and a mixture of probably not related taxa.



**Key** to the extant and fossil (Cretaceous to Palaeogene) subfamilies of the Archaeidae s. l.:

(The extinct Jurassic taxa Jurarchaeinae and *Patarchaea* SELDEN et al. 2008 – both are preserved in stone –: See above and below)

1 Sclerotized ring (\*) around the three pairs (\*\*) of spinnerets (figs. 198-199, photos) existing, femora (more distinct and hump-like on III-IV) bulging dorsally in the basal half (fig. 204). Eight eyes. Prosoma most often rugose, tuberculate or pustulate and opisthosoma usually armoured/furrowed. ♀-pedipalpus distinctly reduced, quite slender and usually short. At least extants are spider eater and dwellers of higher strata of the vegetation. – Cretaceous (ambers from France: *Archaeomecys* and Myanmar: *Burmesarchaea*) – Palaeogene (European ambers: Five genera) – extant: Australia, South Africa and Madagascar (three genera). . . . . ARCHAEINAE

- Sclerotized ring around spinnerets and bulge/hump of the femora absent (most probably in the Jurarchaeinae, too). Six (most *Mecysmaucheniinae*) or eight eyes. One pair of well developed spinnerets (*Mecysmaucheniinae*), two or three pairs. Prosoma most often smooth but see „(\*)“ below fig. E. ♀-pedipalpus long and slender (fig. 218). Prey of the *Lacunaucheniinae* unsure (spiders?), *Mecysmaucheniinae* are generalists. – Cretaceous – extant. . . . . 2

2(1) Median and posterior spinnerets strongly reduced/absent. Usually six eyes (8 eyes in *Aotearoa* from New Zealand). Body usually smooth (but cephalic part of *Mesarchaea* from Chile bearing tubercles). Tarsal organ with a sensory spine. Ground dwelling spiders. – No fossil record (see below: Archaeinae: *Archaeomecys*); extant, Southern Hemisphere: South America and New Zealand. . . . . MECYSMAUCHENIINAE

- Two pairs of well developed spinnerets (the medians may be reduced or even absent, see below); eight eyes. Body surface variable. The existence of a sensory spine of the tarsal organ is unknown. Most probably dwellers of higher strata of the vegetation. – Extinct, Northern Hemisphere, Cretaceous: Burmite: Three genera. (Probably related: The Jurassic *Jurarchaea*, Jurarchaeinae in which eyes, spinnerets and a surrounding ring are unknown). . . . . LACUNAUCHENIINAE

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(\*) Such a ring may be fairly indistinct in females of *Eoarchaea*; males of this genus are unknown. Setose prosomal pustules and an armoured opisthosoma are also absent in this unusual extinct genus.

(\*\*) The median pair is probably absent in the Cretaceous archaeinae genera *Burmesarchaea* WUNDERLICH 2008 (see below) from Myanmar and *Archaeomecys* SAUPE & SELDEN 2009 from France. (These spinnerets are also reduced/absent in the families Huttoniidae, *Mecysmaucheniidae*, Palpimanidae and Stenochilidae).

## Determination of the taxa of Mesozoic Archaeidae s. l.:

- 1 Taxa of the Jurassic from Asia which are preserved in stone. . . . . 2
- Taxa of the Cretaceous from Eurasia which are preserved in amber. . . . . 3
- 2(1) ♂♀: Sclerotized semicircles around anterior sides of the spinnerets. ♂: Cymbium (fig. 217) bearing a large spine. Taxon not placed in a subfamily. . . . .  
. . . . . *Patarchaea* SELDEN et al. 2008
- No sclerotized semicircles around anterior spinnerets. ♀ (♂ unknown) according to the original description with a sclerotized epigyne which may be an artefact in my opinion. Subfamily Jurarchaeinae. . . . . *Jurarchaea zherikhini* ESKOV 1987
- 3(1) Sclerotized ring around spinnerets (fig. 198-199), distinct femoral humps (fig. 204), tarsi basally with unsclerotized ring. France and Myanmar (Burma). Subfamily Archaeinae. . . . . 4
- No sclerotized ring around spinnerets nor unsclerotized tarsal ring, femoral humps absent or quite indistinct (caused by the preservation?). Myanmar (Burma). Subfamily Lacunaucheniinae. . . . . 5
- 4(3) Basal cheliceral articles stout (fig. 198). ad. ♂♀ unknown. France. . . . .  
. . . . . *Archaemecys arcantiensis* SAUPE & SELDEN 2009
- Basal cheliceral articles more slender (figs. 199, 202). The opisthosoma may be distinctly elongated beyond the spinnerets in not deformed specimens (photo 118). ♂-pedipalpus figs. 200, 2005. Myanmar (Burma). . . . .  
. . . . . *Burmesarchaea grimaldii* (PENNEY 2003)
- 5(3) Prosoma low (fig. 218); femur I 1.65 times of the prosomal length. ♂ unknown. . . . .  
. . . . . *Planarchaea kopp* n. gen. n. sp.
- Cephalic part strongly raising (figs. 207, 213). Length of femur I very variable. . . . . 6
- 6(5) Prosoma gradually raising anteriorly (fig. 207). Femur I ca. 1.65 times of the prosomal length. ♂ unknown. . . . . *Eomysmauchenius septentrionalis* WUNDERLICH 2008
- Cephalic part abruptly raising (fig. 213). Femoral/leg length very variable. *Lacunauchenius* WUNDERLICH 2008 (?= *Filiauchenius* WUNDERLICH 2008; female of a single, long-legged, badly preserved and weakly diagnosed species: *F. paucidentatus*) and gen. indet. . . . . 7
- 7(6) Femur I about as long as the prosoma (\*). ♂-pedipalpus (fig. 209): Cymbium covered with numerous long hairs similar to *L. pilosus*, tegular apophysis blunt and slightly bent posteriorly. . . . . *L. speciosus* WUNDERLICH 2008

- Legs very long and slender, femur I ca. 3 times the prosomal length. . . . . 8

8(7) Pedipalpal articles very long (photo), cymbium (fig. 212) covered with numerous long hairs similar to *L. speciosus*, tegular apophysis straight and furcate apically. . . . .  
. . . . . *L. pilosus* n. sp.

- Pedipalpal articles distinctly shorter, pedipalpal tibia with a short dorsal apical spine (fig. 215), cymbium not covered with long hairs (fig. 216), tegular apophysis pointed and bent ventrally. . . . . *L. longissipes* n. sp.

- Pedipalpal articles also relatively short but cymbium with long hairs similar to *L. pilosus* (photo 123). F2541/BU/CJW. . . . . *Gen. indet.*  
. . . . .

(\*) Herewith I correct certain measurements (in mm) of the holotype of *L. speciosus*: Body length without chelicerae 1.7, prosomal length 0.9, its height 0.8.

## Subfamily ARCHAEINAE

See also the key to the subfamilies above.

**Diagnosis:** Prosoma most often rugose, tuberculate or pustulate and opisthosoma usually armoured/furrowed (\*), frequently with rows of sclerotized tubercles, sclerotized ring around the three pairs of spinnerets (figs. 198-199), femora with a dorsal hump in the basal half (fig. 204) (more distinct on III-IV), advanced position of the single tracheal spiracle, very small/short ♀-pedipalpus. Spider eaters. Dwellers of higher strata of the vegetation.  
. . . . .

(\*) fairly indistinct at least in the female (the male is unknown) of the unusual PALAEOGENE genus *Eoarchaea* in which also setose pustules of the prosoma and an armoured opisthosoma are absent.

**Fossil genera:** (a) in Cretaceous ambers: *Burmesarchaea* WUNDERLICH 2008 and *Archaeinae* indet., see below (amber from Myanmar), *Archaeomecys* SAUPE & SELDEN 2009 (amber from France, described under *Mecysmaucheniidae*, see below); (b) Palaeogene ambers from Europe: *Archaea* KOCH & BERENDT 1854, *Baltarchaea* ESKOV 1992, *Eoarchaea* FORSTER & PLATNICK 1984, *Myrmecarchaea* WUNDERLICH 2004 and *Saxonarchaea* WUNDERLICH 2004.

**Relationships:** See fig. E above. Adpressed plumose hairs on body and anterior legs exist in extant taxa; they are absent in the Palaeogene genus *Eoarchaea* and apparently in the Cretaceous genus *Burmesarchaea* – like in the Cretaceous *Lacunaucheniinae* and the *Mysmaucheniinae* (extant).

**Distribution:** Extinct: Northern Hemisphere: Cretaceous (France and Myanmar), Palaeogene (Europe) – extant: Southern Hemisphere: South Africa, Madagascar and Australia. Archaeinae do not share a region with members of the related subfamily Mecysmaucheniinae: see below.

***Archaemecys arcantiensis*** SAUPE & SELDEN 2009 (fig. 198)

The taxon is based on a subadult male (\*) only; it has been described in Lower Cretaceous amber FROM FRANCE (Charente-Maritime) in the Mecysmaucheniinae (under Mecysmaucheniidae) – which is completely restricted to the Southern Hemisphere today –, as first fossil record of this family at all. I doubt the placing in the taxon Mecysmaucheniinae (Mecysmaucheniidae sensu WOOD et al. (2012)) by reasons below, and transfer it to the related subfamily Archaeinae (**n. relat.**) (\*\*):

(1) Like in other Mecysmaucheniinae in *A. arcantiensis* allegedly (really?) only a single tracheal spiracle exists in contrast to the paired spiracle in the Archaeidae. The position of the spiracle in the Mecysmaucheniidae is – like in most spiders – just in front of the spinnerets, but the position of the alleged spiracle in *A. arcantiensis* (figs. 2 A, B in the paper by SAUPE & SELDEN) is far in front of the spinnerets similar to extant Archaeinae. Because of this position this structure is most likely not a tracheal spiracle in my opinion but probably an artefact.

(2) In *A. arcantiensis* the spinnerets are surrounded by a sclerotized ring which exists in members of the Archaeinae but is completely unknown in (extant) Mecysmaucheniinae.

(3) A femoral hump (a dorsally-basally bulging femur) may be reduced and is easily overlooked in certain fossil Archaeinae, see *Eoarchaea*. *A. arcantiensis* (fig. 2 A in the paper by SAUPE & SELDEN) shows a slightly bulging left femur IV; see the arrow in fig. 198.

(4) Within the superfamily Archaeoidea exists the tendency to reduce the median and/or posterior spinnerets, see above (\*\*\*). Therefore a reduction of these spinnerets in the Archaeidae appears not unlikely although *A. arcantiensis* is probably the first known member of the subfamily Archaeinae in which the median spinnerets are strongly reduced or even absent. The small median spinnerets may be hidden by the remaining spinnerets within the sclerotized ring, see *Burmesarchaea grimaldii* below.

(5) According to SAUPE & SELDEN spatulate (!) hairs are absent in *A. arcantiensis* like in members of the Mecysmaucheniinae. SPATULATE leg hairs – see FORSTER & PLATNICK (1984: Fig. 25) – as well as adpressed PLUMOSE hairs – see JOCQUE & DIPPENARE-SHOEMAN (2006: 78) – exist in most fossil and extant Archaeidae s. l. but spatulate leg hairs are absent in *Eoarchaea* and apparently in *Burmesarchaea* like in the Mecysmaucheniinae.

(6) The whole opisthosoma of *A. arcantiensis* appears hardened but it is soft in (extant) Mecysmaucheniinae except ventral plates in certain taxa.

(7) and (8) According to SAUPE & SELDEN (2009: 53) „*Archaemecys* n. gen., like other mecysmaucheniids, does not have tubercles on the carapace, and the chelicerae in the fossil are shorter and stouter than those usually found in archaeids.“. Prosomal tubercles are absent in certain fossil Archaeidae like *Eoarchaea* (now Jurarchaeinae),

relatively stout basal cheliceral articles exist e. g. in *Baltarchaea* (Archaeinae), which both are preserved in Palaeogene Baltic amber.

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(\* ) According to the apparently separate pedipalpal tibia the male is probably adult.

(\*\*) (= family Archaeidae sensu WOOD et al (2012)). The subfamily Archaeinae (extant and extinct taxa) is characterized mainly by the sclerotized ring around the spinnerets and the existence of a femur which is bulging or hump-shaped dorsally in the basal half (fig. 204), see below.

(\*\*\*) In all known extant Mecysmaucheniinae the posterior spinnerets are absent and the median spinnerets are absent or – probably in few species – quite strongly reduced.

### ***Burmesarchaea*** WUNDERLICH 2008 (figs. 199-206) photos 118-122

This genus was introduced by me for *Afrarchaea grimaldii* PENNEY 2003 which is preserved in Burmite. This is the only known taxon of the subfamily Archaeinae in amber from Myanmar as well as in Cretaceous ambers besides *Archaemecys* SAUPE & SELDEN 2009 from France, see above.

**Emended diagnostic characters and relationships:** Lateral eyes widely spaced (fig. 201), cephalic part with spines and bristles (figs. 199, 202), adpressed plumose hairs – as on the legs – apparently absent in contrast to *Afrarchaea* FORSTER & PLATNICK 1984 (extant, Africa and Madagascar), spatulate leg hairs apparently absent, too, opisthosoma – it is frequently deformed – usually distinctly elongated beyond the spinnerets (e. g. F2520) (photo 118) (depressed in fig. 199, arrow), strongly armoured/ scutate, not covered completely by a large undivided shield; apparently only plates/hardenings exist, which bear rows of tubercles in both sexes (fig. 200, photos) in contrast to *Afrarchaea* but similar to the male of *Austrarchaea* FORSTER & PLATNICK 1984 (extant, Australia). In both extant genera spines/bristles of the cephalic region and ROWS of opisthosomal tubercles are absent, and the position of the spinnerets is at or near the end of the opisthosoma. ♂–pedipalpus (figs. 200, 205-206) small, with slender articles and a long embolus and a long conductor (or a seam?). – See also the member of an Archaeinae indet. below.

**Remarks:** (1) In the newly studied specimens the spinnerets are dislocated anteriorly in contrast to the holotype (photo 118) in which the opisthosoma probably is distinctly deformed by the pressure during the preservation, and the spinnerets may be in an unnatural position. (2) Plumose hairs of the body and spatulate hairs of the legs were not mentioned in the original description of the generotype and were not observed by me in the newly studied specimens. (3) The – probably conspecific – female of this taxon is described here for the first time.

**Distribution:** Mid Cretaceous amber from N-Myanmar.

**Material:** 3♂2♀ in Mid Cretaceous amber from N-Myanmar, 1♂ F2519/BU/CJW, 1♂ F2520/BU/CJW, 1♂ F2534/BU/CJW, 1♀ F2521/BU/CJW, 1♀ F27097BU/CJW.

**Preservation:**

F2519: The male is almost completely preserved (only the right leg I is lost beyond the femur), distinctly deformed, darkened and laterally compressed; from that a larger longitudinal dorsal furrow results, most leg articles are shrunked, and the pedipalpi are strongly deformed.

F2520: The male is completely and well preserved in a larger piece of amber together with remains of plants and some arthropods like a large Diptera. The armoured opisthosoma is oval and elongated beyond the spinnerets, its dorsal colour (triangle-shaped marks) is preserved, a ?gas bubble exists on the right side of the prosoma.

F2521: The female is completely and well preserved in a small yellow piece of amber. It is laterally compressed quite similar to the male F2519, so that the body appears distinctly more slender than in the living spider, and the opisthosoma bears a larger longitudinal dorsal furrow. The chelicerae are spread so that the mouth parts are observable, the spinnerets are excellently preserved.

F2534: The male is strongly deformed, its femora (especially the anteriors) are strongly widened/flattened in the basal half, a dorsal opisthosomal furrow exists, the deformed pedipalpus: See fig. 206, the trochanter is quite long.

**Description:**

Males, see PENNEY (2003). In contrast to (the description of) the holotype the cephalic part bears spines/bristles similar to the female, and the spinnerets with their sclerotized ring (this ring is figured but not mentioned in the original description of the species) are set forward (photos). – Measurements (in mm): F2519: Body length 1.8 (holotype 1.97), prosomal length 0.8, femur I 1.0, opisthosoma (deformed!): Length 1.0, width 0.35, height 0.7. F 2520: Body length 2.0, prosomal length 0.9; leg I: Femur I ca. 0.9, patella 0.25, tibia 1.0, femur IV ca. 0.55; opisthosoma: Length 1.0, width 0.8, height 0.85. – Order of the legs I/II/IV/III, femoral humps frequently (!) existing (fig. 204), pedipalpus small, bulbus/tarsus short, embolus apparently long (figs.).

Females (the probably conspecific females are described here for the first time). F2521: The probably adult specimen is completely and well preserved in a clear yellow piece of amber. Measurements (in mm): Body length 2.0, prosomal length 0.9, opisthosoma (deformed!): Length 1.2, width 0.45, height 0.7; leg I: Femur 1.1, patella 0.25, tibia 0.95, metatarsus 0.42, tarsus 0.33, tibia II 0.8, tibia III 0.48, tibia IV 0.65. – Prosoma (figs. 201-203, photos) strongly rugose and spiny, eye field wide, median eyes widely spaced, chelicerae long, bearing numerous long „peg teeth“, lateral files apparently absent but a longitudinal (stridulatory?) edge exists. Labium slender, ca 1 ½ times longer than wide, sternum quite narrow, coxae IV close together. – Pedipalpus (fig. 202) small, with a long trochanter, claw absent. – Legs (photos) long and slender, order I/II/IV/III, bristle-less, unsclerotized basal tarsal area existing, indistinct metatarsal III preening hairs exist, position of the metatarsal II trichobothrium in 0.87. – Opisthosoma (photos) armoured and furrowed, with bristle-bearing tubercles in rows and a well developed sclerotized ring around the anal tubercle and the spinnerets with is set forward, anterior

and posterior spinnerets well developed, the median spinnerets are not observable, probably hidden, strongly reduced or even absent; colulus absent. The opisthosoma bears ventrally a large transverse (epigastric?) furrow in the middle and just in front of it a widely spaced pair of small sclerotized structures which may bear the introductory openings of the vulva.

F2709: The apparently adult and probably egg-bearing female is completely preserved in a clear yellow piece of amber together with a male of *Leclercera* indet. (Psilodercidae). Measurements (in mm): Body length 2.8, prosomal length 1.1, femur I 1.55, tibia I 1.6. Femur IV distinctly bulging dorsally near the base, the spinnerets are fairly well preserved, I did not surely identify the median ones.

**Relationships:** The bulbi of the males are not well preserved and do not allow a sure determination. The body of the four specimens is similar to the holotype but strongly depressed laterally in F2519, F2520 and 2534; as a result exists a longitudinal dorsal furrow in these specimens. An anterior-basal cheliceral bristle is absent in these fossils in contrast to the holotype, probably rubbed off. Therefore I am not quite sure about the conspecificity of the specimens in question. – See also the member of an Archaeinae indet. below.

**Distribution:** Mid Cretaceous amber from N-Myanmar (Burma).

**Archaeinae indet.** (photo 123)

**Material:** 1♂ in Cretaceous amber from N-Myanmar (Burma), F2541/BU/CJW.

Body, legs and pedipalpi of the male are strongly deformed (photo 123); its body is similar to *Burmesarchaea grimaldii* (see above), the prosoma (photo) is strongly raised and bears setose pustules, the opisthosoma is strongly armoured (its ventral part including the spinnerets is lost), the patellae are short, metatarsi III and IV bear an apical wreath of bristle-shaped hairs (not a comb). – Measurements (in mm): Body length >2.0, prosomal length 1.1, length of femur I ca. 3.5. Pedipalpus (photo) with fairly short and hairy articles which are flattened and thickened artificially by the preservation. The long hairs and the furcate tegular apophysis are similar to *Lacunauchenius pilosus*. According to the structures of the body the species may strongly related to the genus *Burmesarchaea*, see above.

An unusual tiny mite, body length 0.15 mm, is preserved just below the surface of the piece of amber above the left patella I of the spider.



**Subfamilies LACUNAUCHENIINAE** WUNDERLICH 2008 and **JURARCHAEINAE** ESKOV 1987

See also the key to the subfamilies above.

**Diagnostic characters of the Lacunaucheniinae:** Basically apparently three pairs of spinnerets (the median pair may be reduced or probably even absent), diastema existing, tracheal spiracle unknown, femoral humps absent or quite indistinct, spatulate leg hairs, opisthosomal folds and scutum as well as sclerotized ring around spinnerets absent, indistinct prosomal pustules may exist (see *Lacunauchenius*), the metatarsal III-IV preening hairs may be reduced/indistinct (fig. 210), a preening comb is absent, cymbium long and slender (figs. 212, 215-216), prey unknown, probably spider eaters (see above and *Lacunauchenius* below), probably dwellers of higher strata of the vegetation.

**Genera:** *Lacunauchenius* WUNDERLICH 2008, *Eomysmauchenius* WUNDERLICH 2008, *Filiauchenius* WUNDERLICH 2008 (probably a synonym of *Lacunauchenius*), and *Plarnarchaea* n. gen.

**Relationships:** See fig. E above. I do not find differences between the still WEAKLY DIAGNOSED monotypic Jurarchaeinae ESKOV 1987 (Jurassic, known from a single female specimen of *Jurarchaea* ESKOV 1987 only) and the Lacunaucheniinae WUNDERLICH 2008 (Cretaceous), see the cladogram of the subfamilies above. Therefore the synonymy cannot be excluded with certainty.

**Possible prey:** It is remarkable that near the two new described species of *Lacunauchenius* five juvenile not archaeoid spiders are preserved.

**Distribution:** Completely extinct, Cretaceous, Northern Hemisphere only up to now: Myanmar (Burma).

***Lacunauchenius*** WUNDERLICH 2008  
(= *Filiauchenius* WUNDERLICH 2008, **quest. n. syn.**)

Only a single female of this genus in amber from Myanmar – of the generotype *L. speciosus* WUNDERLICH 2008 – has been described up to now (see also *Filiauchenius paucidentatus* in the paragraph „synonymy“ below). Here I describe two further species which are based on males; both are strongly deformed. The male sex of this genus is described for the first time and allows a revised diagnosis of the genus.

**Prey:** It is remarkable that together with the two males in question not less than five small juvenile not archaeoid spiders are preserved, some quite near the males. I do not want to exclude that the fossil spiders were araneophagous like the extant relative Archaeinae and at least some Palaeogene Archaeinae, see above.

**Revised diagnosis:** Cephalic part strongly raised with a long „neck“ (fig. 208, 213); male pedipalpus (figs. 209, 212, 215-216): Cymbium very long and slender, bulbus with a long, slender and strongly sclerotized tegular apophysis which is directed ventrally-posteriorly.

Further character: Flattened/spatulate leg hairs are absent. Plumose prosomal hairs exist.

Intragenetic variability: Prosomal pustules are fairly distinct in *pilosus*, fairly distinct in *speciosus* but almost absent in *longissipes*. The legs are relatively short in *speciosus* (femur I 1.65 times the prosomal length) but three times the prosomal length in *pilosus* and *longissipes*. The opisthosoma may be hardened dorsally (in *speciosus*) or probably even scutate in the other species. The cymbium may bear short hairs (figs. 215-216) or numerous long hairs (figs. 209, 212). At least in the male of *longissipes* the basal cheliceral articles bear apparently a large medial outgrowth (fig. 214).

**Synonymy** of *Filiauchenius* WUNDERLICH 2008 (male unknown): The number of peg teeth of the badly preserved female holotype of the generotype – *Filiauchenius paucidentatus* WUNDERLICH 2008 – may be higher than recognized by me previously, see WUNDERLICH (2008: 665, fig. 63), and leg III is probably the shortest like in the (other) species of *Lacunauchenius*. Therefore I regard the monotypic genus *Filiauchenius* as probably synonym with *Lacunauchenius* WUNDERLICH 2008 (**n. quest. syn.**) and **n. quest comb.** of *paucidentatus*.

Key to the species (except *paucidentatus*): See above (determination of the Mesozoic archaetid taxa)

***Lacunauchenius pilosus* n. sp.** (figs. 211-212), photos 125-126

Etymology: *Pilosus* (lat. = hairy) for the numerous long cymbial hairs of the species.

**Material:** Holotype ♂ in Mid Cretaceous amber from Myanmar (Burma), F2536/BU/CJW.

**Preservation and syninclusions** (photos): The spider is strongly deformed, probably dissected, and incompletely preserved in a yellow piece of amber which has been rolled and which consists of numerous layers. The body, the pedipalpi and most parts of the legs are strongly shrunk (fig. 211, photo), the right femur I is abruptly shrunk basally and darkened here by the preservation but normally sized beyond this area; the left leg I is almost complete, the distal part of the femur, the patella, the basal part of the tibia are missing (cut off within the fossil resin), the posterior end of the opisthosoma is also missing. Several spider threads exist, some may be strongly swollen (bubble-shaped) sticky droplets, others are thin; some needle-shaped possible plant hairs and some „stellate hairs“ are existing, too, as well as a small Hymenoptera, a Psocoptera, and a small juvenile spider indet.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (fig. 209; both pedipalpi are strongly deformed): Cymbium covered with numerous partly very long hairs, bulbus with a long, slender tegular apophysis which is furcate apically.

**Description** (♂):

Measurements (in mm): Body length 3.5, prosomal length 1.7, basal cheliceral article 1.0; leg I: Femur (the distal part is missing) probably about 5.0, diameter in the middle 0.11, patella lost, tibia (the basal part is lost) probably about 4.0, metatarsus 5.4, tarsus 2.0, tarsus III 1.0; pedipalpus: Femur 1.5, patella 0.5, tibia 1.35, cymbium 0.8.

Colour: Femora medium brown, remaining parts dark brown (darkened by the preservation).

Prosoma (photo 125; it is strongly deformed) with a high cephalic part and a large gap between gnathocoxae and chelicerae (diastema), pustules only fairly distinct, eye position unknown, basal cheliceral articles long, bearing peg teeth probably in two rows, lateral files apparently absent, fangs long and strongly bent. – Legs (photos, fig. 210) extremely long and slender, more or less shrunk by the preservation, hairs short and indistinct, bristles absent; I: femur ca. 3 times the prosomal length, patella missing, metatarsi longest, metatarsal III-IV preening comb and tarsal trichobothria absent, metatarsal trichobothria unknown, unpaired tarsal claw long and strongly bent. – Opisthosoma (photo) strongly deformed, posterior part lost. – Pedipalpus (photo 226, fig. 212): Articles very long and slender (their diameter is shrunk by the preservation), femur almost as long as the prosoma, cymbium slender, distinctly longer than the bulbus, covered with numerous hairs which partly are very long, the bulbus is strongly deformed and bears a long, slender, straight and strongly sclerotized tegular apophysis which is directed ventrally-posteriorly and has a furcate end, another apophysis exists near the thin embolus.

**Relationships:** See the key above and *L. longissipes* n. sp. below in which the legs are extremely long and slender, too.

**Distribution:** Mit Cretaceous amber forest of Myanmar (Burma).

***Lacunauchenius longissipes* n. sp.** (figs. 213-216), photo 124

**Etymology:** From longus (lat. = long) and pes (lat. = leg) for the extremely long legs of the species.

**Material:** Holotype ♂ in Mid Cretaceous amber of Myanmar (Burma) and a separated piece of amber, F2537/BU/CJW.

**Preservation and syninclusions** (photos): The spider is deformed/dissected and incompletely preserved in a yellow piece of amber which has been rolled and which consists of numerous layers, the opisthosoma is lost, the right leg II is completely pre-

served, several loose leg articles are preserved behind the spiders prosoma. – Two and four mm below and in front of the holotype two juvenile spiders are preserved, both ca. 0.7 mm long, a female member of the genus *Burmorchestina* WUNDERLICH 2008 (Oonopidae), and a questionable member of the superfamily Araneoidea; remains of opisthosoma and legs of a small and probably juvenile spider indet. and a tiny mite exist behind the spider. Remains of a small and deformed insect are preserved behind/below the prosoma of the holotype, and numerous small ?gas bubbles above the prosoma. Few spider threads and remains of plants like „stellate hairs“ exist also. A forth small juv. Araneae indet. is preserved in the separated piece of amber near an insect indet. together with two leg articles of the holotype.

I do not want to exclude that at least one of the small spiders near the holotypes' prosoma may have been a potential prey of the archaeid spider.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (figs. 215-216, photo; both are strongly deformed): Tibia with a dorsal-apical spine-shaped apophysis, the bulbous bears a long, slender and strongly sclerotized tegular apophysis which is bent ventrally.

### **Description** (♂):

Measurements (in mm): Body length (the opisthosoma is lost) probably not much longer than 2.0, prosoma: Length 1.1, height 0.9; legs: The right femur I is cut off beyond its basal 2.7 mms, leg II: Femur > 2.5, patella 0.35, tibia 2.1, metatarsus 2.0, tarsus 1.1, tibia III > 1.0; pedipalpus (parts are hidden): Femur probably > 0.4, tibia probably > 0.35, cymbium (deformed) ca. 0.45.

Colour: Legs medium brown, prosoma dark brown.

Prosoma (figs. 213-214, photo) (it is strongly deformed) with a high cephalic part and a large gap between chelicerae and gnathocoxae (diastema), cuticula almost smooth (very finely corniculate), eye position unknown, basal cheliceral articles long, with a large medial outgrowth (probably not an artefact); I did not recognize long peg teeth or retrolateral files. The fangs are long and strongly bent. – Legs (photos) extremely long and slender, order I/II/IV/III, hairs short and indistinct, bristles and metatarsal III-IV preening comb absent, I distinctly the longest, III distinctly the shortest, femoral humps absent, femur I ca. 3 times the prosomal length, metatarsi long, tarsi relatively short, metatarsal trichobothria unknown, tarsal trichobothria apparently absent, metatarsal III-IV preening comb absent. – Opisthosoma lost. – Pedipalpus (figs. 215-216, photo) strongly deformed, articles only fairly long but cymbium long and slender, its hairs short, the bulbous bears a long, slender and strongly sclerotized tegular apophysis which is bent ventrally, another apophysis exists ventrally of the thin embolus.

**Relationships:** *L. pilosus* n. sp. is larger, its pedipalpal articles are much longer, the tibia bears no apical spine-shaped apophysis, the cymbium bears numerous hairs which partly are very long, and the tegular apophysis is furcate apically.

**Distribution:** Mit Cretaceous amber forest of Myanmar (Burma).

***Lacunauchenius* sp. indet.** photos 127-128

**Material:** 1 ♀ in Mid Cretaceous amber from Myanmar (Burma) and a separated piece of amber, F2627/BU/CJW.

**Remark:** According to the relatively voluminous opisthosoma this appears to be an egg-bearing female.

**Description** (♀): The spider is partly very well preserved in a clear yellow piece of amber, the prosoma is laterally distinctly compressed..

Measurements (in mm): Body length 2.1, prosomal length 1.0, length of a basal cheliceral article 0.85, opisthosoma: Length 1.2, height 1.0, tibia I ca. 0.6.

Like in other members of *Lucauchenius* the prosoma is distinctly rugose and overhanging posteriorly; an anterior cheliceral bristle, a ring around the spinnerets and probably cheliceral files are absent. The cheliceral articles are very large and bear very long peg teeth (photo), the legs are not very long (photo). The anterior and posterior spinnerets are large, median spinnerets are not observable, probably strongly reduced.

According to the measurements of body and legs the this species may be **related** to *L. speciosus* WUNDERLICH 2008.

***Eomysmauchenius*** WUNDERLICH 2008 (fig. 207)

Only a single species of this genus – *E. septentrionalis* WUNDERLICH 2008 (fig. 207), based on a single female (the male of this genus is still unknown) – has been described from Burmese amber. Relationships: See the key to the mesozoic archaeid taxa above.

***Planarchaea* n. gen.**

**Etymology:** Plan (lat. = flat) for the low prosoma, archaea for the related archaeid genus *Archaea*. – The gender of the name is feminine.

**Type species** (by monotypy): *Planarchaea kopp* n. sp.

**Diagnosis** (?ad. ♀): Cephalic part (fig. 218) not raised, position of the eyes as in figs. 218-219.

Further character: Femur I 1.65 times of the prosomal length.

**Relationships:** According – and in contrast to the Archaeinae – to the absence of femoral humps, spatulate leg hairs, an armoured opisthosoma, and a ring around the three pairs of spinnerets I regard *Planarchaea* as most probably being a member of the subfamily Lacunaucheniinae. In contrast to the remaining genera of the Lacunaucheniinae the cephalic part is not raised. In the subfamily Mecysmaucheniinae exists only a single pair of well developed spinnerets.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

***Planarchaea kopp* n. sp.** (figs. 218-219) photos 129-130

Derivatio nominis: The spider is dedicated to KARIN and LUDWIG KOPP in Ritterhude which selected fossil spiders in Burmite for me in a joint excursion in Myanmar (Burma) 2013.

**Material:** Holotype adult or juvenile ♀ in Mid Cretaceous amber of Myanmar (Burma), F2522/BU/CJW.

**Preservation and syninclusions:** The spider is very well and almost completely preserved, only the tips of the tarsi of the left legs I and IV are cut off. Parts of body and legs are fairly shrunked by the preservation, parts of both femora IV are compressed laterally and artificially enlarged dorsally, some ventral parts of the opisthosoma have been inclined and are covered with a bubble. – A dark grey and pear-shaped „bubble“ is preserved at the margin of the clear yellow piece of amber behind the spider. A tiny wasp is preserved left of the spider.

**Diagnosis:** See the genus.

**Description** (?ad. ♀):

Measurements (in mm): Body length 1.65, prosoma: Length 0.85, width 0.5, height 0.35; leg I: Femur 1.4, patella 0.3, tibia 1.35, metatarsus 1.4, tarsus 0.8, tibia II ca. 0.8, tibia III 0.4, tibia IV 0.55, femur IV 1.0; opisthosoma: Length 1.0, width 0.4, height 0.4.

Colour: Prosoma and legs medium to dark brown, opisthosoma light brown.

Prosoma (figs. 218-219, photos) (fairly shrunked) 1.7 times longer than wide, slender and low, distinctly narrowed anteriorly, not wrinkled/pustulate, fovea indistinct, hairs fairly short, plumose hairs apparently existing, eyes small, field wide, anterior medians largest, posterior row procurved, lateral eyes contiguous, the anterior larger, clypeus ca. 1 ½ times longer than the diameter of the anterior median eyes, basal cheliceral articles large, slender distally, lateral files probably absent, fang furrow with two rows of long peg teeth, fangs fairly stout. The deformed labium is about 1 ½ times longer than wide, the deformed gnathocoxae are about twice as long as wide at its base, serrula well developed, sternum ca. 1.33 times longer than wide, a posterior „knob“ is absent.

– Pedipalpus (fig. 218-219) quite long and very slender, its trochanter apparently not elongated, tarsal claw absent. – Legs long and slender, order I/II/IV/III, III distinctly smallest, patellae short, metatarsi distinctly longer than tarsi, bristles absent, femoral humps and adpressed spatulate hairs absent, femur IV not bent, metatarsal III-IV preening hairs indistinct, building no comb, similar to *Lacunauchenius speciosus* (fig. 210). Position of the metatarsal II trichobothrium in 0.65, tarsal trichobothria absent. Tarsal claws apparently toothless, unpaired claws about as long as the paired claws and bent in a right angle. – Opisthosoma (photos) more than twice as long as wide, soft, hairs short, no sclerotized ring around the 3 pairs of well developed spinnerets, colulus most probably absent, anal tubercle large. I did not recognize lung covers or a tracheal spiracle.

**Relationships:** See above.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

**Subfamily MECYSMAUCHENIINAE** PETRUNKEVITCH 1928

(= Mecysmaucheniidae auct.; the taxon may be regarded as a family of its own).

See also the key to the subfamilies above. – No sure fossil proof.

**Diagnosis:** Strong reduction/absence of the median and posterior spinnerets, usually smooth body, sensory spine of the tarsal organ, absence of the anterior median eyes, but 8 eyes in *Aotearoa* FORSTER & PLATNICK 1984 (corresponding to the Archaeidae), smooth prosoma, but tubercles exist on the cephalic part in *Mesarchaea* FORSTER & PLATNICK 1984 (corresponding to the Archaeidae); feeding as generalists, ground spiders, no capture web.

**Genera:** Several extant genera.

**Relationships:** See fig. E above.

**Distribution:** Fossils unknown (see *Archaeomecys* above under Archaeinae). Extant: Southern Hemisphere: South America and New Zealand. In these regions Archaeinae are absent. Such substitution (vicariance) is not rare in related subfamilies (and other lower subtaxa).



## Family HUTTONIIDAE SIMON 1893

**Diagnosis and relationships:** See Micropalpimanidae below and the discussion of the relationships of selected archaeoid families above. In the extant members exist a compact eye field similar to the Spatiatoridae: Vetiatorinae.

**Distribution:** New Zealand. Questionable Huttoniidae fossils (see below): Late Cretaceous amber forest of North America: Canada and New Jersey (including the present fossil).

**Questionable taxon indet.** (figs. 220-221) photo 139

**Material:** 1 apparently juv. female in Late Cretaceous amber from New Jersey, F2464/NJ/CJW.

**Preservation:** The spider is very well and almost completely preserved in a yellow-orange piece of amber, the tip of the right tarsus I is cut off; bubbles exist ventrally on the opisthosoma, the mouth parts and some leg articles. The opisthosoma has been somewhat deformed by the preservation by a layer within the fossil resin. A thin spiders thread originated from the left leg IV.

### **Description** (?juv. ♀):

Measurements (in mm): Body length 1.5, prosomal length 0.8; leg I: Femur ca. 0.5, patella 0.28, tibia 0.35, metatarsus 0.28, tarsus 0.28; leg IV: Femur 0.6, patella 0.24, tibia ca. 0.3, metatarsus 0.34, tarsus 0.25.

Colour light brown.

Prosoma (photos): Cephalic part not raised, bearing very few short hairs, cuticula almost smooth, 8 eyes in two wide rows, fovea hard to detect, apparently absent, diastema absent, clypeus at least as long as the length of the eye field, basal cheliceral articles long, not diverging, fine lateral stridulatory files probably existing, fangs hidden besides a basal part, mouth parts and teeth of the fang furrow hidden by bubbles, coxae IV spaced by less than their diameter. Pedipalpus (fig. 221) not reduced, bearing strong retrolateral tarsal hairs, tarsal claw apparently absent. – Legs (photo) fairly short, order IV/II/III/III, patellae relatively long (see above), true bristles very rare, a distinct straight dorsal-apical bristle exists on the right patella III (fig. 220), tarsal trichobothria absent, position of the metatarsal trichobothria unknown, metatarsal III-IV preening comb well developed, prolateral spatulate hairs on tarsi and metatarsi I-II difficult to observe, 3 tarsal claws. – Opisthosoma (photo) deformed by a layer in the amber, raised in the basal half, covered with thin hairs, genital area hidden by a bubble, anterior spinnerets large and close together, remaining spinnerets hidden.

**Relationships:** The low cephalic part and the existence of true leg bristles/spines (fig. 220), the position of the 8 eyes in a wide field and the possible absence of a fovea of the present specimen are similar in the Huttoniidae sensu PENNEY (2006). Extant Huttoniidae are known from New Zealand only. Fossils: Up to now only juveniles in Late Cretaceous amber have been described from North America (Canadian and New Jersey ambers) only, see PENNEY (2006). I am quite unsure sure about the correct determination of these fossils on the family level until adults will have been studied, and a revision of the extant taxa from New Zealand has been carried out. In contrast to extant Huttoniidae the pedipalpus of the female 2464 is not reduced. See also Micropalpimanidae below and the discussion of the relationships of selected archaeoid families above.

## **The LAGONOMEGOPID BRANCH of the Archaeoidea**

This diverse extinct branch – including the families Lagonomegopidae and Micropalpimanidae – may be the most basal branch of the superfamily Archaeoidea. The high frequency of its members in the fossil resins may point to its dwelling in higher strata of the vegetation.

The branch is **diagnosed** by the existence of (long) tarsal and several metatarsal trichobothria (figs. 228, 245-246, 259, 267 photo 112) (unique within the Archaeoidea) in an irregular position (they may be numerous but may be absent in juveniles), probably basically the existence of (few and usually thin ones in juveniles) leg bristles (figs. 228 (s), 267-268, 271, 273, 278) (also existing in the Huttoniidae, including adults), probably the loss of cheliceral stridulatory files (at least in the Lagonomegopidae, see figs. 236, 269), and thin (NOT widened or flattened) and usually dense hairs of the „scopulate“ legs I-II (figs. 259, 272, photos 103, 107, 117).

Further important characters are e. g. the false claw tufts (thin hairs) which may be well developed (fig. 266), and with a more or less long/slender cymbium (figs. 222, 227, 239-240, 243, 249). Eight eyes exist probably in all taxa (I found eight eyes in all larger/adult and well preserved specimens).

**Relationships:** See above, the Archaeidae, the cladogram, and the chapter „Phylogenetics“ in which „similarities“ and probable relationships to the RTA-clade are discussed.

**Family LAGONOMEGOPIDAE** ESKOV & WUNDERLICH 1995 figs. 222-266, photos 92-117, family key no. 12

The fast and enormous progress in the knowledge of the Mesozoic spider fauna is best demonstrated by the new finds of well preserved and even adult specimens of the extinct family Lagonomegopidae which is only known from the Cretaceous. The first taxon – based on juveniles – has been described from Siberian amber only two decades before – see ESKOV & WUNDERLICH (1995) -, and now (in 2015) we know 22 species of about 14 genera (8 or 9 in Burmite) from 7 kinds of ambers, including several adult specimens of both sexes of the same species. It has turned out that the ancient extinct Lagonomegopidae was one of the most diverse families of haplogyne spiders which are preserved in Cretaceous ambers besides the Segestriidae, Praeterleptonetidae (?), Archaeidae and Uloboridae (besides the Praeterleptonetidae members of these families survived up to now in contrast to the Lagonomegopidae). Lagonomegopidae is known by a single subfamily only, Segestriidae, Archaeidae and Uloboridae by several subfamilies each.

The taxa of the Lagonomegopidae, their distribution, stade and known sex:

Burmite = amber from Myanmar (Burma). Generotypes are marked with an asterix.

Archaelagonops WUNDERLICH 2012d, ♂ ♀, Myanmar (type area) and Spain. See below: *Soplaogonomegops unzuei*. ♀: See *Archaelagonops* sp. indet;  
– *alavensis* (PENNEY 2006) (under *Burlagonomegops* a., **n. comb.**), juv., Spain: Alava,  
– *propinquus* **n. sp.**, ♂, Burmite,  
– *\*salticoides* WUNDERLICH 2012d, ♂, Burmite,  
– *scorsum* **n. sp.**, ♂, Burmite,

Burlagonomegops PENNEY 2005 b, juv., Burmite,  
– *\*eskovi* PENNEY 2005b, Burmite,  
(*B. alavensis*: See *Archaelagonops*),

Cymbiolagonops **n. gen.**, ♂, Burmite,  
– *\*cymbiocalcar* **n. sp.**, ♂, Burmite,

Grandoculus PENNEY 2004b, ?ad. ♀, Canadian amber,  
– *\*chemahawinensis* PENNEY 2004b, ?ad. ♀, Burmite,

Lagonoburmops WUNDERLICH 2012d, juv., ♀, Burmite,  
– *\*plumosus* WUNDERLICH 2012d, juv., ♀: see below, Burmite,

Lagonomegops ESKOV & WUNDERLICH 1995, type genus of the family, juvenile, Siberia (type area), probably Burmite and USA (det. questionable),  
– ?*americanus* PENNEY 2005b, juv., USA: New Jersey,  
– \**sukatchaevae* ESKOV & WUNDERLICH 1995, juv., Siberia: Taimyr,  
– ?*L. tuber* **n. sp.**, juv., Burmite,

Lineaburmops **n. gen.**, ♂, Burmite,  
– \**beigeli* **n. sp.**, ♂, Burmite,  
– *hirsutipes* **n. sp.**, ♂, Burmite,

Myanlagonops WUNDERLICH 2012d, ♂, Burmite,  
– \**gracilipes* WUNDERLICH 2012, ♂, Burmite,

Parviburmops **n. gen.**, ♂, Burmite,  
– \**brevipalpus* **n. sp.**, ♂, Burmite;

Paxillomegops **n. gen.**, ♂, Burmite,  
– ?*P. brevipes* **n. sp.**, ♂, Burmite,  
– \**longipes* **n. sp.**, ♂, Burmite,

Picturmegops **n. gen.**, ♀, Burmite,  
– \**signatus* **n. sp.**, ♀, Burmite,

Soplaogonomegops FUENTE et al. 2013, juv., Spain; probably synonym of *Archaelagonops* (**quest. n. syn.**),  
– \**unzuei* FUENTE et al. 2013, juv., Spain: Cantabria,

Spinomegops FUENTE et al. 2013, juv., Spain,  
– \**arcanus* FUENTE et al. 2013, juv., Spain: Alava,  
– *aragonensis* FUENTE et al., juv., Spain: Aragon,

Zarqagonomegops KADDUMI 2007, juv., Jordanian amber,  
– \**wunderlichi* KADDUMI 2007, juv.; WUNDERLICH (2008: 615), Jordanian amber.

### Suprageneric synonymy:

(a) The family Grandoculidae PENNEY 2011 was first synonymized by WUNDERLICH (2012: 199-200) and afterwards independently by FUENTE et al. (2013). The synonymy was not accepted by PENNEY (2013: 298) who overlooked or ignored the arguments in the paper by WUNDERLICH (2012). In my opinion the weak argumentation by PENNEY does not at all justify the acceptance of a family Grandoculidae of its own (even not a subfamily); see the emended diagnosis of the Lagonomegopidae below.

(b) The subfamily Archaelagonopinae WUNDERLICH 2012: After the study of new and well preserved specimens of *Archaelagonops* (see below) the alleged huge posterior median eyes (in a typical position of the anterior median eyes in other families!) of the holotype of *Archaelagonops salticoides* turned out to be nothing else than larger humps

of the clypeus which are covered with an emulsion. Furthermore: Long and more or less diverging basal cheliceral articles also exist in *Myanlagonops* WUNDERLICH 2012 and *Paxillomegops* n. gen.. Therefore I now regard *Archaelagonopinae* as a junior synonym of the *Lagonomegopidae*: *Lagonomegopinae* ESKOV & WUNDERLICH 1995 (**n. syn.**).

The intrafamilial arrangement of the taxa of the *Lagonomegopidae* – several tribus may exist – is still unclear; their investigation is still on its beginning. Adult males of most genera are still unknown, and the structures of the male pedipalpi of several genera have to be studied more closely in the future by well preserved specimens and with the help of the microCT.

### Synonymy of genera:

*Soplaogonomegops* FUENTE et al. 2013 may be a junior synonym of *Archaelagonomegops* WUNDERLICH 2012 (**quest. n. syn.**), see below, *Archaelagonomegops*. – Probably certain other genera – known up to now only by juvenile stages – may turn out in the future as synonyms after the knowledge of adult stages or males. I do not want to exclude that *Burlagonomegops* PENNEY 2005 may be an older synonym of *Myanlagonops* WUNDERLICH 2012. This author (2005b) described probably species of two different genera under *Burlagonomegops*, see the list of the taxa above. – Remark: In my opinion the creation of new genera based on badly preserved and furthermore very young specimens in which typical generic characters are not observable or still not developed (see below) – an example is *Burlagonomegops* – is not wise, and may cause strong confusions in the taxonomy and the biogeography.

**Emended diagnosis of the *Lagonomegopidae*:** Existence of several tarsal as well as several metatarsal trichobothria (figs. 228, 245-246, 259, photo 112) usually in an irregular row (see below) (1) 8 eyes (figs. A-B, 231-233, photos) (probably a less number in certain taxa after the loss of the posterior lateral eyes, see below) in four rows, peculiar long and wide eye field with huge anterior (2) median eyes in a lateral position at the prosomal margin which are directed more sideways, remaining eyes tiny, clypeus bearing usually a pair of humps (figs. 224, 231, 241-242, photos) (weakly developed and almost absent e. g. in *Paxillomegops* and *Picturmegops*), diastema/foramen existing (3) (fig. 256, photos 92, 116) or absent. Leg bristles: Probably basically existence of few – e. g. femoral – bristles in certain taxa (fig. 228 (s) (4).

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(1) Existing less distinct in the *Micropalpimanidae* and probably absent in small juveniles.

(2) These ANTERIOR median eyes were previously erroneously regarded as POSTERIOR median eyes, following ESKOV & WUNDERLICH (1995); this error is corrected herewith after a comparison with the eye position of the related family *Micropalpimanidae* and the con-suprafamiliar *Archaeidae* in which the anterior and posterior lateral eyes also are close together. In the derived and unique eye position of the *Lagonomegopidae* the enlarged anterior median eyes are placed (translocated) behind and above the posterior lateral eyes, see figs. A, B. The lateral position of the huge eyes which are directed

more laterally may be connected with the nocturnal life style of these spiders, see below. – Remark: Enlarged anterior median eyes exist also in the DIURNAL Salticidae but in this family these eyes remain in their median position and are directed anteriorly. (In the extant nocturnal Deinopidae exist huge POSTERIOR median eyes, see fig. 335).

(3) For example in *Picturmegops signatus*. According to FUENTE et al. (2013: 4) diastema and foramen are absent in the Lagonomegopidae. Probably these structures are not well developed or even absent in certain Lagonomegopidae at least in juvenile specimens.

(4) It seems to me that leg bristles (or strong bristle-shaped hairs) may exist in juveniles of certain species but are absent in conspecific adults. – The existence of leg bristles in certain members of the lagonomegopid branch (Lagonomegopidae + Micropalpimanidae) may be a reversal.

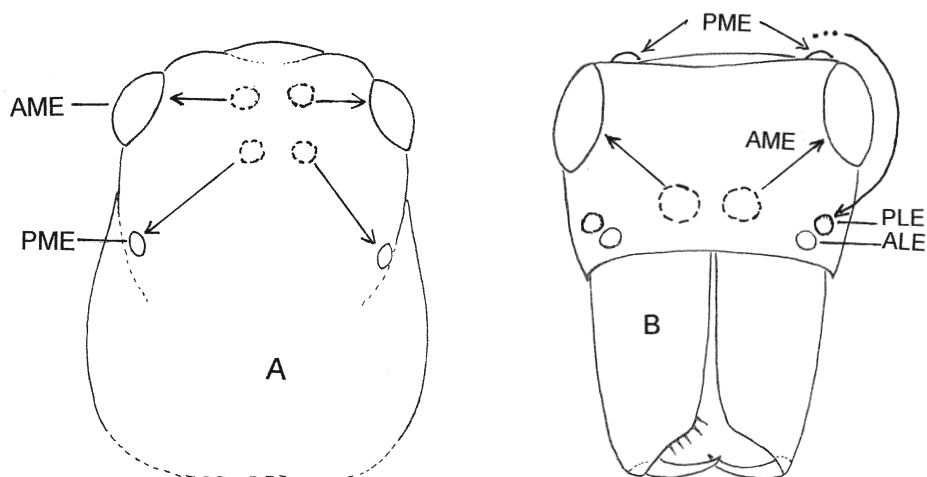
Further important characters: Prosoma dorsally not rugose, eye region raised in certain taxa at least in adult spiders, anterior lateral eyes quite close to the posterior lateral eyes (figs. 224, 232-233) (one of these TINY eyes or both may be hidden by hairs or emulsions!), basal cheliceral articles quite variable (figs., photos): Position diverging or parallel, protruding or not, stout or long and slender, true teeth on the cheliceral fang furrow absent, on the posterior margin, too, anterior fang furrow bearing cheliceral peg teeth of medium length or long ones (figs. 257), elevated gland mound existing (fig. 257), chelical-pedipalpal femoral stridulatory organ existing at least in *Lineaburmops beigeli* n. sp. (see fig. 236), labium very long, slender and pointed (fig. 258), leg I most often longer than IV, legs (false) scopulae (thin hairs) dense to very dense, quite variable, false claw tufts may be well developed (fig. 266), metatarsal III-IV preening comb usually well developed (figs. 225, 245), patellae shortest in long-legged species, at least in adults (tendency to) markings – white and black hairs – of the body (see e. g. *Picturmegops signatus* n. sp., fig. 255, photos 214; they are also existing in *Archaelagonops*, *Lineaburmops* and *Myanlagonops*). Probably no (distinct) sexual colour or body size dimorphism (adults of both sexes are surely known only in *Archaelagonops*, see below). Male pedipalpus (e. g. figs. 222-223) usually with slender articles, the tibia may bear e. g. a retroapical apophysis similar to members of the RTA-clade (so in *Archaelagonops*, figs. 222, 227) or „peg teeth“ (figs. 227, 248), cymbium most often long and slender, hairy, in some taxa prolonged basally, enclosing most parts of the bulbus which bears several tegular apophyses, the embolus may be long. Body length of adult spiders 3-8 mm (♀) (adult spiders are only known from some genera). – See also the apomorphic characters of the superfamily Archaeoidea listed in fig. D above, and the characters of behaviour and ecology below.

Remarks concerning two important structures: Mainly because of incomplete preservation, decomposition, deformations as well as covers by emulsions and bubbles the existence of dense hairs the existence and the number of eyes and leg trichobothria may be difficult to recognize. In the following I discuss selected examples:

(1) The eye pattern: (a) The alleged large posterior median eyes of *Archaelagonops salticoides* WUNDERLICH 2012: 232, fig. 68 turned out – after the study of new and better preserved spiders – as nothing else than emulsions on larger humps. – (b) *Picturmegops signatus* n. sp. (fig. 256, photos) as well as *Lagonomegops suchatchevae* – see ESKOV & WUNDERLICH 1995 (figs. 231.233) – show four pairs of eyes. A similar case may occur in *Spinomegops aragonensis* FUENTE et al. (2013: Fig. 6 C) in which

A PAIR of lateral eyes exists. – (c) Based on facts in (e. g.) in *Lagonomegops* (and probably in *Burlagonomegops*) not two or three but four pairs of eyes exist and one pair of tiny lateral eyes has been overlooked, e. g. in fig. 263, see below. – (d) Only two pairs of eyes were reported from *Grandoculus chemahawinensis* PENNEY but parts of the prosoma are not preserved and three or four pairs of eyes may well exist. – (e) In *Soplaogonomegops unzuei* FUENTE et al. (2013) only a single pair of „visible“ eyes is noted (p. 20; see p. 16) but also two, three or four pairs of eyes may well exist on the deformed prosoma of this species. – Therefore I suppose that four pairs of eyes exist most probably in most or even all described Lagonomegopidae, although only three pairs of eyes (not the posterior lateral eyes) were well recognized by me in *Cymbiolagonops cymbiocalcar* and are shown in *Zarqaraneus* (fig. 263).

Possible translocation of the eye pattern: See the family diagnosis above and figs. A–B below.



Figs. A-B. Likely translocation of the eyes of the hypothetical pre-precursor of a lagonomegopid spider (dotted) towards a Cretaceous member of the family Lagonomegopidae; dorsal (A) and anterior (B) aspects. The original position of the PLE is not shown (they are hidden here), see the curved arrowed line. – AME = anterior median eyes, PME = posterior median eyes, ALE = anterior lateral eyes, PLE = posterior lateral eyes.

(2) The pattern of tarsal and metatarsal trichobothria: The identification of real trichobothria in fossil spiders with the help of a light microscope is difficult, see the helpful paragraph in FUENTE et al. (2013: 3). According to tab. 1 in FUENTE et al. (2013) tarsal trichobothria are „absent“ in most Lagonomegopidae but most described taxa are based on incomplete, deformed not well preserved small specimens; almost all previously described spiders are juvenile (!). In juvenile specimens tarsal trichobothria are probably not (well) developed or quite hard to recognize. In the present study I found tarsal trichobothria in all ten well or fairly well preserved adult specimens, and thus it seems quite likely to me that tarsal trichobothria exist in all lagonomegopid taxa – at least in adult specimens – as an apomorphic character of the lagonomegopid sub-branch. – More than a single metatarsal trichobothrium (and usually tarsal ones, too) are well observable e. g. in *Picturmegops signatus* (fig. 259), and exist apparently in all other taxa, too, see above.



**Relationships:** See the discussion on relationships of selected arachaeoid families, and the possible cladograms above, figs. D, F. According to the numerous characters in common with the Archaeoidea I am sure that Lagonomegopidae belongs to this superfamily. The existence of tarsal trichobothria – and furthermore more than a single metatarsal trichobothrium (fig...) – is shared by the Micropalpimanidae within the Archaeoidea (\*). According to the pattern of trichobothria, (occasionally few) leg bristles, the not flattened hairs of legs I-II (see fig. 276) (as well as the long and slender cymbium, which encloses parts of the bulbus) (not unique to these families) I regard the family Micropalpimanidae as the sister group of the Lagonomegopidae, see fig. D. The shape of the prosoma and the pattern of the lagonomegopid eyes – including huge anterior median eyes in a lateral position, figs. 231-233, photos – are absolutely unique in spiders (four eye „rows“ in contrast to two eye rows in the Micropalpimanidae, the leg IV is longer than I, the body length of the Micropalpimanidae is 1-5-2.5 mm in contrast to the larger Lagonomegopidae (3.2-8 mm). Because of certain distinct differences one may doubt close relationships of these families. The characters of behaviour and ecology (see below) may (also) indicate the relationships of the Lagonomegopidae and Micropalpimanidae. – See the discussion in FUENTE et al. (2013: 17 and 21).

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 (\*) The existence of tarsal trichobothria is an ancient character of the Araneae, existing, e. g., in the Mygalomorpha. They evolved (regained) in my opinion convergently in the RTA-clade, separately in the lagonomegopid subbranch of the superfamily Archaeoidea as well as in the Caponiidae of the superfamily Dysderoidea.

**Ecology and behaviour:** Most members of the superfamily Archaeoidea (= Palpiman-  
 oidea) are spider eaters (araneophagous), except several Mecysmaucheniinae. Ara-  
 neophagy is unknown from Cretaceous archaeoid spiders (\*) but it has been reported  
 from Eocene Archaeidae and Spatiatoridae (\*), see above: Fig. D, remark 8. Apparently  
 most archaeoid spiders feed only on members of OTHER superfamilies, e. g. on Ara-  
 neoidea (probably Lagonomegopidae is an exception (\*)). How does this work? Most  
 Archaeoidea stridulate with the help of retrolateral cheliceral files. Such stridulating is  
 known to be used in connection with the mating behaviour, e. g., in the family Linyphi-  
 dae, but recently LIZNAROVA et al. – Abstract Book of the 19. Internat. Congress of  
 Arachnology, Taiwan (2013: 208) – reported a quite different function of stridulating in  
 spiders: of a family of the superfamily Archaeoidea, the Palpimanidae: „We assume  
 that stridulation is used in intraspecific communication to avoid cannibalism.“. This idea  
 makes sense in the whole superfamily Archaeoidea whose members mainly feed on  
 spiders but may spare specimens of related taxa. Note: Cheliceral files are probably  
 absent in the Huttoniidae, their existence is not quite sure in the Micropalpimanidae.  
 Did spiders of the lagonomegopid branch – members of a quite basal archaeoid branch  
 – still not feed on spiders? (\*).

Archaeoidea construct no capture web, and the existence of modifications of legs I-II  
 (usually peculiar prolateral hairs as well as metatarsal III-IV preening combs (fig. 225)  
 in Cretaceous archaeoid spiders – they exist in extant archaeoid spiders, too – support  
 the absence of a capture web in extinct spiders, too. False claw tufts and legs pseudo-  
 scopulae – see the lagonomegopid branch – indicate also the absence of an capture  
 web in these spiders.

At least some extant Archaeidae are reported to be night-active sit-and-wait predators.  
 This lifestyle may be connected in the Lagonomegopidae (a) with the highest devel-  
 oped optical sensory apparatus in Cretaceous spiders (working probably even at night,

see below: Members of the Sparassidae and Thomisidae,) with a very wide eye field and a view in almost all directions similar to certain sit-and-wait predators of the family Thomisidae (in these spiders the anterior LATERAL eyes are largest), and with a pair of huge and laterally directed eyes (figs. 233–234, photos) (\*\*) – in contrast to active hunting spiders like Salticidae whose huge anterior median eyes are close together and are directed anteriorly –; (b) with the existence of several sensory tarsal trichobothria in the Lagonomegopidae (fig. 245) and Micropalpimanidae, (c) with the well developed dense scopula-like hairs on the legs I(-II) in most spiders of these families (fig. 239, photos 103, 107, 117) (such hairs are extremely strongly developed in the spider capturing Palpimanidae), and (d) probably with a striking body „COLOUR“ (white and black structural colour hairs) (fig. 226, photos 106, 114) which is strongly developed in *Lineaburmops* and *Picturmegops signatus* n. gen. n. sp., and which may not be a kind of camouflage. – Considering all these characters together a sit-and-wait life style of members of the Lagonomegopidae (at least of the long-legged spiders) – and probably certain other Archaeoidea – appears quite likely to me. On the other hand I do not want to exclude that members of shorter-legged genera like *Picturmegops* may have been active hunters; a case of intrageneric separation.

The function of the body colour (possible camouflage: See above): As far as I know from the fossil spiders a sexual dimorphism in the body colour is absent in the Lagonomegopidae – thus a courtship function of the body colour may be unlikely? – YUN-JIAO LO – Abstract Book of the 19. Internat. Congress of Arachnology, Taiwan (2013: 209) – reports on the function of body colour mainly of diurnal East Asian Thomisidae. „However, such cost could be refused by higher prey intake of these spider’s nocturnal hunting.“.

In the also mainly nocturnal Sparassidae exists usually a single pair of eyes which is larger developed than the remaining eyes: The anterior medians or the anterior laterals (in contrast to the anterior medians in the Lagonomegopidae which have a quite unusual lateral position in this family), and the tarsi and metatarsi are usually strongly scopulated similar to certain Lagonomegopidae. Recently TSO (2014) reported a striking colour on the clypeus of the extant nocturnal Sparassidae *Heteropoda venatoria*. (Remark: Colouration is surely less important in nocturnal animals than a dark-light contrast).

This colouration „seems to exhibit dual functions of visually attracting flying prey and courting females.“ To our actual knowledge members of the Sparassidae appear first in the Eocene (\*\*\*). Did the entelegyne Sparassidae displace the extinct and probably haplogyne Lagonomegopidae (and the Micropalpimanidae) at the beginning of the Tertiary or at the end of the Cretaceous?

Apparently we have more unsolved questions than answers in this matter!

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(\*) A recently discovered Cretaceous member of the Spatiatoridae in Burmite (see below) may indicate araneophagy of this family already in the Cretaceous: A congeneric member of this family feeding on a spider has been found in Eocene Baltic amber, see the paper on „Frozen behaviour“ in this volume. – Possible prey (Diptera) of a Lagonomegopidae: See the genus *Archaelagonops*.

(\*\*) Several night active animals possess large eyes which are directed more laterally, e. g. geckos.

(\*\*\*) In contrast to the fossil report of the Sparassidae the writers MORADMAD et al. (2014: 45) published: „According to molecular clock analyses, the divergence time of Sparassidae and *Eusparassus* was estimated with 186 and 70 million years ago respectively.“ – This is really a „funny story“ in the fabulous world of molecular genetic.

**Distribution in space and time:** (a) Geographical distribution: Cretaceous, widely distributed in the Northern Hemisphere: North America: Canada and USA (New Jersey); Europe: Spain (Alava and Cantabria); Middle East: Jordan (still not reported from the Lebanon); Asia: N-Myanmar (Burma) (the best studied and most diverse deposit) and Siberia (Taimyr). See the key below (remarks). Unknown from Ethiopian amber which may be younger than Cretaceous, see above. – (b) Epochs: The oldest proof of Lagonomegopidae in amber comes from the Earliest Cretaceous (almost 140 million years old, near the border of the Jurassic) (\*) of Jordan (*Zarqagonomegops*), Burmite has an age of about 100 million years, and the age of most Canadian ambers is almost 80 million years (*Grandoculus*).

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(\*) So the proof of this family from the Jurassic might be only a matter of time.

Taxonomical note: The intrageneric variability of certain structures like the different development of the leg hairs and the claw tufts may be striking, see the new genus *Lineaburmops* – if the two species which are described in this genus are really congeneric!

#### Provisional **key** to the genera of the family Lagonomegopidae:

Remarks: Several characters are usable only in a restricted sense and in adult spiders: Probably caused by allometric growth the proportions of the prosoma and the chelicerae may be different in juvenile spiders (stouter?) compared to adult spiders; see no. 2 in the key. Because of the preservation the chelicerae may have an unnatural position in the fossils. The colour/markings of the body are distinct in well preserved LARGE fossil spiders – see *Archaelagonops*, *Lineaburmops*, *Myanlagonops* and *Picturmegops* – but absent or only weakly developed in small/juvenile specimens resp. in species which only are known from juvenile stages. The leg bristles/spines may also be developed differently in such spiders (they may be rubbed off, too). Most species are known from juveniles, and therefore the characters in question can be used only in quite a limited way and with hesitation in a key. – See also the remarks above on the eye pattern and on the structures of the legs like the tarsal trichobothria. The position of the eyes of the anterior row close to the clypeal margin (figs. 232-233) is probably unique in *Lagonomegops* (key no. 9), at least in juvenile (!) spiders.

For these reasons the characters of tab. 1 („Character distribution...“) by FUENTE et al. (2013) cannot be used for a determination. It is remarkable that the number of eyes in this table is noted as „number of VISIBLE eyes“(!). What about the number of „invisible“ eyes?

The geographic DISTRIBUTION may be helpful for the determination although the relationships of some taxa are unsure:

Most – 9 or 10 – genera are known from the best studied Burmite:

*Archaelagonops* (in my opinion from Spain, too), *Burlagonomegops*, *Cymbiolagonops*, *Lagonoburmops*, ?*Lagononomegops* (questionable proof), *Lineaburmops*, *Myananlagonops*, *Parviburmops*, *Paxillomegops* and *Picturmegops*;

*Granodoculus* is known only from Canadian amber;

*Zarqagonomegops* is known only from Jordanian amber;

*Lagonomegops* has probably been distributed most widely during the Cretaceous; it has been reported from Siberia (Taimyr, type area) and – questionably – from Myanmar/Burma and the USA (New Jersey);

from Spain *Spinomegops* and *Soplaogonomegops* have been described; the latter may be a junior synonym of *Archaelagonomegops* in my opinion, the first is similar to *Lagonomegops* e.g. according to the shape of the prosoma.

1 Spine-like bristles exist on distal parts of metatarsi and tarsi I-II and on the femora of the type species *arcanus* (fig. 261) from Alava, only thin bristles on metatarsi and tarsi I-II in *aragonensis* from Aragon (Teruel). Prosoma not much longer than wide (fig. 261) but see the remark above. Two poorly preserved specimens – both juveniles in my opinion – of two (really congeneric?) species in amber from Spain. . . . . *Spinomegops*

- Leg bristles existing – e. g. in *Burlagonomegops*, no. 5 – or absent: e. g. in other taxa from Alava (no. 3). Shape of the prosoma variable. . . . . 2

2(1) Basal cheliceral articles long and slender, 2-3 times longer than wide (fig. 244, photos), prosoma at least 1.3 times longer than wide (shorter in ?*Paxillomegops brevipes*) (key no. 4), legs usually long and slender (photos) but relatively short in ?*Paxillomegops brevipes*. . . . . 3

- Basal cheliceral articles stouter, prosoma compact, not (much) longer than wide or even wider than long, legs more stout (photos). . . . . 6

3(2) Opisthosoma long and slender, ca. 3 times longer than wide/high (fig. 226, photos), legs also very long and slender (but see ?*Paxillomegops brevipes* (no. 4) and below, *Lagonomegopidae* indet., F2628). . . . . 4

- Opisthosoma stouter, up to 2 times longer than high (fig. 241, photos). Legs long or short. . . . . 5

4(3) ♂-pedipalpus (figs. 248-249): Tibia bearing a long row of retrolaretal „peg teeth“, in *brevipes* a field ♀ unknown. *P. longipes* and ?*P. brevipes*. Burmite. . . . . *Paxillomegops*

- ♂-pedipalpus (figs. 290-230): Tibia without „peg teeth“, cymbium with a very long and slender basal outgrowth. ♀ unknown. Only *cymbiumcalcar*. Burmite. . . . . *Cymbiolagonops*

5(3) Prosoma with a distinct wide median field of dark hairs, clypeal humps weak, low depression between the large anterior median eyes, lateral prosomal constriction existing but dorsal ridges absent. See WUNDERLICH (2012). ♂. Pedipalpus: Figs. 239-240. Only *gracilipes*. Burmite. . . . . Myanlagonops

- Prosoma without a distinct median field of dark hairs, with a pair of large humps on the clypeus, a well developed depression anteriorly between the large anterior median eyes which are limited on both sides by a sharp and distinct ridge, a lateral and a dorsal constriction exist between the wide cephalic and the narrow thoracic part (fig. 224, photos 92-97). ♂♀. ♂-pedipalpus (figs. 222-223, 227): Tibia with a (serrated) retroapical and a ventral-apical apophysis (in *unzuei*, too?). – *A. salticoides*, *propinquus* and *scorsum* from Myanmar (Burma) as well as *A.* (= *Burlagonomegops*) *alavensis* from Spain (Alava); (?= *Soplaogonomegops unzuei*) from Spain (Cantabria). . . . . Archaelagonops

- Prosoma (in badly preserved juveniles!) without dark hairs or modifications. Thin dorsal-distal bristles exist on femora I, II and IV. Figs. 228-228a. Juv. Burmite. Only *eskovi*. . . . . Burlagonomegops

6(2) Prosoma and opisthosoma bear paired lateral longitudinal bands of white hairs (photo 106). Two species in Burmite. . . . . Lineaburmops

- No such bands of white hairs. . . . . 7

7(6) Leg hairs long and very dense, especially on the anterior metatarsi (figs. 255, photo 117). Burmite. . . . . 8

- Leg hairs shorter and much less dense. Burmite and other kinds of amber. . . . . 9

8(7) Largest known member of the family, body length ♀ ca. 8.5 mm, prosomal length 3-3.5 mm, body markings absent (or not preserved?). ♂ unknown. Only *plumosus*. . . . . Lagonoburmops

- Body length 3.6 mm. Prosoma and opisthosoma bear distinct dorsal markings of black and white hairs (fig. 255, photos 114-117), prosoma distinctly narrowed posteriorly, distinct clypeal humps absent, clypeus convex. ♀. Only *signatus*. Burmite. . . . . Picturmegops

9(8) Leg I strongly enlarged, see WUNDERLICH (2008: 666, fig. 68. Larger spiders, prosomal length of the ad. (or juv.?) ♀ ca. 2.3 mm. Canadian amber. Only *chemahawinensis*. . . . . Grandoculus

- Leg I not strongly enlarged. Reported in Burmite, Jordanian and Siberian ambers. 10

10(9) Position of the tiny lateral eyes near the clypeal margin (apparently unique within the Lagonomegopidae), position of the tiny posterior median eyes far behind the huge anterior median eyes (figs. 231-233). Juv. Amber from Myanmar (?), Siberia (Taimyr), and probably USA (New Jersey), see the list above. . . . . Lagonomegops

- Position of the tiny lateral eyes far from the clypeal margin (similar to most or even all other lagonomegopid genera), position of the tiny posterior median eyes nearer to the huge anterior median eyes (figs. 241-242). . . . . 11

11(10) Position of the tiny posterior median eyes fairly far behind the huge anterior median eyes (fig. 241), clypeal humps well developed (figs. 241-242). ♀ unknown. ♂: Body length only 3.2 mm (one of the smallest species of the family), pedipalpus (fig. 243) with stout articles including the cymbium, bulbus enlarged prolaterally. Only *brevipalpus*. Burmite. . . . . *Parviburmops*

- Position of the tiny posterior median eyes nearer to the huge anterior median eyes (fig. 263), clypeal humps huge (fig. 263). Juv. Only *wunderlichi*. Jordanian amber. . . . . *Zarqagonomegops*

## **Archaelagonops WUNDERLICH 2012**

Type species (by monotypy): *Archaelagonops salticoides* WUNDERLICH 2012.

Further species: *A. alavensis* (PENNEY 2005a) and *A. propinquus* n. sp.

**Synonymy**: The „neck-like“ (lateral) constriction of the prosoma as well as the „chelicerae inserted at an elevated point of the carapace,...“ are the main diagnostic characters of *Soplaogonomegops* FUENTE et al. 2013 (Cretaceous of Spain: Cantabria) which is based most probably on a juvenile. The prosomal constriction as well as the depression between the posterior median eyes are as in *Archaelagonops*, the elevated insertion of the chelicerae are probably a result of the preservation. Only a single pair of eyes is „observable“ (but the existence of further eyes has been not excluded in *Soplaogonomegops*. Tarsal trichobothria are reported as absent but trichobothria are easily to be overlooked in juvenile spiders or are still not developed. In my opinion *Soplaogonomegops* is likely to be a junior synonym of *Archaelagonops* (**n. quest. syn.**). – According to the shape of the prosoma I regard *Burlagonomegops alavensis* PENNEY 2006 from the Cretaceous of Spain (Alava) as a member of *Archaelagonops* (**n. comb.**). Do to its bad preservation in the only known juv. specimen only the large posterior median eyes are observable.

**Diagnosis** (♂♀): Prosoma (fig. 224, photos 92f) distinctly longer than wide, bearing three peculiar features: (a) a distinct anterior depression between (in front of) the large posterior median eyes which is limited on each side by a ridge; (b) a „constriction“ between the wide thoracic and the narrow cephalic part; (c) a pair of well developed humps on the clypeus. Clypeus very long and sloping vertically. – The existence of indistinct dark prosomal hairs (?) and an anterior outgrowth of the cymbium (fig. 227)



may be further diagnostic characters. The existence of scale-shaped hairs – see WUNDERLICH (2012: 232, fig. 70) – may be questioned.

**Relationships:** See the key to the genera above and *Picturmegops*. *Myanlagonops* WUNDERLICH 2012, *Paxillomegops* n. gen. and *Burlagonomegops* PENNEY 2005 may be most related.

**Prey:** See below, *Archaelagonops* sp. indet.

**Distribution:** Mid Cretaceous amber forest of N-Myanmar (Burma) and probably Cretaceous amber from Spain, see above.

**Description of the hitherto unknown female of *Archaelagonops* in Burmite from N-Myanmar (2♀):**

**(a) F2605/BU/CJW:**

The ventral surface of the opisthosoma and some leg articles are cut off; the right pedipalpus is lost beyond the coxa by autotomy.

Measurements (in mm): Body length 4.1, prosoma: Length 1.9, width 1.4; femur I 1.7, leg IV: Femur 1.7, patella 0.55, tibia 1.3, metatarsus 1.2, tarsus 0.7; length of a basal cheliceral article 1.0.

Colour (photos 95-97): Prosoma and legs dark grey brown, opisthosoma dorsally light grey, with spots on dark hairs on two longitudinal median bands.

Prosoma (photo...) as in the male, anteriorly raised and with a pair of large humps on the high clypeus which is sloping ventrally. Two pairs of eyes in a lateral position – the anterior medians and the anterior laterals – are observable. Basal cheliceral articles long, slender and not diverging. Pedipalpus long and slender (the right one is broken off near its base), tarsal claw absent. Legs fairly long, bristles absent, hairs distinct. Opisthosoma long ovally, hairs fairly short. Most spinnerets and the genital area are cut off.

**(b) F2606/BU/CJW:**

The spider is fairly deformed, partly covered with an hiding emulsion, some leg articles are cut off.

Measurements (in mm): Body length 4.1, prosomal length 2.3; femur I ca. 1.9, tibia I 1.8, femur II 2.0, femur III 1.6, femur IV ca. 2.0; length of a basal cheliceral article 1.1.

Colour dark grey brown.

Prosoma deformed, eyes strongly deformed, apparently as in the genus. Pedipalpus long and slender tarsal claw absent. Legs fairly long, hairs distinct. Opisthosoma long ovally, genital area darkened.



## ***Archaelagonops* sp. indet. and its prey**

**Material:** 1 juv. and 2 Diptera: Nematocera indet. as its prey in Burmite; unnamed Inst.

**Preservation:** The arthropods are completely and fairly well preserved in a slightly muddy/cloudy piece of amber.

### **Description:**

Body length of the spider ca. 3 mm, of the Diptera almost 1 mm.

The prosoma of the spider possesses the typical shape of the genus *Archaelagonops*. Most legs are bent under its body. Position of the Diptera: One right under the spider's mouth parts almost in contact with them, the other one left of the prosoma under the basal parts of the anterior leg.

**Discussion:** According to the position of the inclusions I regard the Diptera most likely to be the prey of the lagonomegopid spider. The present spider is the first report of a Cretaceous member of the superfamily Archaeoidea (= Palpimanoidea) which is preserved together with its prey. Almost all extant spiders of this superfamily are araneophagous (except certain Archaeidae: Mecysmaucheniinae which feed on spiders and insects), and also Eocene members of the Archaeidae and Spatiatoridae fed on spiders, see the paper „Frozen behaviour...“ in this volume. This find may be a hint that members of the Lagonomegopidae fed on insects but not on spiders. Extant Palpimanidae – and probably other Archaeoidea, too – are known to use their retrolateral cheliceral stridulatory files not in their courtship behaviour but for a different special intraspecific communication: to prevent cannibalism, see LIZNAROVA et al. (2013: 208). Interestingly such stridulatory files are absent in the extinct Lagonomegopidae which apparently did not feed on spiders, and therefore did not need such prevention.

**Distribution:** Mid Cretaceous amber forest of N-Myanmar (Burma).

### **Key to the species of *Archaelagonops* (♂):**

1 Cymbium elongated basally, ventral-apical tibial apophysis of the pedipalpus well developed (fig. 227). Ventral aspect of the bulbus unknown . . . . . *propinquus*

- Cymbium not elongated basally. . . . . 2

2(1) Ventral tibial apophysis of the pedipalpus slender (fig. 222), ventral aspect of the bulbus as in fig. 223. . . . . *scorsum*

- Cymbium and bulbus more slender, ventral tibial apophysis of the pedipalpus and ventral structures of the bulbus badly preserved, see WUNDERLICH (2012: 232, fig. 72). . . . . salticoides

***Archaelagonops scorsum* n. sp.** (figs. 222-223) photo 94

Derivatio nominis: The name refers to the relationships of the species rather apart from the remaining species of the genus; scorsum (lat.) = apart.

**Material**: Holotype ♂ in Mid Cretaceous Burmite, F2681/BU/CJW.

**Preservation and syninclusions**: The spider is completely and well preserved in a clear yellow orange piece of amber. The left bulbus is observable in the ventral aspect, some anterior parts of the prosoma are covered with an emulsion. – Remains of plants like hairs and of two Diptera: Nematocera are preserved in the same piece of amber.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (figs. 222-223): Ventral tibial apophysis slender, bulbus with a long questionable embolus and four tegular apophyses including a sickle-shaped one.

**Description** (♂):

Measurements (in mm): Body length 3.8, prosomal length 1.8, opisthosoma: Length 2.0, height 1.3; femur I ca. 1.7, tibia I ca. 1.7.

Colour mainly medium brown, opisthosoma lighter, without markings, legs not annulated.

Prosoma (photo 94) not much longer than wide, dorsal and anterior shape as in the genus, covered with few short hairs, fovea well developed, eyes partly covered with emulsions, posterior medians as well as anterior and posterior laterals tiny and close together, basal cheliceral articles long and slender, peg teeth well developed, fangs long, labium and gnathocoxae hidden. – Legs (photo) fairly long and slender, bristles absent, hairs/scopulae short, metatarsal III-IV comb well developed, paired claws with long teeth. – Opisthosoma (parts are hidden by an emulsion) oval, hairs indistinct. – Pedipalpus (figs. 222-223): Tibia with a longer retrolateral-apical apophysis which is serrated apically and a slender ventral-distal apophysis, bulbus with a long questionable embolus and four tegular apophyses including a sickle-shaped one.

**Relationships**: See the key above.

**Distribution**: Mid Cretaceous amber forest of Myanmar (Burma).

***Archaelagonops propinquus* n. sp.** (figs. 224-227) photo 92-93

Etymology of the species name: From *propinquus* (lat.) = similar, related. The new species is apparently strongly related to *A. salticoides* WUNDERLICH 2012.

**Material:** Holotype ♂ and a separated piece of amber in Mid Cretaceous Burmite, F2570/BU/CJW.

**Preservation and syninclusions:** The spider is fairly well preserved in a muddy piece of amber, prosoma, legs and pedipalpi are slightly deformed, some leg articles are cut off: The left legs I and II through their metatarsi and the left legs III and IV through the base of their tibiae. – A bubble exists between the opisthosoma and the left femur I; numerous tiny bubbles are also preserved.

**Diagnosis** (♂; ♀ unknown): Marks of the opisthosoma as in fig. 226, pedipalpus (fig. 227): The tibia bears a blunt retroventral apical and a serrated retroapical apophysis.

**Description** (♂):

Measurements (in mm): Body length 3.5, prosomal length 1.6, opisthosoma: Length 2.0, height 0.7; leg I: Femur 1.9, patella 0.75, tibia 2.45, metatarsus ca. 2.9, tarsus 0.7, tibia II 2.4, tibia III 1.5, tibia IV ca. 2.3, diameter of a posterior median eye 0.25, cymbium ca. 0.67; distance between the clypeal humps and the clypeal margin 0.3 as in *A. salticoides*.

Colour/marks: Prosoma and legs medium to dark brown, legs not annulated, opisthosoma dorsally grey with a pair of longitudinal dark hairs (fig. 226).

Prosoma (fig. 224, photo) distinctly longer than wide, fovea deep, bearing an anterior depression which is limited at both sides by a ridge similar to other congeneric species (the anterior prosomal depression of the holotype of *A. salticoides* is quite similar but has not been drawn), 4 pairs of eyes, anterior medians very large, the remaining three pairs of eyes tiny and not well observable like in the generotype *salticoides*, fovea well developed, clypeus long, clypeal humps large and protruding, basal cheliceral articles slender and longer than the prosomal height, peg teeth existing, fangs long and slender, foramen well developed, mouth parts not well observable. – Legs (photo) slender and long, I longest, III distinctly shortest, bristles absent, I and II with long and thin proventral hairs, scaly hairs apparently absent (such hairs reported from *A. salticoides* are most probably artefacts). Trichobothria long and numerous, about a dozen on tarsus IV in two (?) rows, metatarsus IV bears at least two long trichobothria in a distal position. Three tarsal claws, the paired ones bear long teeth. Metatarsal preening comb: fig. 225. – Opisthosoma (fig. 226) distinctly longer than wide, apparently pointed anteriorly, most probably three pairs of spinnerets, anteriors large and closely together, a larger structure in front of the spinnerets may be a colulus. – Pedipalpus (fig. 227 photo) with slender articles, tibia slightly bent, apically with a blunt retroventral and a serrated retrolateral apophysis, cymbium long and hairy, bearing a pointed posterior outgrowth, the left cymbium is slightly longer and stronger bent apically than the right one, bulbus fairly protruding, structures hard to observe.

**Relationships:** See the key above.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

**Cymbiolagonops n. gen.**

Derivatio nominis: The name points to the basally strongly elongated cymbium and to the family name Lagonomegopidae; a part is the genus name Lagonomegops.

The gender of the name is masculine.

**Diagnosis** (based on a strongly deformed male): Pedipalpus (figs. 229-230): Tibia with a divided retroapical apophysis, cymbium with a long and slender (spoon-shaped) basal apophysis which is directed backwards.

Further characters: Body, legs and pedipalpus long and slender (deformed!), cephalic part raised (fig. 229).

**Relationships** (see the key): In *Paxillomegops longipes* long legs and a long opisthosoma exist, too, but the pedipalpal tibia bears „peg teeth“.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

**Cymbiolagonops cymbiocalcar n. gen. n. sp.** (figs. 229-230) photo 100

Etymology of the species name: „calcar“ (lat. = spoon) points to the peculiar cymbium which is basally strongly elongated.

**Material:** Holotype ♂ in Mid Cretaceous Burmite, F2687/BU/CJW.

**Preservation and syninclusions:** The spider is preserved in a larger piece of amber, almost completely and strongly deformed by heating and apparently by decomposition, a larger decompository bubble exists ventrally on the opisthosoma (see the photo and the fig.), mainly the tibia of the right leg II is cut off, the prosoma is empty, the opisthosoma is strongly compressed laterally and bent downwards (all caused by decomposition). – Dorsally of the male several spider threads are preserved – parts of a capture web, originating most probably from a member of the ecribellate Araneoidea – which bear sticky droplets of quite various size, diameter up to more than one mm. These threads are not preserved in the amber layer of the holotype which is not a member of a capture web building taxon. Near the surface of the piece of amber this web includes a white

plate-shaped structure which may be remains of excrement of the spider which built this capture web. This object may be build e. g. by guanine and includes tiny crystals of pyrite. A small leg of a spider, the leg of an insect, a beetle, few midges, the part of a longer leaf, plant hairs and insects excrement are also preserved in this piece of amber.

**Diagnosis:** See above.

**Description** (strongly deformed ♂):

Measurements (in mm): Body length ca 4 mm, prosoma: Length 2.0, width 1.35, opisthosoma: Length 2.9, width ca. 0.4; leg I: Femur ca. 4.0, patella ca. 1.0, tibia ca. 4.5, metatarsus ca. 2.9, tarsus ca. 0.9, tibia III ca. 1.0, tibia IV ca. 2.4.

Colour light brown.

Prosoma (figs. 229-300, photo 100; deformed and empty) ca. 1.5 times longer than wide, cephalic part raised, eyes basically as in the genus but posterior median eyes not recognizable, lateral eyes far away from the clypeal margin, clypeal humps indistinct, basal cheliceral articles long and slender. – Legs (photo) long and slender, order apparently I/III/IV/III, I distinctly the longest, III distinctly the shortest, bristles absent, hairs not distinct but longer dense and thin hairs on some articles, several metatarsal and tarsal hairs exist. – Opisthosoma (fig. 229, photo; it is strongly deformed) probably more than 7 times longer than wide. – Pedipalpus (figs. 229-230, photo) with long articles, see the diagnosis of the genus, tibial „peg teeth“ absent, bulbus strongly deformed. The cymbium is loose, separated from the tibia, caused by the preservation.

**Relationships and distribution:** See above.

### **Lagonoburmops** WUNDERLICH 2012: 203

Only the type species *plumipes* and only the female sex are known from a single specimen in Burmite. Here I shortly describe a second female which I regard as probably conspecific and as adult, F2601/ BU/CJW:

Preservation: The spider is incompletely preserved in a fairly muddy piece of amber; parts of body and legs are hidden, the body is filled with resin, the ventral parts of pro- and opisthosoma including the spinnerets as well as most leg articles are cut off, the peltidium, the chelicerae, the pedipalpi and the anterior pair of legs are preserved. Two pairs of eyes in an anterior lateral position are probably existing (these eyes are not observable in the holotype of *L. plumipes*). – A Diptera and two Auchenorrhynha exist in the same piece of amber.

Measurements (in mm): Body length almost 7.0, prosomal length and width 3.5; leg I: Patella 1.5, tibia 3.0, metatarsus 2.2, tarsus 1.0.

Colour light to medium brown.

Prosoma as wide as long, most parts are hidden. Legs fairly long, bristles absent, hairs dense as in the holotype but shorter.

**Lagonomegops** ESKOV & WUNDERLICH 1995 (figs. 231-233)

Type species (by monotypy): *Lagonomegops sukatchevae* ESKOV & WUNDERLICH 1995.

The gender has not been noted in the original description, therefore it is considered as masculine, see IRZN 30.1.4.3.

**New material:** (1) A juv. of ?*Lagonomegops ?americanus* PENNEY 2005 (\*) which is poorly preserved in a muddy piece of amber from New Jersey, USA, F2565/NJ/CJW, and two pieces of amber which were separated. In this specimen one of the huge posterior median eyes in the typical generic lateral position is observable. Because of its poor preservation and its young stage the generic relationships of this specimen are unsure. – (2) ?*Lagonomegops tuber n. sp.*: See the description below.

(\*) „*Lagonomegops*“ *americanus* PENNEY 2005: See fig. 235.

**Diagnosis** (only juveniles are known): Prosoma (figs. 231-234) about as long as wide, position of the tiny posterior median eyes far behind the large anterior median eyes, position of the two pairs of tiny lateral eyes near the clypeal margin, basal cheliceral articles fairly short.

**Remark:** Four pairs of eyes exist (figs. 231-234), the lateral eyes are contiguous. In the description of the holotype of the generotype I regarded one pair of the anterior row as questionable artefacts.

**Relationships:** *Zarqagonomegops* of Jordanian amber may be most related, see the key to the genera above (the position of the tiny eyes is quite different). The shape of the prosoma is similar to *Spinomegops* FUENTE et al. in amber from Spain.

**Distribution:** Probably widely distributed on the Northern Hemisphere during the Cretaceous (adult males are needed for a sure determination):

- *americanus* PENNEY 2005b, juv., USA: New Jersey (determination questionable);
- *sukatchevae* ESKOV & WUNDERLICH 1995, generotype, juv., Siberia: Taimyr;
- *tuber n. sp.*, juv., Burmite (generic assignment questionable).

**Remark:** I do not want to exclude that *Spinomegops* (preserved in amber from Spain) may be a member of *Lagonomegops*, see above („Relationships“).

?*Lagonomegops tuber n. sp.* (fig. 234) photos 98-99

Etymology: The species is named after its clypeal hooks: tuber (lat.) = hook.

**Material:** Two juveniles in Mid Cretaceous amber from N-Myanmar (Burma): Holotype F2017/BU/CJW (published under *Burlagonomegops ?eskovi* PENNEY 2005 by WUNDERLICH (2008: 615)); paratype F1918/BU/CJW (published under *Burlagonomegops ?eskovi* PENNEY 2005 by WUNDERLICH (2008: 615)).

**Preservation and syninclusions:** (a) The holotype is completely and excellently preserved in a clear yellow-orange piece of amber which has a fissure in front of the spiders body. – (b) The paratype is well and almost completely preserved (only tarsus and metatarsus I-II are cut off), the prosoma is dorsally strongly depressed, the opisthosoma is deformed. A larger fissure runs through the piece of amber in front of the spider, few „stellate“ plant hairs are preserved in the same piece.

**Diagnosis** (juv.): A pair of protruding and well developed humps exist above the lateral eyes near the large anterior median eyes (fig. 234).

**Description** (juv.):

Measurements (in mm): Body length 1.2 (holotype) and 1.4 (paratype); prosomal length and width ca. 0.65; leg I (paratype): Femur ca. 0.5, patella 0.22, tibia 0.36, metatarsus 0.3, tarsus 0.3, tibia III 0.23, tibia IV 0.35.

Colour medium to light brown, markings and leg annulations absent.

Prosoma (fig. 234, photos) as wide as long, hairs of medium length, fovea absent, the anterior two thirds are raised and bordered posteriorly. 8 eyes, laterals tiny and close together, well observable in the paratype, their position near the clypeal margin, anterior medians huge, in a lateral position and directed laterally, position of the tiny posterior median eyes far behind the anterior median eyes; the anterior median eyes are situated below well developed and protruding humps and directed ventrally-laterally. Basal cheliceral articles only fairly large, peg teeth apparently not observable, probably not well developed, fangs slender, labium long and triangular, gnathocoxae long, slender and converging, almost touching apically. Sternum not elongated between coxae IV. – Legs (photos) stout, bristles absent beside a questionable thin basal one on tibia IV – see WUNDERLICH (2008: 666, fig. 67) – as well as some one on patellae and femora distally. A questionable long trichobothrium exists in the middle of the right tarsus I of the paratype; metatarsal trichobothria probably not developed in these juveniles. A metatarsal III-IV preening comb is absent in these juvenile spiders. Tarsi about as long as metatarsi, paired claws toothed, unpaired claws small. – Pedipalpus not reduced. – Opisthosoma (photo) oval, hairs of medium length. Three pairs of spinnerets, the anteriors stout, the medians well developed (holotype). Colulus probably absent.

**Relationships:** The congenerity with *Lagonomegops* can probably be confirmed after the discovery of males from Taimyr and Myanmar (Burma) as well. – In *?L. americanus* PENNEY 2005 (amber from New Jersey, USA) – according to PENNEY – femur I bears a dorsal-distal bristle/ spine. In *L. sukatchevae* ESKOV & WUNDERLICH (Siberian amber from Taimyr) the anterior prosomal humps are wider, less narrowish/ protruding (fig. 231).

**Distribution:** Mid Cretaceous amber from N-Myanmar (Burma).



***Lineaburmops* n. gen.**

Etymology: The name is a combination of linea (lat.) = line, according to the longitudinal bands of pro- and opisthosoma, and a part of the lagonomegopid genus name *Lagonoburmops* WUNDERLICH.

The gender of the name is neuter.

Type species: *Lineaburmops beigeli* n. sp.

Further species: *L. hirsutipes* n. sp.

**Diagnosis** (♂; ♀ unknown): Prosoma and opisthosoma with longitudinal lateral bands of white hairs (photos 104-105).

Further diagnostic characters: Position of the lateral eyes far from the clypeal margin (photo), paired clypeal humps large and near the huge anterior median eyes, dorsal depression between the huge eyes low, prosoma 1.35-1.6 times longer than wide, basal cheliceral articles robust, bearing stridulatory files and pedipalpal femoral stridulatory teeth (fig. 236) at least in *beigeli*, gap between gnathocoxae and chelicerae apparently small, leg hairs and claw tufts indistinct (*beigeli*, photo) or well developed (*hirsutipes*, photo), cymbium elongated apically in *beigeli* (fig. 236), body length 3-5 mm.

**Relationships**: See the key. *Lagonomegops* and *Picturmegops* may be most related.

**Distribution**: Mid Cretaceous amber forest of Myanmar (Burma).

***Lineaburmops beigeli* n. gen. n. sp.** (figs. 236-237) photos 104-105

Derivatio nominis: The species is dedicated to Alexander Beigel in Aachen, the actual owner of the piece of Burmite which later probably will be kept in the SMF.

**Material**: Holotype ♂ in Mid Cretaceous Burmite, coll. Alexander Beigel.

**Preservation and syninclusions**: The spider is excellently and completely preserved in a yellow-orange piece of amber, a ?gas bubble is preserved left of and ventrally on the opisthosoma as well as on the left legs. – Syninclusion: 1 Acari, 1 large Hemiptera, few small/tiny insects like Diptera: Nematocera, Coccinea and Thysanoptera, remains of plants including hairs and detritus.

**Diagnosis** (♂; ♀ unknown): Leg hairs and claw tufts weakly developed (photo), pedipalpus (figs. 236-237): Cymbium long and slender, distinctly longer than the questionable embolus. The clypeus bears a large field of white hairs (photo).

**Description (♂):**

Measurements (in mm): Body length ca. 3.0; prosoma: Length at least 1.6, width ca. 1.0; opisthosomal length ca. 1.25, width at least 0.75; leg I: Femur 1.4, patella 0.4, tibia 1.5, metatarsus 1.1, tarsus 0.75; tibia II 1.4, tibia III 1.1, tibia IV 1.3.

Colour (photo) mainly dark brown, prosoma dorsally with a pair of longitudinal bands of white hairs in a position away from the prosomal margin, clypeus with a large field of white hairs, opisthosoma with a pair of narrow longitudinal bands of white hairs, legs not annulated.

Prosoma (photos) ca. 1.6 times longer than wide, 8 eyes, weak lowering between the huge anterior median eyes, humps between these eyes existing, inclination behind the huge eyes existing, tiny posterior median and lateral eyes, lateral eyes closely together as in the genus, clypeus very large, in a vertical position, basal cheliceral articles stout, not diverging, hairs short and indistinct, retrolateral files indistinct, „peg teeth“ hard to observe, fangs widely hidden. Gnathocoxae large and strongly converging, coxae IV widely spaced. – Legs (photos) slender and rather long, bristleless, hairs short and indistinct, order I/II/IV/III, II almost as long as I III distinctly the shortest, metatarsi III–IV apically-ventrally with longer bristle-like hairs, tarsi and metatarsi bear several long trichobothria, 3 tarsal claws, tufts rather weak. – Opisthosoma (photo) distinctly longer than wide, ventrally hidden, hairs short and dense, spinnerets hidden, apparently quite short. – Pedipalpus (figs. 236–237) with stout articles, femur probably with few teeth which I regard as stridulatory teeth, cymbium slender and hairy, distinctly longer than the bulbus and the questionable straight embolus; I did not surely identify a conductor.

**Relationships:** The white pro- and opisthosomal bands are as in *L. hirsutipes* n. sp.; therefore I regard both species as congeneric although other characters – leg hairs, claw tufts (both are strongly developed in *hirsutipes*), the shape of the cymbium (shorter in *hirsutipes*) and apparently the structures of the bulbus – are remarkably different. If both species are really congeneric this is a quite remarkable case of intraspecific variability of several structures. – In *hirsutipes* the legs are annulated and a large field of white hairs on the clypeus is absent in contrast to *beigeli*.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

***Lineaburmops hirsutipes* n. gen. n. sp.** (fig. 238) photos 106–107

**Etymology:** The species name refers to the quite hairy legs, from *hirsutus* (lat.) = hairy.

**Material:** Holotype ♂ in Mid Cretaceous Burmite, F27537/BU/CJW.

**Preservation and syninclusions:** The spider is well preserved in a muddy piece of amber in which numerous brown droplets exist, the right pedipalpus is lost beyond the femur, the tips of the left femora I and II, the left tarsus III and parts of the legs IV are cut off. – Syninclusions: A larger flat and rectangularly segmented organic object – which

reminds me on remains of a Diplopoda or scales of certain snakes – is preserved above the right legs II and III; insect's excrement and particles of detritus are also preserved.

**Diagnosis** (♂; ♀ unknown): The anterior metatarsus and tibia distally are covered densely with long hairs (photo), the claw tufts are well developed. Pedipalpus (fig. 238): Cymbium relatively short, a strongly sclerotized sclerite of the bulbus is standing out apically. The clypeus bears apparently a transverse band of white hairs.

**Description** (♂):

Measurements (in mm): Body length ca. 5.0, prosoma: Length 2.8, width ca. 2.2; opisthosoma: Length at least 2.7, width 1.1; leg I: Femur ca. 3.2, patella ca. 1.1, femur IV 2.8.

Colour (photo) mainly dark brown, prosoma dorsally with a pair of longitudinal bands of white hairs in a position away from the prosomal margin, clypeus with a transverse band of white hairs, opisthosoma with a pair of narrow longitudinal bands of white hairs, legs annulated, most distinct on the anterior tibiae: At the base and in the middle exist anterior fields of white hairs.

Prosoma (photo) ca. 1.3 times longer than wide, with a low depression between the large anterior median eyes, bulgings between these eyes (at their margins) well developed, inclination behind these eyes existing, remaining eyes tiny and hard to observe, fovea low and indistinct, clypeus large, in a vertical position, basal cheliceral articles stout, retrolateral files, teeth, mouth parts and sternum hidden. – Legs (photo) only fairly long, bristleless, order I/II/IV/III, III distinctly the shortest, tarsal and metatarsal trichobothria existing; in contrast to the remaining ones the anterior metatarsi and tibiae distally are densely covered with long hairs, claw tufts strongly developed. – Opisthosoma at least 2 ½ times longer than wide, hairs numerous and short, spinnerets hidden, apparently short. – Pedipalpus (fig. 238; insufficiently preserved and partly hidden, the right one is lost beyond the femur, the left patella bears dorsally an artificial structure): Articles not thickened, cymbium relatively short, a strongly sclerotized sclerite of the bulbus is standing out apically.

**Relationships:** See *L. beigeli* n. sp.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

**Myanlagonops** WUNDERLICH 2012 (figs. 239-240)

Only the type species of this genus – *M. gracilipes* WUNDERLICH 2012 – has been described up to now, a male in Burmite. – Diagnostic characters of the genus: See the key to the genera above and WUNDERLICH (2012: 204). (Leg bristles are absent, tarsal trichobothria exist).

## **Parviburmops n. gen.**

**Etymology:** From parvus (lat. = small) according to the small body size of the holotype, and burmops after the second part of the confamiliar genus name Lagonoburmops.

The gender of the name is masculine.

Type species (by monotypy): *Parviburmops brevipalpus* n. sp.

**Diagnosis** (♂; ♀ unknown): Prosoma (figs. 241-242) as wide as long, eye position as in the figs., clypeal humps well developed (figs.), legs only fairly long, pedipalpus (figs. 241-243) with stout articles, tibia without apophysis or „peg teeth“, cymbium short, enclosing most parts of the bulbus which is enlarged/protruding prolaterally, sickle-shaped tegular apophysis well developed, questionable embolus long, in a retrolateral position.

**Relationships** (see the key to the genera): In *Lagonomegops* (locus typicus Taimyr, Siberia) the position of the tiny lateral eyes is close to the clypeal margin. In *Zarqagonomegops* (amber from Jordan) the position of the posterior lateral eyes is much more anteriorly, near the huge posterior median eyes.

Further characters: See the diagnosis of the genus.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

*Parviburmops brevipalpus* n. gen. n. sp. (figs. 241-243) photos 108-109

**Etymology:** Brevis (lat. = short) according to the short articles of the pedipalpus.

Material: Holotype ♂ in Mid Cretaceous Burmite, F2682/BU/CJW.

**Preservation and syninclusions:** The spider is fairly well and incompletely preserved in a fairly muddy piece of amber, the right legs I and II and the left leg IV are completely preserved, the remaining legs are cut off through the tibia or the tarsus. – A Thysanoptera is preserved right behind above the spider, a thin spider thread exists dorsally along the right leg I, numerous questionable pollen grains are preserved mainly right of the spider's body.

**Diagnosis** (see above): Legs distinctly annulated, II longer than I.

**Description** (♂):

Measurements (in mm): Body length 3.2, prosoma: Length 1.6, width 1.6, opisthosoma: Length 1.6, width 1.4; leg I: Femur 1.6, patella 0.7, tibia 1.7, metatarsus 1.1, tarsus 0.55, tibia II 1.8.

Colour medium grey brown, legs distinctly annulated.

Prosoma (figs. 241-242, photo) as wide as long, hairs very short, fovea a large depression, 8 eyes, position of the posterior median eyes only fairly wide behind the huge anterior median eyes, the tiny lateral eyes are close together and widely spaced from the clypeal margin. Clypeal humps well developed, basal cheliceral articles rather stout, most of the (other) mouth parts hidden – Legs only fairly long, order II/I/IV/III, III and IV distinctly smaller than I and II, bristleless, hairs and scopulae indistinct/short, metatarsal III-IV preening comb well developed, several metatarsal and tarsal trichobothria existing, paired tarsal claws with long teeth. – Opisthosoma (fig. 241, photo) oval, 1.14 times longer than wide, ventrally covered with an emulsion, hairs short, spinnerets well observable, the anteriors stout, converging, close together. – Pedipalpus: See the diagnosis of the genus.

**Relationships and distribution:** See above.

### **Paxillomegops n. gen.**

**Etymology:** The first part of the name is taken from *paxillus* (lat.) = peg, pointing to the „peg bristles“ of the pedipalpal tibia; the second part of the name is taken from the family name *Lagonomegopidae*.

The gender of the name is masculine.

Type species: *Paxillomegops longipes* n. sp.

Further species: ?*Paxillomegops brevipes* n. sp.

**Diagnosis** (♂; ♀ unknown): Opisthosoma apparently long and slender, tibia of the ♂-pedipalpus (figs. 247, 252) with a long row (or rows) of numerous „peg bristles“ (and a field), and an indistinct small and blunt RTA.

**Further characters:** Legs I and II (photo) very long (ca. 4 times longer than the body), 8 eyes (see below), clypeus (fig. 244) long and sloping, basal cheliceral articles 2.7 times longer than wide, diverging distally, cheliceral „peg teeth“ (fig. 248) quite long, leg bristles absent, tarsi and metatarsi with long trichobothria.

**Relationships:** According to the long and sloping clypeus and the long basal cheliceral articles – see the key to the genera no. 2f – *Archaelagonops* and *Myanlagonops* are most related. A depression between the large posterior median eyes exist (fig. 244) as in *Archaelagonops* but sharp cephalic ridges and clypeal humps as well as tibial „peg bristles“ of the pedipalpus are absent. Tibial „peg teeth“ are unique within the lagonomegopid genera. Retrolateral tibial „peg teeth“/spines of the male pedipalpus exist also in certain members of the *Mecysmaucheniinae*.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

?*Paxillomegops brevipes* n. gen. n. sp. (figs. 250-254) photo 113

Derivatio nominis: According to the short legs: brevis (lat. = short) and pes (lat. = leg.).

**Material**: Holotype ♂ in Burmite, F2684/BU/CJW.

**Preservation and syninclusions**: Some distal leg articles (right legs I and II, left leg I) are cut off. The spider probably has been the prey of a spider: It is enclosed in irregular three-dimensional, fairly dense spider's threads without sticky droplets, probably part of a capture web, body and legs are crumbled, the remains of the opisthosoma a probably have been sucked out, some leg articles are broken or lose. I do not want to exclude that the spider has been the prey of a member of the capture web building mygalomorph family Dipluridae whose members were not rare in the ancient amber forest of Myanmar, and which were large enough to capture a spider of a body length of 4 mm. – Remains of questionable white digestive secretion are preserved on parts of the prosoma and on both anterior femora. A Diptera, remains of Collembola, parts of an insect's leg, decomposed wood and plant hairs are also preserved in this piece of amber. – In a separated piece of amber, F2754/BU/CJW, two hairs of a mammal are preserved.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (figs. 252-254): Tibia with a retroventral-apical apophysis, a retroventral row of „peg teeth“ and a retrolateral field of „peg teeth“.

Further characters: Posterior median eyes widely spaced, clypeal humps quite weakly developed, legs only fairly long.

### **Description ( ):**

Measurements (in mm): Body length 4.0, prosoma: Length 2.0, width 1.9; leg I: Femur 2.0, patella 0.8, leg II: Femur 2.1, patella 0.8, tibia 2.5, metatarsus 1.85, tarsus 0.8, tibia III ca. 1.5, tibia IV ca. 1.8.

Colour dark brown.

Prosoma (figs. 250-251, photo) slightly longer than wide, cephalic part fairly raised, 8 eyes, the large anterior median eyes and the tiny posterior median eyes widely spaced, lateral eyes far away from the clypeal margin and contiguous, clypeus long, its humps quite weak, basal cheliceral articles ca. 1.45 times longer than wide, fangs long. – Legs only fairly long, bristles absent, scopula hairs of medium length, long tarsal and metatarsal trichobothria existing, 3 tarsal claws, paired claws with long teeth, hairs of a pseudotuft existing. – Opisthosoma crumbled and apparently sucked out by a spider, see above. – Pedipalpus (figs. 252-254) with stout articles, tibia with a retroventral-apical apophysis, a retroventral row of „pegteeth“ and a retrolateral field of „peg teeth“, cymbium fairly long, wide and hairy, elongated basally, bulbus (its structures are partly hidden by emulsions) protruding probasally, position of the questionable embolus prolatrally, sickle-shaped tegular apophysis long.

**Relationships**: The tibial „peg teeth“ are similar in *P. longipes* but in *longipes* the legs are much longer and much more slender. Therefore I am not sure about the congenerity of both species.

**Distribution**: Mid Cretaceous amber forest of Myanmar (Burma).

Etymology: According to the long legs: longus (lat.) = long, pes (lat.) = leg, foot.

**Material**: Holotype ♂ in Mid Cretaceous amber from Myanmar (Burma), F2626/BU/CJW.

**Preservation and syninclusions**: The spider is well but incompletely preserved in a larger piece of amber (4.7x3.7x1cm); some legs are stretched sideways, the deformed opisthosoma is situated deeper in the amber, its distal part may be lost, most parts of the left tarsus II and both legs IV except the left metatarsus and tarsus are cut off. – 5 mm in front of the holotype a juvenile Lagonomegopidae indet. is badly preserved which may be conspecific, its body length is 1.3 mm. A thin spider's thread runs forwards from the left patella III of the holotype. The piece of amber is full of microfossils, tiny droplets, plant hairs, insects excrement and detritus. Also preserved are remains of few Diptera as well as a questionable Isoptera and a questionable Ephemeroptera.

**Diagnosis**: See above.

**Description** (♂):

Measurements (in mm): Body length at most 4 mm, prosoma: Length at least 1.8, width 1.5; opisthosomal width near the middle ca. 1.1; leg I: Femur 3.6, patella 0.9, tibia 4.5, metatarsus 3.2, tarsus 1.0 (= 13.2), leg II quite similar, tibia III ca. 2.0, basal cheliceral articles 0.75; cymbium more than 1.0.

Colour: Prosoma probably uniformly medium brown, legs light brown, opisthosoma light grey.

Prosoma (fig. 244, photo) not wrinkled, distinctly v-shaped declined behind the narrowed cephalic part, with a distinct depression between the large anterior median eyes, dorsal ridges absent, hairs short, position of the small posterior median eyes at the prosomal margin, anterior median eyes very large and sitting on humps. I did not recognize the posterior median eyes which may be hidden by hairs. Clypeus long and sloping, distinct bulges absent. Basal cheliceral articles long and slender, in a parallel position, diverging only distally, bearing at least 5 long and slender „peg teeth“, lateral files absent, fangs only fairly long. Most parts of the mouth parts and the sternum hidden, gnathocoxae vera long, a diastema may exist. – Legs (fig. 245-247, photo) long and slender, order I=II/IV/III, I and II very long, ca. 4 times the body's length, III distinctly the shortest, patellae short, bristles absent, hairs short, partly dense but indistinct, preening bristles on metatarsus III-IV existing, tarsi and metatarsi bear several long trichobothria as well some differing but similar sensory hairs, e. g., distally on the left metatarsus III (not drawn), and ventrally on femur III. Unpaired tarsal claws large, paired claws with two large teeth. – Opisthosoma (it is badly preserved) and pedipalpal articles with fairly short hairs. – Pedipalpus (fig. 248-249) with long and slender articles, tibia with several dorsal trichobothria, a small blunt RTA, and retrolaterally with an irregular row of short and blunt „peg bristles“ which function appears enigmatic, cymbium slender, bulbus fairly protruding, bearing apophyses, the identity of the embolus remains unsure.



**Relationships:** See ?*P. brevipes* n. sp. in which prosoma, leg and pedipalpal articles are stouter, the prosoma is not narrowed anteriorly, and the RTA is well developed.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

### **Picturmegops n. gen.**

**Etymology:** The genus is named after the distinct markings of its body by white and black hairs: *pictura* (lat.) = picture.

The gender of the name is masculine.

**Type species** (by monotypy): *Picturmegops signatus* n. sp.

**Diagnosis** (♀; ♂ unknown): Prosoma and opisthosoma bear distinct dorsal markings of white (prosoma) and black (opisthosoma) hairs as in fig. 255 e. g. a wide transverse prosomal band as well as spots, and 2 pairs of longitudinal opisthosomal bands. Prosoma distinctly narrowed posteriorly, slightly wider than long, clypeus convex (fig. 255, photo), patellae I-II relatively long.

**Relationships:** See the key to the genera above. Differing markings of the body exist also in *Archaelagonops* and *Myanlagonops* in which the shape of prosoma and chelicerae are different, and the patellae I-II are shorter.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

### ***Picturmegops signatus* n. gen. n. sp. (figs. 255-259) photos 114-117**

**Etymology:** The species is named after the distinct markings of its body: *signum* (lat.) = marking.

**Material:** Holotype ♀ (according to the proportions of prosoma, opisthosoma and legs adult in my opinion) in amber from N-Myanmar (Burma), F2451/BU/CJW.

**Preservation and syninclusions:** The spider is excellently preserved in a yellow-orange piece of amber, the left metatarsus and tarsus I and II are cut off, some leg articles – especially the left femora – are depressed dorso-ventrally, a secretion of a gland mound (arrow in fig. 257) is preserved on the left chelicera. A ?gas bubble cov-

ers some dorsal-right parts of the opisthosoma. – Few remains of – apparently sticky – larger spider's threads exist 2 cm right of the spider; few Acari, 1 Diplopoda, 4 Collembola, dissected remains of a further insect, thin remains of insect's legs (right and left of the spider), a strongly bent thin hair of a mammal, at least 2 mm long – a part of it is cut off – left and behind the holotype, remains of plant hairs, a questionable tiny seed and numerous tiny ?gas bubbles are also preserved in the piece of fossil resin.

**Diagnosis** (♀): See the genus.

**Description** (♀):

Measurements (in mm): Body length 3.6, prosoma: Length 1.5, width 1.6, height ca. 0.6, diameter of a posterior median eye 0.25, basal cheliceral article: Length 0.7, width 0.5; opisthosoma: Length 2.4, width 1.4; leg I: Femur 1.15, patella 0.6, tibia 1.1, metatarsus 0.75, tarsus 0.5, tibia II 1.2, tibia III ca. 0.7, tibia IV 0.9.

Colour (fig. 255, photos): Prosoma dark brown, dorsally with spots and a transverse band of white hairs, pedipalpus and legs dark brown (femur I prolaterally light brown, white hairs exist on femur IV), opisthosoma dorsally covered with white hairs and 2 pairs of irregular longitudinal bands of black hairs, the lateral pair is indistinct.

Prosoma (figs. 255-258, photos) slightly wider than long, hairs see above, posteriorly gradually sloping and distinctly narrowing, fovea absent, clypeus convex, 8 eyes, anterior medians huge, directed sideward, remaining eyes tiny (the right anterior lateral eye is connected with a bubble), clypeus fairly short and fairly protruding, distinct humps absent, diastema large, foramen fully sclerotized, encircling the chelicerae, basal cheliceral articles fairly weak, lateral files absent, gland mound distinctly elevated (the left one bears a secretion as a bubble, fig. 257), peg teeth well developed, in a single row, fangs long, slender, slightly bent, labium triangular, longer than wide, gnathocoxae long, slender and fairly converging, narrowing distally, sternum rugose, not elongated between the coxae IV. – Pedipalpus (figs. 255-256) long and slender, tarsus hairy, claw absent. – Legs (fig. 259, photos) fairly stout, IV apparently longest, III distinctly shortest, I and II about equal in length, bristles absent, metatarsi with several long trichobothria, tarsi also with several trichobothria, in a single row, preening comb on metatarsus III-IV existing, hairs on I-II long and dense – especially prolaterally on tibiae, metatarsi and tarsi –, not thickened. Paired tarsal claws bearing long teeth, unpaired claw only fairly long. – Opisthosoma (fig. 255, photos) long ovally, 1.7 times longer than wide, anteriorly pointed, soft, hairs see above, lung covers indistinct, tracheal spiracle hidden, genital area bulging and dark brown, not sclerotized, colulus apparently absent, anterior spinnerets fairly long, biarticulate, posterior spinnerets shorter, medians not observable.

**Relationships and distribution:** See the genus.

*Spinomegops aragonensis* FUENTE et al. 2013, juv., in Cretaceous amber from Spain, fig. 260).

*Spinomegops arcanus* FUENTE et al. 2013, juv., in Cretaceous amber from Spain, fig. 261.

Saplaogonomegops unzei FUENTE et al. 2013, juv. in Cretaceous amber from Spain, fig. 262.

Zarqagonomegops wunderlichi KADDUMI 2007, juv. in Cretaceous Jordanian amber, figs. 263 (1) and (2).

### **Lagonomegopidae indet. preserved in Burmite**

Few juveniles (Lagonomegopidae indet.) exist in the coll. of ALEX BEIGEL in Aachen, Two further juveniles indet. are preserved together with two Uloboridae in a larger piece of amber, F2775/BU/CJW.

Except the first one the spiders are shortly described.

F2628/BU/CJW: 1♀, most probably adult in my opinion, and a separated piece of amber. Figs. 264-266.

**Preservation and syninclusions:** The spider is only fairly well preserved, it is „captured“ and deformed within several layers of the fossil resin, the ventral and (partly) intern parts of the opisthosoma including the spinnerets are missing, the prosoma is also deformed and dorsally partly covered with an emulsion, the large lense of the right anterior median eye is missing, some articles of the left legs are cut off. Probably the female has been the prey of an arthropod. – Just above the spider's opisthosoma anteriorly a tiny and slender member of the family Mymarommatidae indet. (Hymenoptera) indet., J. JANZEN det. in IV 2014, is preserved, which antennae are very long; its body length is 0.65 mm. I took a photo which is not published. Members of this family are probably egg parasitoids of insects. Remains of few Diptera, plant hairs, insects excrement and detritus are also preserved.

### **Description:**

Measurements (in mm): Body length 5.0, prosoma: Length 2.0, width ca. 1.4; opisthosoma: Length 3.1, width 1.4; leg I: Femur 2.3, patella 0.7, tibia 1.8, metatarsus 1.2, tarsus 0.7, tibia II 1.7, tibia III 0.95, tibia IV > 1.5, femur IV 2.5.

Colour: Prosoma and legs medium brown, opisthosoma medium grey brown.

Prosoma (fig. 264) (dorsally deformed and partly covered with an emulsion): Ca. 1.4 times longer than wide, weakly inclined between cephalic and thoracic part, numerous hairs of medium length are observable on the left posterior area; anterior median eyes large, weakly concavity between these eyes, remaining eyes tiny, lateral eyes contiguous and far away from the clypeal margin, posterior lateral eyes not observable, clypeus long and sloping, anterior humps weakly developed. – Pedipalpus fairly long and slender, tarsus quite hairy, claw absent. – Legs long, order IV/II/III, III distinctly the shortest, I and II not very long, bristles absent but bristle-shaped hairs exist dorsally on the patellae, especially on the anteriors, metatarsal III-IV preening combs quite well developed, tibiae, metatarsi and tarsi bear dense hairs, the tarsi bear distinct false

claw tufts (figs. 265-266), tarsi and metatarsi bear long trichobothria. – Opisthosoma (most ventral parts are empty), 3 times longer than high in the middle, bearing longitudinal lateral furrows, hairs fairly short, spinnerets missing.

**Relationships:** See the key no. 3.

F2602/BU/CJW: Juv. in my opinion, body length 3 mm. All eyes are cut off.

F2603/BU/CJW: Juv., body length 2 mm. The right eyes are preserved, the opisthosoma is filled with a white substance.

F2604/BU/CJW: Juv., body length 2.7 mm. Most legs are strongly bent below the body, the prosoma is quite hairy. Remains of an insect are preserved in the same piece of amber.

F2673/BU/CJW: ♀, strongly deformed, body length ca. 4 mm, preserved together with a juv. Hersiliidae indet. and a Tetrablemmidae indet.

F2677/BU/CJW: ♀. The spider is preserved in a large and muddy piece of amber. Body length 7.5 mm, eyes hidden, leg bristles apparently absent, opisthosoma long oval. – Syninclusions (besides Diptera etc): A small part of a feather is preserved 1.2 mm above and in front of the spider, small particles of moss are preserved in a large separated piece of amber.

F2678/BU/CJW: A ?juv. ♀, body length 4 mm. The spider is preserved in a fairly muddy piece of amber.

F2679/BU/CJW: A ?juv. ♀, body length 4 mm. The spider is preserved in a clear yellow piece of mber.

F2680/BU/CJW: ?Adult ♀, body length 5.3 mm. The spider is not well observable in a yellow piece of amber.

F2683/BU/CJW: Subad. ♂, body length ca. 4.5 mm. The spider is not well and incompletely preserved, dorsal parts of the prosoma and several leg articles are cut off, the opisthosoma is inclined dorsally. The prosoma is not much longer than wide, the basal cheliceral articles are only fairly long. The cymbium is long and slender. Eight eyes, position of the lateral eyes far from the clypeal margin, leg hairs short, tarsal and metatarsal trichobothria long and numerous. – Two Acari are preserved in the same piece of amber.

**Family MICROPALPIMANIDAE** WUNDERLICH 2008 figs. 267-278, photos 134-138, family key no. 19

Recently discovered – partly well preserved – fossils of this extinct monotypic family in Burmite lead to closer conclusions on the relationships of this family and related taxa; in these specimens I discovered the existence of several tarsal and metatarsal trichobothria. In this paper I describe some – probably conspecific – specimens of *Micropalpimanus poinari* WUNDERLICH 2008 as well as specimens indet..

**Diagnostic characters and relationships of the family:** See the paragraph „discussion“ above within the superfamily Archaeoidea, the key to the families, fig. D, the lagonomegopid branch and the family Lagonomegopidae above.

Several tarsal and several metatarsal trichobothria (fig. 267) (\*). I regard this character as an autapomorphy of the lagonomegopid branch of the Archaeoidea. Lagonomegopidae and Micropalpimanidae share furthermore the existence of leg bristles (which exist elsewhere only in the Huttoniidae within the Archaeoidea), but other characters of the Huttoniidae are quite different; Huttoniidae is not strongly related, see above.

Thickened/flattened leg hairs are absent in the Micropalpimanidae (as in the Lagonomegopidae); the thin and dense leg hairs may bear apical droplets (artefacts) which may „simulate“ flattened/widened hairs (fig. 276); compare fig. 272) and see also below.

Leg bristles (see the figs.). Tibia III bears usually (!) a prodistal bristles which is well developed. The number of leg bristles may be quite variable even within the same species, and some bristles may be rubbed off. Therefore the number of leg bristles apparently is not well usable as a diagnostic character for the species.

Eight eyes (fig. 275).

The epigaster is strongly sclerotized in both sexes.

The body length is 1.5- 2.5 mm.

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(\*). They also exist in the Caponiidae and Lagonomegopidae, and can easily be overlooked in the fossils. Additional long sensory hairs in a ca. prolateral position may exist (fig. 276) which are probably not trichobothria.

***Micropalpimanus ?poinari*** WUNDERLICH 2008 (figs. 267-271f), photos 134-135f

New **material**: 3♂1♀ in Mid Cretaceous Burmese amber from N-Myanmar, F2511/ BU/CJW, F2512/BU/CJW with a larger separated piece of amber, F2445/BU/CJW and F2734/BU/CJW as well some spiders from an unnamed institution, see below.

**Preservation and syninclusions:** The spider is completely and well preserved in a clear yellowish light green piece of amber; most legs are laterally depressed, the prosoma – especially the eyes and the thoracic region – are deformed, some air bubbles cover mainly the right side of the spider's body. – Numerous tiny (water/air?) bubbles, a „stellate“ hair, remains of a tiny insect and of a questionable leaf are preserved in the same piece of amber.

**Description:**

Measurements (in mm): Body length 1.5, prosoma: Length ca. 0.7, width ca. 0.6; leg I: Femur 0.55, patella 0.25, tibia 0.4, metatarsus 0.27, tarsus 0.32, tibia III 0.35, tibia IV 0.43.

Colour: Prosoma and epigaster dark brown, legs medium brown, opisthosoma medium grey.

Prosoma (it is deformed, especially the field of the 8 eyes) wide, cephalic part raised and bearing long erect dorsal hairs, cuticula distinctly wrinkled like in the holotype, fovea absent, basal cheliceral articles strongly deformed, large, bearing at least two „peg teeth“, lateral sides only restrictedly observable, files not observable but blunt (!) denticles on the pedipalpal femur exist, see below, fangs very stout, labium distinctly longer than wide, gnathocoxae strongly converging, sternum distinctly wrinkled, separating the coxae IV by about their diameter. – Legs (figs. 267-268) slender, order IV/II/II/III, femur I NOT enlarged (the previously reported thickened femur of *M. poinari* is apparently an artefact), metatarsus IV with a „preening comb“, constriction of tarsus I indistinct or absent. True bristles/spines absent but a long and bent bristle-shaped hair exists on all femora; prodistal bristle on tibia II apparently absent. Some of the tarsi and metatarsi I-II bear proventral hairs which are distinctly „thickened“ apically (apparently nothing else than artefacts). Tarsi and metatarsi bear long trichobothria, false claw tufts well developed. – Opisthosoma oval, bearing short hairs, lung covers and epigaster strongly sclerotized, no sclerotized ring around spinnerets, colulus absent, 3 pairs of spinnerets. – Pedipalpus (figs. 269-270; it is fairly deformed): Femur only fairly enlarged (the distinctly enlarged femur of the holotype is apparently an artefact caused by the preservation), bearing two blunt – PROBABLY stridulatory – teeth in a probasal position (fig. 269), tibia only fairly thickened (not thickened as the artificial thickened tibia of the holotype), cymbium and bulb slender, cymbium laterally with dense long hairs, embolus fairly long, in a prodistal position.

**Relationships:** The male is probably conspecific with the holotype of *M. poinari* WUNDERLICH 2008, but the fang is more stout in the present male, the tarsi are longer than the metatarsi, and the pattern of the bristle-shaped hairs of the legs (partly rubbed off?) may be different.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

**Preservation and syninclusions:** The spider is completely and very well preserved between two layers of the fossil resin. Parts of an irregular capture web (the threads bear tiny droplets) are preserved mainly above the spider in a different layer of the fossil resin.

**Description:**

Measurement (in mm): Body length 1.9, prosomal length 1.0, tibia I 0.45, metatarsus II 0.4, tarsus II 0.32.

Colour: Prosoma dark brown, legs medium brown, tibiae slightly darker, opisthosoma grey.

Prosoma (as far as observable) (photo) similar to the holotype stronger raised and larger. Fovea unknown. – Legs (fig. 271) only fairly long, metatarsus II longer than tarsus II (see above). Few thin bent hair-shaped bristles (or bristle-shaped hairs?) on femora, patellae and tibiae; tibia III bears a true prodistal bristle which is well developed. Position of one of the metatarsal I trichobothria in 0.83. Metatarsi III and IV bear few apical-ventral preening bristles. – Opisthosoma similar to the holotype; no sclerotized ring around the three pairs of spinnerets. – Pedipalpus: Cymbium slender, bulbus hidden.

**Relationships:** Probably conspecific with *M. poinari* WUNDERLICH 2008 but larger, and prosoma stronger raised.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

?Ad. ♀ F2445/BU/CJW.

**Preservation and syninclusions:** The spider is fairly well and almost completely preserved, embedded in artificial resin, the left side of the opisthosoma has been cut off within the fossil resin, the opisthosoma is transparent in this area. The prosoma is covered with an emulsion.

**Description:**

Measurements (in mm): Body length 2.0, prosomal length 0.7; leg I: Femur 0.5, patella 0.26, tibia 0.31, metatarsus 0.31, tarsus 0.26, tibia IV 0.44, pedipalpal tarsus 0.23.

Prosoma (photo) distinctly raised but eye area lower than in the holotype, dorsally (as well as the clypeus) with long erect hairs, cuticula rugose. Foramen probably absent, chelicerae and mouth parts partly hidden. – Pedipalpus large, tarsus with long bristles, claw absent or strongly reduced (the apical area is hidden by hairs). – Legs only fairly long, order IV/II/III, patellae I-II quite long, metatarsi longer than tarsi, few bristle-shaped hairs exist, e. g. a single one prodistally on femur IV. Metatarsal III-IV preening bristles existing. A trichobothrium on tarsus I exists probably in the middle of the article. – Opisthosoma oval, hairs of medium length, genital area hidden.

The **relationships** are not sure. The eye region (photo) is lower than in the holotype, the prosoma is stronger raised than in the probably conspecific female F2285/BU/ CJW



– see WUNDERLICH (2012: 228, fig. 51) – but that female is deformed and the prosoma apparently depressed dorso-ventrally.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

♂ F2734/BU/CJW and three separated pieces of amber.

The male is completely but not well preserved, pro- and opisthosoma are strongly deformed, the body length is 1.3 mm. I did not observe leg bristles or trichobothria. – Just behind right above the spider a questionable colony of Bacteria is preserved; in the larger one of the separated pieces a member of Auchenorrhyncha is preserved.

?Ad. ♀, kept in an institution which remains unnamed here, photo 136

The female is excellently preserved, its body length is 2.4 mm.

♂, sp. indet. (a), kept in an institution which remains unnamed here, figs. 272-274, photo 137

The male is well preserved, its body length is 1.9 mm.

♂, sp. indet. (b), kept in an institution which remains unnamed here, figs. 275-278, photo 138

The male is well preserved, its body length is 1.5 mm.

**Family SPATIATORIDAE** PETRUNKEVITCH 1942 (figs. 279-283, photo 131)

The extinct family Spatiatoridae was known up to now only from the genus *Spatiator* PETRUNKEVITCH 1942 (3 species) in Eocene Baltic amber, see WUNDERLICH (1986: 21-23, figs. 7-11), (2004: 757, 767, 806-807, figs. 48-56), (2006: 213-218, figs. 1-5). The geological age of the family Spatiatoridae is more than doubled by the discovery of the present fossils.

With some hesitation – remarkable differences exist – I regard the new genus *Vetiator* as a member of the family Spatiatoridae, and of the new subfamily Vetiatorinae. The inclusion of *Vetiator* in the Spatiatoridae causes a dramatic change of the family diagnosis.

Emended **diagnostic characters** of the family Spatiatoridae (see the key to the subfamilies below):

Prosoma (figs. 279, 284-285, photos) slender and elongated anteriorly and especially posteriorly; ♂-pedipalpus (figs. 281-283, 286-287): cymbium widely enclosing the flat bulbus, conductor existing at least in *Spatiator* (not surely known in *Vetiator*), embolus slender.

Further character: Eye field not wide, anterior and posterior eyes close together, patellae long but not very long: Tibia I 1.8-2.2 times longer than patella I, cheliceral-pedipalpal femoral stridulatory organ existing, see fig. 281.

Questionable araneophagy of *Spatiator*. See the paper on araneophagy in the Eocene in this vol. on „Frozen behaviour“, Beitr. Araneol., 9. With the discovery of the present member of the araneophagous genus *Spatiator* the existence of araneophagy already in the Mid Cretaceous appears quite likely.

Possible weak myrmecomorphy of the slender members of *Spatiator*. See WUNDERLICH (2006: 317).

**Relationships**: Stenochilidae may be most related, see the cladogram of the families of the Archaeoidea. In a questionable member of the Huttoniidae in amber from New Jersey (F2464/NJ/CJW) tibia I is only 1.1 times longer than patella I. See above: „Further characters of the Spatiatoridae“.

**Distribution**: Mid Cretaceous Burmite (*Vetiator* and *Spatiator*) to Eocene (*Spatiator*, Baltic amber).

### **Key to the subfamilies:**

1 Prosoma (photo 131) distinctly wrinkled, twice as long as wide, cephalic part strongly raised, opisthosoma dorsally leathery or sclerotized basally, epigaster distinctly sclerotized, legs only fairly slender (photo), tarsi I-II distinctly shorter than metatarsi I-II (photo). *Spatiator*, Mid Cretaceous Burmite and Eocene. . . . . Spatiatorinae

- Prosoma only weakly corniculate, 1.33 times longer than wide, low (figs. 284-285, photo 132), opisthosoma including the epigaster soft, legs more slender (photo), tarsi I-II about as long as the metatarsi. *Vetiator*, Mid Cretaceous Burmite. . . . Vetiatorinae

***Spatiator putescens* n. sp.** (figs. 279-283) photo 131

**Etymology:** The species name refers to the decomposed and injured opisthosoma of the holotype, from *putesco* (lat.) = rot.

**Material:** Holotype ♂ in Mid Cretaceous Burmite, F2740/BU/CJW.

**Preservation and syninclusions:** The spider is almost completely preserved in a yellow-orange piece of amber, only the tips of some tarsi are lost within the amber. Prosoma and pedipalpi are well preserved, the opisthosoma (fig. 280, photo) is injured and decomposed, the legs are ventrally partly covered with bubbles. – Left behind and below the spider a tiny Acari: ?Gamalina (det. E. SIDORCHUK) is preserved. Further syninclusions are remains of a Diplopoda as well as of a ?winged questionable Formicidae, detritus, insect excrement and plant hairs.

**Diagnosis** (♂; ♀ unknown): Opisthosoma with a dorsal basal scutum (photo) besides a scutate epigaster; pedipalpus (figs. 281-283) with a large and not sclerotized questionable conductor which stands out.

**Description** (♂):

Measurements (in mm): Body length 3.2, prosoma: Length 1.5, width 0.75; legs: I: Femur 1.25, patella ca. 0.45, tibia 1.0, metatarsus 0.75, tarsus 0.65, tibia III ca. 0.7, tibia IV ca. 1.1.

Colour: Prosoma dark brown, legs and opisthosomal scutum medium brown, opisthosoma light grey brown.

Prosoma (fig. 279, photo) twice as long as wide, distinctly wrinkled, hairless, cephalic part distinctly raised, anteriorly and posteriorly distinctly narrowed, fovea long and well developed, 8 eyes, field not wide, the anterior medians largest, posterior row distinctly procurved, anterior and posterior lateral eyes close together, clypeus long, basal cheliceral articles large, lateral files indistinct, few small „peg teeth“, fangs fairly long, gnathocoxae strongly converging, labium distinctly longer than wide, with a seam to the sternum which is distinctly wrinkled, spacing the coxae IV by about their diameter. – Legs (photo) only fairly long, order IV/III/III, bristleless, hairs quite indistinct. The tarsi I-II are bent retrolaterally from their metatarsus, see WUNDERLICH (2004: 768, 807, fig. 52). Tarsal claws lost, hidden or decomposed. I did not recognize thickened prolateral hairs on legs I-II which are only insufficiently preserved. – Opisthosoma (photo): Most parts are decomposed, a larger dorsal-anterior scutum exists, the epigaster is strongly sclerotized. – Pedipalpus (figs. 281-283): Femur probasally with at least one pointed stridulatory tooth, tibia long, fairly thickened, cymbium slender and wide, questionable conductor large, not sclerotized, standing out, embolus long.

**Relationships:** The shape of the body and the strongly sclerotized prosomal cuticula are as in the Eocene species of *Spatiator*; the Eocene species are at least 50% larger in size, and an outgrowth of the bulbus is absent. The existence of this outgrowth may justify the creation of a separate genus for *putescens*.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

## VETIATORINAE n. subfam.

Etymology: See the type genus *Vetiator* n. gen.

**Diagnosis** (♂; ♀ unknown): Prosoma (figs. 284-285, photos 132) low and abruptly narrowed anteriorly, dorsal part of the opisthosoma and epigaster not sclerotized; pedipalpus (figs. 285-286) with a distinctly bent questionable embolus.

Further characters: Prosoma slender, not wrinkled, finely corniculate, eyes (fig. 284): the anterior medians are the largest, posterior row distinctly procurved, basal cheliceral articles slightly divergent and not protruding, „peg teeth“ existing, legs slender tarsal trichobothria absent, cheliceral-pedipalpal femoral stridulatory organ apparently existing, small spiders, body length 1.8 mm.

The **relationships** are not sure, the shape of the slender prosoma which is elongated posteriorly, the position of the eyes and the structures of the pedipalpus are similar or even very similar to *Spatiator* PETRUNKEVITCH 1942 (Spatiatorinae, Eocene). In the Spatiatorinae the prosoma (photo) is distinctly raised and distinctly wrinkled, and the epigaster is strongly sclerotized. I do not want to exclude with certainty that *Spatiator* and *Vetiator* may be regarded as member of different families.

**Distribution**: Mid Cretaceous amber forest of Myanmar (Burma).

### *Vetiator* n. gen.

Etymology: The name is based on *vetus* (lat.) = ancient and the genus *Spatiator* which may be well related to *Vetiator*.

Type species (by monotypy): *Vetiator gracilipes* n. sp.

**Diagnosis, relationships and distribution**: See above.

***Vetiator gracilipes* n. gen. n. sp.** (figs. 284-287) photos 132-133

**Etymology:** The species name refers to the quite slender legs, from *gracilis* (lat.) = slender and *pes* (lat.) = foot, leg.

**Material:** Holotype ♂ in Mid Cretaceous Burmite, F2739/BU/CJW.

**Preservation and syninclusions:** The spider is completely and well preserved in a flat yellow-orange piece of amber; some fissure in the amber exist ventrally of the spider. – Larger organic structures are absent within the piece of amber.

**Diagnosis** (♂; ♀ unknown) (see the subfamily): Pedipalpus (figs. 286-287): Questionable embolus distinctly bent, of medium length.

### **Description** (♂):

Measurements (in mm): Body length 1.8; prosoma: Length 0.8, width 0.6; opisthosoma: Length 0.95, width 0.55; leg I: Femur 0.9, patella ca. 0.35, tibia ca. 0.65, metatarsus 0.42, tarsus ca. 0.42; tibia II ca. 0.62, tibia III 0.43, tibia IV 0.7.

Colour: Prosoma and legs dark brown, opisthosoma medium grey brown.

Prosoma (figs. 284-285, photo) 1.33 times longer than wide, finely corniculate, probably hairless, low, anteriorly abruptly narrowed, posteriorly elongated, fovea probably long, 8 eyes in a narrow field, posterior row distinctly procurved, the anteriors largest and well separated, the laterals close together, basal cheliceral articles only fairly large, clypeus long, lateral files not observable (but probably existing), few „peg teeth“ which are hard to observe, fangs only fairly long, gnathocoxae strongly converging, labium probably wide and free, sternum finely corniculate, spacing the coxae IV by about their diameter. – Legs (photo) long and slender, bristleless, hairs indistinct, I longest, III distinctly the shortest, tarsi I and II as long as metatarsi I and II, tarsi III and IV shorter, longer strong hairs (apparently no true combs) exist ventrally-apically on the metatarsi III-IV. I found indistinctly club-shaped prolateral hairs on tarsus I. Tarsi and metatarsi bear long erect hairs which are not bent backwards and are no trichobothria. Tarsal trichobothria absent. Paired tarsal claws slender, unpaired claws well developed. – Opisthosoma ca. 1.7 times longer than wide, soft, hairs indistinct, spinnerets only fairly well preserved, the anteriors slender and not widely spaced, medians not observable, anal tubercle of medium size, lung covers not observable. Pedipalpus (figs. 286-287, photo): Femur probasally with few indistinct stridulatory teeth, cymbium long, hairy retrolaterally, enclosing most parts of the long bulbus which is not standing out distinctly, questionable embolus distinctly bent; I cannot identify a conductor with certainty.

**Relationships:** See above.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

## THE RELATIONSHIPS OF THE HAPLOGYNE SUPERFAMILIES AND FAMILIES, WITH A FOCUS ON THE TAXA ARCHAEOIDEA, CAPONIIDAE AND LEPTONE-TOIDEA, AND ON REMARKABLE CONVERGENCES, „REVERSALS“, „TENDENCIES“ AND LOSSES OF CHARACTERS IN THESE TAXA

See WUNDERLICH (2011: 567-590)

Because of the tricky mixture of numerous convergent developments, „reversals“ and losses of characters – partly combined with „tendencies“ – the diagnoses and limits of some haplogyne superfamilies as well as the relationships of families like Caponiidae and Tetrablemmidae (see below) are confusing and still controversially discussed. Decisions on the existence of LOSSES or CONVERGENT DEVELOPMENTS (or both?) or „REVERSALS“ („regains“) of certain characters are very hard and frequently not sure. My conclusions may hopefully be correct in most parts.

The term „REVERSALS“ is used here in a „descriptive/functional sense“; their origins may not be monocausal. See the discussion on important characters like „metatarsal and tarsal trichobothria“, „leg bristles“, „cribellum“ and „cheliceral stridulatory files“ below as well as the family Caponiidae which is chosen as a model. The existence of „reversals“ appears quite rare to me.

The (genetical) background and the kinds of selection pressure regarding the „TENDENCIES“ used in this paper – they are mainly losses – are unknown to me but the existence of such „(pre)dispositions“ is obvious.

We still do not have enough information about the characters of the – probably numerous – extinct branches of spiders. The discovery of higher taxa of such branches should be a great help in the future to find out the sequence of losses, „reversals“ and convergent developments of characters; see e. g. the genus *Zhizhu*.

### (1) THE RELATIONSHIPS OF THE PECULIAR FAMILY CAPONIIDAE

**Diagnosistic/apomorphic characters of the family Caponiidae:** Existence/ absence of ...

- several tarsal and metatarsal trichobothria in an irregular position (fig. 291),
- position of the anterior median and lateral spinnerets in a single transverse row (fig. 293),
- existence of retrolateral cheliceral stridulatory files and corresponding pedipalpal femoral picks (fig. 289),

- only fairly thickened articles of the ♂-pedipalpus,
- a large cymbium which usually bears dense hairs like the tarsus of the ♀-pedipalpus (fig. 294),
- absence (loss) of lungs (fig. 292),
- absence (loss) of leg bristles,
- absence (loss) of the claw of the female pedipalpal tarsus (fig. 294),
- absence (loss) of the colulus (fig. 293),
- absence (loss) of marginal teeth of the fang furrow,
- tendency to the reduction of the number of (the basically four pairs of) eyes and
- reduction/absence of the posterior median spinnerets in males.

Further characters (besides basic ones): A quite variable number of the eyes: 2 or 4 (most often), 6 or (rarely) 8, prosomal cuticula only weakly or not rugose, a low cephalic part, a strongly reduced/absent fovea, a non-protruding clypeus, a translucent lobe-shaped medial-distal cheliceral membrane which covers the fang furrow (fig. 289), strongly bent fangs and strongly converging gnathocoxae (fig. 289), sternum bearing intercoxal sclerites, quite long anterior patellae, free chelicerae, no metatarsal III-IV preening combs, two pairs of tracheae in an anterior position, colour of prosoma and legs usually orange-red, body length 6-13 mm, ground dwellers, hunters (no capture web builders). – Characters OF CERTAIN TAXA/TENDENCIES (see also above: The reduction of the eye numbers): Strongly sclerotized ♂-epigaster, legs I-II: Metatarsi ventrally with a longitudinal translucent keel and tarsi with a translucent ventral-basal lobe (Nopinæ, fig. 290), tarsi subdivided (fig. 290), unpaired tarsal claw reduced and hidden by a „tuft“, spider eaters (at least some taxa).

**Relationships:** JOCQUE & DIPPENAAR-SCHOEMAN (2007: 88) wrote under „Taxonomical status“: „Lehtinen (1967) regarded Caponiidae as a superfamily of its own (\*). Platnick et al. (1991), Coddington & Levi (1991) regarded the Tetrablemmidae and Caponiidae together as the sister-group of the Dysderoidea, but Coddington et al. (1994) place them as sister to the Dysderoidea, thus including the Tetrablemmidae.“. According to RAMIREZ (2000) Tetrablemmidae is a member of the Pholcoidea (under Scytodoidea), like the opinion of WUNDERLICH (2004: 645).

I regard the Caponiidae and the Tetrablemmidae as members of different superfamilies: The Caponiidae as a basal family of the dysderid branch of the Dysderoidea and the Tetrablemmidae as a member of the Pholcoidea, related to the Pholcidae, see below and the paragraph „Discussion“. Further basal members of the dysderoid branch may be the families Trogloraptoridae and Periegopidae, see below, the family Periegopidae.

**Distribution of the Caponiidae:** Extant: The Americas, Southern Asia, Africa. Fossil: Miocene (Dominican amber, see WUNDERLICH (1988)); no report of the Mesozoic up to now.

The following characters are SHARED by the Caponiidae and the Tetrablemmidae:

(a) The existence of a medial cheliceral membrane which is widened distally (fig. 289). (Basic characters: Both families are ecibellate, haplogyne, and possess an unpaired tarsal claw).



(b) Losses/reductions: Losses of: Leg bristles, the tarsal claw of the ♀-pedipalpus, marginal teeth of the fang furrow. Tendency to the reduction of the number of the eyes (to 6, 4, 2 or even a single one) (\*\*), strong reduction of the colulus (loss in the Caponiidae), of the fovea, and reduction of the lungs (loss in the Caponiidae).

**Discussion:** In general losses of characters/structures are of relatively weak taxonomical value. LUNGS exist in almost all members of the haplogyne spiders (lost besides in the Caponiidae in the Ochyroceratidae s. str. and in the Telemidae). The tracheal system is reduced or even lost several times independently. The reduction of the respiratory system (and other reductions/losses) are most likely caused by dwarfism in certain Tetrablemmidae.

The existence of partly FUSED BASAL CHELICERAL ARTICLES, a medial CHELICERAL LAMINA and a distal CHELICERAL LOBE (fig. 289) are typical characters of the superfamilies Filistatoidea and Pholcoidea; fused chelicerae exist e. g. in several taxa of the families Ochyroceratidae, Pholcidae, Psilodercidae and Sicariidae, see fig. F; a distal cheliceral lobe is QUITE STRONGLY developed – convergently evolved in my opinion – (a) in the Caponiidae (fig. 289) and (b) in the Tetrablemmidae.

TARSAL AND METATARSAL TRICHOBOTHRIA (see also below): Several TARSAL (as well as several metatarsal) trichobothria of the Caponiidae (fig. 291): They are completely absent in the Tetrablemmidae as well as in other haplogyne spiders with the exception of two extinct Cretaceous families of the Archaeoidea (= Palpimanoidea): The Lagonomegopidae and in the Micropalpimanidae, the lagonomegopid branch of the Archaeoidea. This character is shared by Archaeoidea and Caponiidae besides the following further characters, which are all absent in the Tetrablemmidae and other Dysderoidea except the Caponiidae (with few exceptions/“reversals”):

- strongly bent fangs (fig. 289),
- only slightly or fairly thickened articles of the male pedipalpus,
- a long/large cymbium which may hide parts of the bulbus,
- dense or even brush-like hairs of the ♂♀-pedipalpal tarsus, see the fig. 294,
- a ground living life style and free hunting behaviour (no capture web building),
- no egg-carrying behaviour by females, in contrast to the members of the „female egg carrying branch“ which includes the Tetrablemmidae, see WUNDERLICH (2004: 645),
- feeding on spiders: At least some taxa of the Caponiidae as in almost all members of the Archaeoidea.

Note: Strongly converging gnathocoxae of the Caponiidae (fig. 289) is a frequent character of the Haplogynae; lengthened anterior patellae are typical characters of several Archaeoidea and of the Dysderidae as well.

In the Tetrablemmidae – in contrast to the Caponiidae – FURTHERMORE exists (see directly below):

- a quite different respiratory system,
- large/various opisthosomal scuta,
- a long/protruding clypeus (rather similar to other Pholcoidea),
- usually modifications/outgrowths of the male chelicerae (occasionally of the clypeus or the eye region) (rather similar outgrowths exist in the Pholcidae),
- no cheliceral stridulatory files (like in numerous Pholcidae),

- egg-carrying behaviour by females – see KOH & MING (2013: Photo p. 251) – (like in the members of the Pholcoidea).

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(\*) I did not find a designation/diagnosis of a SUPERfamily Caponoidea in the paper by LEHTINEN (1967).

(\*\*) Within the Caponiidae and the Tetrablemmidae the highest intrafamilial variability in the number of eyes in spiders exists.

**Conclusions:** (1) In spite of numerous convergences with the superfamily Archaeoidea (= Palpimanoidea) the family Caponiidae is regarded here as a member of the superfamily Dysderoidea (and not of a member of a separate superfamily or related to the Tetrablemmidae or to the Archaeoidea). – (2) Apparently Caponiidae and Dysderidae are related; both families share e. g. the long anterior patellae, intracoxal sclerites, a compact eye field and – basically – an orange-red colour of prosoma and legs; members of both are hunters. Differences of both families (see the diagnosis of the Caponiidae above) exist in the eyes, the spinnerets, the respiratory system as well as in the absence of cheliceral files and several tarsal and metatarsal trichobothria in the Dysderidae. According to the existence of cheliceral files and the basal existence of eight eyes the Caponiidae may be the most basal family of the dysderid branch; the existence of numerous tarsal and metatarsal trichobothria (in an irregular position) is regarded as a „reversal“ combined with multiplication, see below (\*). – (3) The family Tetrablemmidae is surely not strongly related to the Caponiidae but it is a member of the „female egg-carrying branch“ as well as of the „branch of capture web dwellers“ of the superfamily Pholcoidea, a member of the pholcid branch, and related to the Pholcidae, see KOH & MING (2013: Photo p. 251), fig. F and WUNDERLICH (2004: 645).

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(\*) These trichobothria exists also in the lagonomegopid branch of the Archaeoidea (!). Losses and „regains“ of metatarsal trichobothria exist in the entelegyne families Theridiidae and Tetragnathidae: See WUNDERLICH (2011: 576).

## **(2) RELATIONSHIPS OF THE FAMILY PERIEGOPIDAE with remarks on the Trogloraptoridae**

The relationships of the enigmatic monotypic haplogyne extant family Periegopidae SIMON 1893 (New Zealand) are quite unsure, and the placing as sister group of the Plectreuridae – see WUNDERLICH (2004: 645) – appears unlikely to me at present. The main autapomorphic characters of this family may be the bipectinate anterior tarsal claws and the thick embolus.

Taxonomic history: According to JOCQUE & DIPPENAAR-SCHOEMAN (2007: 202) „The family belongs to the Scytodoidea but was suggested to be the sister-group of the Drymusidae (Forster, 1995), although it was not included in a family level cladistic analysis.“. See the list of diagnostic characters for haplogyne spiders presented by GRISWOLD et al. (2012: 79-80).

The mixture of characters – free chelicerae which bear a lamina, existence of a well developed onychium, numerous THIN leg bristles, position of the wide groove of the tracheal system more in front of the spinnerets (\*), a redbrown colour of the prosoma and a retreat as well as the absence of a capture web – does apparently not allow a sure placing of the Periegopidae in one of the described superfamilies, see fig. F.

According to the advanced position of the tracheal system, the loss of a capture web, the existence of a retreat (like, e. g., in Dysderidae), the free chelicerae, and the redbrown colour of the prosoma I place the Periegopidae with some hesitation in – or quite near to – the dysderid branch of the Dysderoidea. It is remarkable that bipectinate paired tarsal claws (a rare character!) exist in the Oonopidae and Orsolobidae of the dysderid branch and that a thick embolus exists in several taxa of this branch. Due to these characters I exclude a periegopid membership of the Pholcoidea and relationships to the Drymusidae. Furthermore a typical character of the Pholcoidea – the egg-carrying behaviour by females – is unknown, and its existence in the Periegopidae appears unlikely to me because of its life style.

The family Trogloraptoridae GRISWOLD et al. 2012 – extant, North America – is placed by these authors „as sister group of other Dysderoidea“; that means it is excluded from the dysderid branch (as well as from the segestriid branch) in which I like to include it because of the quite more basal position of the segestriid branch, see fig. F. Most of the trogloraptorid characters – e. g. the position of the median eyes, the leg position, the structure of the tarsal claws and structures of the copulatory/genital organs – are quite different from the Periegopidae, but the structures of the basal cheliceral articles and the position of the advanced tracheal system are similar. Caponiidae – see the existence of four pairs of eyes and of cheliceral stridulatory files – may be more basal within the dysderid branch than the position of the Periegopidae and Trochanteriidae.

NOTE: Retrolateral thin bristle-shaped hairs on the male anterior tibia are shared by the Periegopidae and the Eopsilodercidae, but in the Eopsilodercidae the chelicerae are fused basally, the anterior paired tarsal claws possess a single row of teeth, the legs are long and thin, leg I is longer than IV and the embolus is thin. So the retrolateral tibial bristle-shaped hairs are surely convergent developments of these families.

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(\* ) But a „posterior“ tracheal position exists according to GRISWOLD et al. (2012: 79) contra JOCQUE & DIPPENAAR-SCHOEMAN (2007: 202). The position of the tracheal system in the family Trogloraptoridae is said to be “posterior” although fig. 12 shows a position of the tracheal fold distinctly more in front of the spinnerets.

### **(3) THE FAMILY LEPTONETIDAE AND THE SUPERFAMILY LEPTONETOIDA**

„Leptonetiids don't sit easily in the haplogynae due to their apparent cylindrical gland spigots, expandable basal haematodochae, and now the cribellum in *Archoleptonata* complicates their placement even further.“ – E-mail by CHARLES GRISWOLD to the present author in February 2010.

The fossil and extant taxa have been recently treated by WUNDERLICH (2012: 182-200). The cylindrical gland spigots may be added to the derived characters p. 182, and are shared with the Entelegynae, see LEDFORD & GRISWOLD (2010). The overground three-dimensional capure web may be an apomorphic character of this branch, probably convergently developed in the Pholcoidea.

The Pholcoidea and the Leptonetoidea possess some similar characters, see WUNDERLICH (2012: 190) which I now regard as convergences. See LEDFORD & GRISWOLD (2010: 109). My current opinion of the leptonetoid relationships – related to the Archaeoidea and the Entelegynae as well – is shown in fig. F. Leptonetoidea is probably not a monophyletic taxon, see the chapter on the Leptonetoidea above.

### **(4) LOSSES, CONVERGENCES, „REVERSALS“ and MULTIPLICATIONS of selected structures in haplogyne spiders**

See the chapters on different superfamilies and the discussion above and below.

#### **Tarsal and metatarsal trichobothria** (see WUNDERLICH (2011: 573-576):

TARSAL trichobothria is an ancient character in spiders, existing e. g. in the Mygalomorpha, apparently lost in the Dipneumonomorpha, and existing within the araneomorph spiders as a „reverse“ character of the RTA-clade. In EXTANT haplogyne spiders tarsal trichobothria are extremely rare, existing only in the family Caponiidae (fig. 291).

In almost all extant and extinct haplogyne taxa which are treated here tarsal trichobothria are absent, and only a single metatarsal trichobothrium exists.

The existence of tarsal trichobothria is partly linked with the existence of more than a single metatarsal trichobothrium (\*) as demonstrated by the three of four families in question: Caponiidae, Lagonomegopidae and Micropalpimanidae (Filistatidae is an exception).

More than a single metatarsal trichobothrium exists in the following families (see fig. F):

- Filistatidae (Filistatoidea): in a single row at least in the European species (person. observ., see below (\*)). Tarsal trichobothria are absent;
- Caponiidae (Dysderoidea): in an irregular position. Tarsal trichobothria exist additionally, in an irregular position;

- Lagonomegopidae and Micropalpimanidae (Archaeoidea = Palpimanoidea), the only families of this superfamily, the lagonomegopid branch: frequently in a more or less single row. Tarsal trichobothria exist additionally, probably usually in a single row.

It appears not unlikely to me that the existence of tarsal trichobothria in the Caponiidae and within the Archaeoidea may be two cases of „reversals“ (or new developments), and the existence of several metatarsal trichobothria may be multiplications of a single one. Alternatively the tarsal trichobothria should have been lost about ten times separately within the haplogyne spider superfamilies and/or families, see fig. E.

The ALSO SPORADIC existence of more than a single metatarsal trichobothrium in entelegyne spiders may support the above interpretation: (1) In members of the superfamily Araneoidea s. l. (= Orbiculariae) the metatarsi bear only a single trichobothrium. The only exception known to me is *Allomengea scopigera* (GRUBE), in which all metatarsi bear several trichobothria (tarsal trichobothria are absent). The remaining congeneric species are not known to have more than a single metatarsal trichobothrium. (2) More than a single metatarsal trichobothrium exists only in a single taxon of the superfamily Oecobioidea: in the Hersiliidae (figs. 328-329) in which tarsal trichobothria are absent.

Both cases may be caused by multiplications of a single trichobothrium, see WUNDERLICH (2011: 574).

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 (\*) The only exceptions within the haplogyne spiders known to me are certain (all?) members of the family Filistatidae: I found several short metatarsal trichobothria (but no tarsal trichobothrium) in all European members of the genera *Filistata* and *Pritha*. Long metatarsal (but no tarsal) ones were reported and drawn of *Misionella jaminawa* GRISMADO & RAMIREZ 2000 (two trichobothria), and *Pikelinia uspollata* GRISMADO 2003 (three trichobothria). Tarsal trichobothria of the family Filistatidae – their existence has been erroneously reported by HARVEY (1995: 284) – are actually absent. Leg trichobothria of the Filistatidae are yet not well studied; they are frequently rubbed off in alcohol material but their bothria still exist. – In the Hypochilidae (Hypochilomorpha) the metatarsi bear a double row of trichobothria or a single trichobothrium, tarsal trichobothria are absent, see JOCQUE & DIPPENAAR-SCHOEMAN (2007).

**A cribellum** exists besides in the Hypochilomorpha in the haplogyne spiders (a) in the ancient Filistatidae (Filistatoidea) – see LEHTINEN (2013) and fig. G – and (b) in the derived Leptonetoidea – Archoleptonetinae (part: *Archoleptoneta*) of the Leptonetidae and Pholcochyroceridae; see also Mongolarachnidae and Juraraneidae –, two basal branches of this superfamily.

We know from extant and fossil taxa – e. g. from the Oecobiidae, Amaurobiidae and Dictynidae – that the cribellum became lost numerous times, and no indication exists for a „reversal“ or a new development. Within high haplogyne taxa one may suppose a loss of the cribellum five times (but see fig. G!): (a) In the ancestor of Dysderoidea + Pholcoidea, but see fig. G p. 287, (b) in the ancestor of the Archaeoidea (the loss may be connected with the loss of the capture web in this superfamily), and (c) in the Leptonetoidea (probably three times).

**Fused chelicerae** evolved in the Filistatidae and within the Pholcoidea: (a) in the Pholcidae of the „pholcid branch“ – widely fused – and (b) (differently and probably convergently developed) only in the basal part – in the „scytodid branch“ (= Drymusidae, Eopsilodercidae, Scytodidae and Sicariidae), see WUNDERLICH (2004: 645).

**Modifications outgrowths/clasping structures of the ♂-chelicerae** evolved mainly within the Eopsilodercidae, Pholcidae and Tetrablemmidae but also within the Ochyroceridae: Theotiminae (some *Spheocera*).

A strongly **armoured opisthosoma** evolved various times, (a) in several Archaeoidea, (b) in several Dysderoidea (Dysderidae: e. g. *Rhode*, Oonopidae: Gamasomorphinae, and Caponiidae: ventrally/laterally in the male of *Iraponia scutata* KRANTZ-BALTENS-PERGER et al. 2009 (extant, Iran)), as well as (c) in the Pholcoidea: Tetrablemmidae.

A **posteriorly displaced tracheal system** was developed independently by the Filistatidae, the Pholcoidea, the Psilodercidae, and the “LAE-clade”.

A **translocation of the alveolus to the tip of the cymbium (tarsus)** within the families in question exists mainly in certain members of the Pholcoidea: Some members of the Ochyroceratidae and Psilodercidae as well as in the Drymusidae, Eopsilodercidae and Sicariidae. It is connected with the loss of additional structures of the bulbus.

**Losses** exist in several characters (see below, „convergences“ and above, especially the family Caponiidae), and are much more frequent than „reversals“/“regains“). Convergent losses are frequent, especially of the cheliceral files, the anterior median eyes, the leg bristles, the lungs, and additional structures of the bulbus after their development e. g. in the “LAD-clade”.

The **anterior median eyes** exist in the Caponiidae (only in basal taxa), the Filistatidae, the Pholcidae (only in basal taxa) and in the Plectreuridae (basically: in the Plectreurinae; they are lost in the Diguettinae). In basal Caponiidae and basal Pholcidae the eye triad retained.

**Cheliceral stridulatory files connected with stridulatory picks of the pedipalpal femur** exist in the following taxa which are treated here: (a) Dysderoidea: The segestrid branch: Plectreuridae (s. l.); (b) Dysderoidea: The dysderid branch: Caponiidae; (c) Pholcoidea: Sicariidae, several Pholcidae: The most basal subfamilies, as well as some Ochyroceratidae (published by BRIGNOLI); (d) Archaeoidea: Most families; (e) Leptoneoidea: Rarely.

Remarks: (1) Numerous losses of these structures exist as well as numerous convergent developments. We know, e. g., several losses within the family Linyphiidae of the superfamily Araneoidea. On the other hand we know sure convergent developments of these structures, e. g. within the family Tetragnathidae of the Araneoidea. – (2) Most extant members of the classical Haplogynae are ecribellate, and their scaly prosomal cuticula may be a good pre-condition for the development of stridulatory files. To my knowledge only very rarely cheliceral stridulatory files exist in cribellate spiders (e. g. in some Hypochilomorpha, see the chapter on this taxon above) which have a different structure of the prosomal cuticula.

**Lungs** are lost in the Caponiidae, Ochyroceratidae (s. str.) (not in the Psilodercidae), Telemidae; they are strongly reduced – especially in minute – Tetrablemmidae.

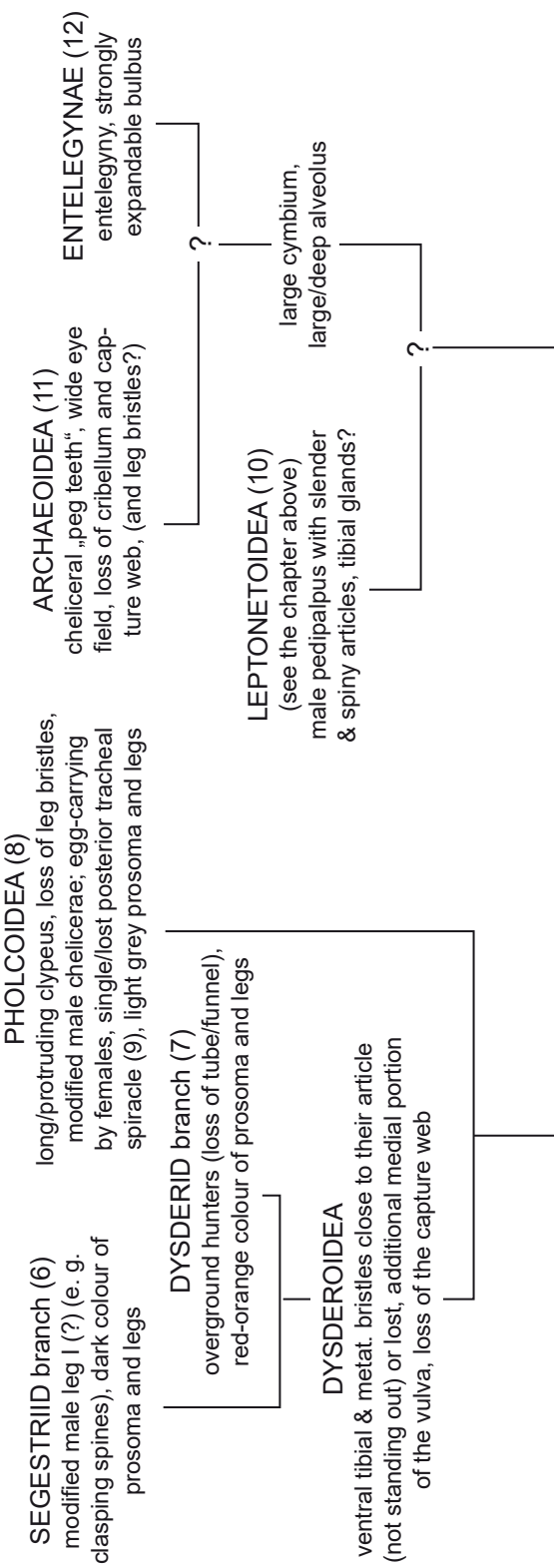


The **unpaired tarsal claw** has been lost (a) in the Dysderidae: Dysderinae and Oonopidae + Orsolobidae of the Dysderoidea and (b) in the Sicariidae of the Pholcoidea. It may be strongly reduced (or probably even absent) in the families Epsilodercidae, Ochyroceratidae and Scytodidae of the Pholcoidea.

**Leg bristles** are frequently lost in haplogyne spiders: (a) in the Plectreuridae (bristle-shaped hairs exist in the Diguetiinae) of the segestriid branch of the Dysderoidea, (b) in the Caponiidae and in numerous Dysderidae as well as in several Oonopidae and Orsolobidae of the dysderiid branch, (c) apparently apomorphic in the Pholcoidea: Drymusidae, Epsilodercidae (note the occasional existence of bristle-shaped hairs, Tetrablemmidae, Pholcidae, Ochyroceratidae, Psilodercidae, Scytodidae (very rare „reversals“ on the legs III/IV exist in the last four families), Sicariidae: Loxoscelinae (in the Sicariinae numerous short spines but no bristles exist), (d) in most taxa of the Archaeoidea except in certain members of the lagonomegopid branch and the Huttoniidae (regain in the Huttoniidae?).

Frequently the loss of the ancient **underground tube/funnel** is connected with the development of a three-dimensional (overground) capture web: Within the Hypochilidae, within the Pholcoidea (existing not only in the families of the „three-dimesional capture web branch“, see WUNDERLICH (2004: 645), the Leptonetoidea (and furthermore as apomorphy of the RTA-clade). I regard the absence of a three-dimensional capture web of the Dysderoidea (they are basically ground spiders) and of the Archaeoidea (in my opinion they most probably are basically dwellers of higher strata of the vegetation) as convergent losses while „funnels“ may still exist in families like the Filistatidae.

**(5) THE RELATIONSHIPS OF THE HAPLOGYNAE, THEIR SUPERFAMILIES AND SELECTED FAMILIES**





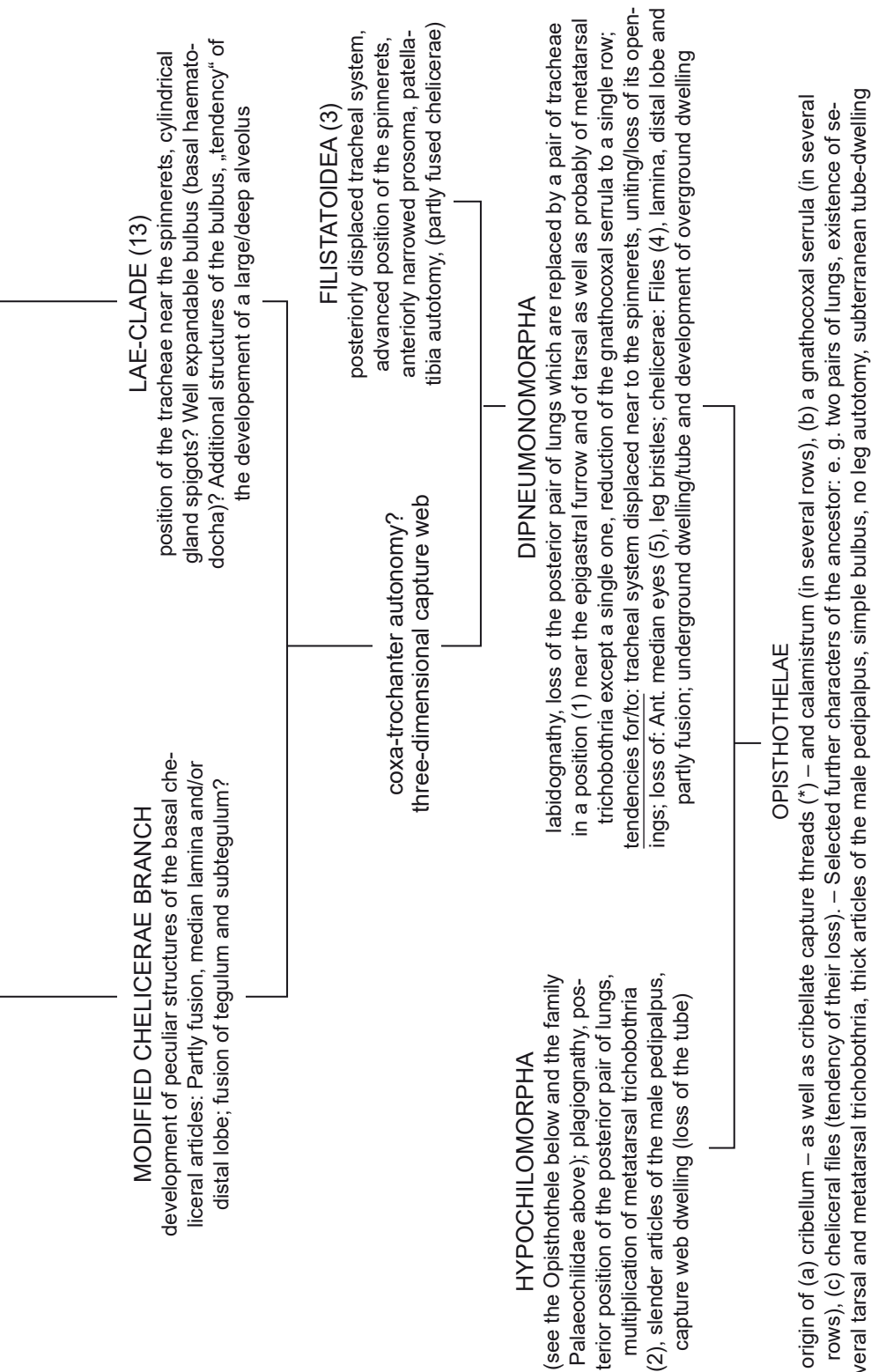


Fig. F. POSSIBLE RELATIONSHIPS OF THE HAPLOGYNE SPIDERS (\*), and their main branchings (Superfamilies and selected families: See above). **See the alternative fig. G!**

(\*) Included are the Hypochilomorpha s. l. and the classical Haplogynae: Filistatoidea, Dysderoidea, Pholcoidea, Leptonetoidea and Archaeoidea (= Palpimanoidea). „Haplogynae“ is a polyphyletic taxon in my opinion. Archaeoidea has – at least partly – probably a secondary haplogyne stage.

Remarks: (a) Only few of the numerous – partly quite unsure! – convergences, reversals and losses are noted. (b) „Tendencies“ mean the existence of genetical (pre-) dispositions. They include convergences and losses.

#### NOTES:

(1) The ANTERIOR – but not the posterior – position of the tracheal spiracle corresponds to the anterior position of the posterior pair of lungs in the more basal Mygalomomorpha. It is remarkable that in the Hypochilomorpha the posterior pair of lungs has a quite POSTERIOR position compared with the Mygalomorpha.

(2) Families of this branch: Thaididae (= Austrochilidae), Gradungulidae and Hypochilidae, see above: The chapter on the Hypochilomorpha.

(3) Only the cribellate family Filistatidae.

(4) Retrolateral cheliceral stridulatory files (as well as prolateral stridulatory picks of the pedipalpal femur in both sexes) exist in the Plectreuridae, recognized by me in the subfamilies Plectreurinae (a single pick) and Diguatinae (several picks, fig. 288) (apparently overlooked by previous investigators). Plectreuridae is the single member of the plectreurid subbranch in which leg bristles are absent or quite rare on the male leg I. In the second the – segestriid subbranch – (well developed) leg bristles exist, and cheliceral files are absent. This subbranch includes the families Segestriidae and the extinct Plumorsolidae.

(5) The basal number of EIGHT EYES remains in the following taxa: Dysderoidea: Plectreuridae: Plectreurinae of the Segestriid branch and some species of the family Caponiidae of the dysderid branch, as well as certain members of the Pholcidae of the Pholcoidea.

(6) The colour of the prosoma varies from medium to dark grey and dark brown.

I regard the funnel (hiding of the spiders in a subterranean retreat) as an ancient character of spiders, still existing in the segestriid branch, but not as a derived „regain“. A modified male anterior leg developed probably only in – in the geological sense – younger taxa like in the subfamily Ariadninae.

Families: (a) Plumorsolidae (extinct) and Segestriidae: Leg III directed forwards in both families (see above), leg bristles numerous, and cheliceral lamina lost; (b) Plectreuridae, including the subfamilies Plectreurinae and Diguatinae which share: A strongly reduced/absent posterior tracheal system, existence of – quite fine and narrow – retrolateral cheliceral stridulatory files in both sexes as well as prolateral stridulatory picks of the pedipalpal femur (several picks in the Diguatinae, fig. 288), a distal cheliceral outgrowth which is pointed, well developed and distinctly sclerotized, loss of leg bristles (bristle-shaped hairs exist in the Diguatinae) as well as a peculiar actual distribution in North and Central America but a wide distribution in Eurasia in the Eocene and in the Mesozoic. – NOTE on the family Periegopidae (extant, New Zealand): See the remark at the superfamily Pholcoidea above.

(7) The families Caponiidae (probably the most basal one, see above), Dysderidae (they have quite long patellae), Oonopidae, Orsolobidae (in most members of these two families bipectinate paired tarsal claws exist), the recently described Trogloraptoridae of North America, and probably the family Periegopidae (see above). In the CAPONIIDAE – the single family of the caponiid subbranch – several tarsal (fig. 291) and metatarsal trichobothria exist as well as lateral cheliceral files, and in certain basal members the basic number of eight eyes. These three characters are completely absent (lost) in the second, the dysderid subbranch. – GRISWOLD et al. (2012) regarded the family TROGLORAPTORIDAE as sister group of the dysderoid branch. In my opinion this advanced six-eyed family, has a position WITHIN the dysderid subbranch, and may be more related to the Dysderidae, see above (the family Periegopidae).

(8) The families Drymusidae, Eopsilodercidae, Ochyroceratidae s. str. (excl. Psilodercinae and probably including Theotiminae), Psilodercidae, Pholcidae, Scytodidae, Sicariidae (Loxoscelinae and Sicariinae) and Tetrablemmidae which possesses a darker (reddish) colour because of its strong sclerotization in contrast to related families. (Periegopidae FORSTER 1995: See the remark at the superfamily Pholcoidea above). Leg bristles exist – in my opinion as „reversals“ only on tibia/metatarsus III/IV in VERY FEW members of the Ochyroceratidae (*Speocera*), Pholcidae and probably Scytodidae. In the Sicariidae: Sicariinae no true leg bristles but short spines exist. – The unpaired tarsal claw is lost in this branch in the Sicariidae. A strongly armoured opisthosoma exists in the Tetrablemmidae. (This character may be mistaken for fairly similar Oonopidae: Gamasomorphinae of the Dysderoidea).

(9) The position of the posterior spiracle is quite variable in this branch; furthermore it may be strongly reduced or even absent (in the Pholcidae).

(10) At least three or four families: (a) Leptonetidae (extant and extinct, 6 eyes, cribellate – the extant *Archoleptoneta* (part.) but see the extinct *Palaeoleptoneta* – or ecribellate); the large/wide questionable colulus („pseudocribellum“) of *Palaeoleptoneta* points to a „recent“ cribellate ancestor, (b) Praeterleptonetidae (extinct, 8 eyes, ecribellate), (c) Pholcochyroceridae (extinct, 8 eyes, cribellate); see above, the superfamily Leptonetoidea, and probably (d) probably Mongolarachnidae and Juraraneidae (extinct, cribellate). – Praeterleptonetidae and Pholcochyroceridae (as well as probably Mongolarachnidae and Juraraneidae) may be members of a separate branch in which a large/deep alveolus exist and tibial glands may be absent.

(11) (= Palpimanoidea). Eight families. Several tarsal and metatarsal trichobothria exist in the extinct lagonomegopid branch (the families Lagonomegopidae and Micropalpimanidae). See the superfamily Archaeoidea (= Palpimanoidea) above.

(12) Branchings of the Entelegynae are supposed in this order: (a) Eresoidea (cribellate, only Eresidae), (b) Oecobioidea (cribellate or ecribellate, with the latest origin of FEATHERY HAIRS, Hersiliidae and Oecobiidae), (c) Araneoidea s. l. (= „Orbiculariae“) (incl. the ecribellate Araneoidea s. str. and the cribellate „Deinopoidea“: Deinopidae, Uloboridae and the extinct Mongolarachnidae), (d) **the first defined DTA-clade** (the **dorsal tibial apophysis** clade) which is characterized by the existence of a DORSAL tibial apophysis of the male pedipalpus, probably basically by the absence of tarsal trichobothria („regain“ in the Amaurobiidae) as well as the existence of ground-living

funnel-dwelling (probably a plesiomorphic character). This clade includes e. g. Amaurobiidae, Phyxelidae, Titanoecidae, Nicodamidae and probably the enigmatic Dictynidae, and (e) the most diverse RTA-clade (the retrolateral tibial apophysis clade) in which numerous metatarsal and tarsal trichobothria exist. Two main groups are included in this clade: (a) the three-clawed *Trionycha* which are mainly capture web dwellers (so the frequent cribellate spiders (\*)), with the exception of certain ecribellate Zoropsidae s. l.) but also including (ecribellate) hunters like Lycosidae and Zodariidae; (b) the derived *Dionycha* which all are ecribellate and mainly hunters like, e. g., the Salticidae (few Salticidae are dwellers of capture webs in a “functional reverse”).

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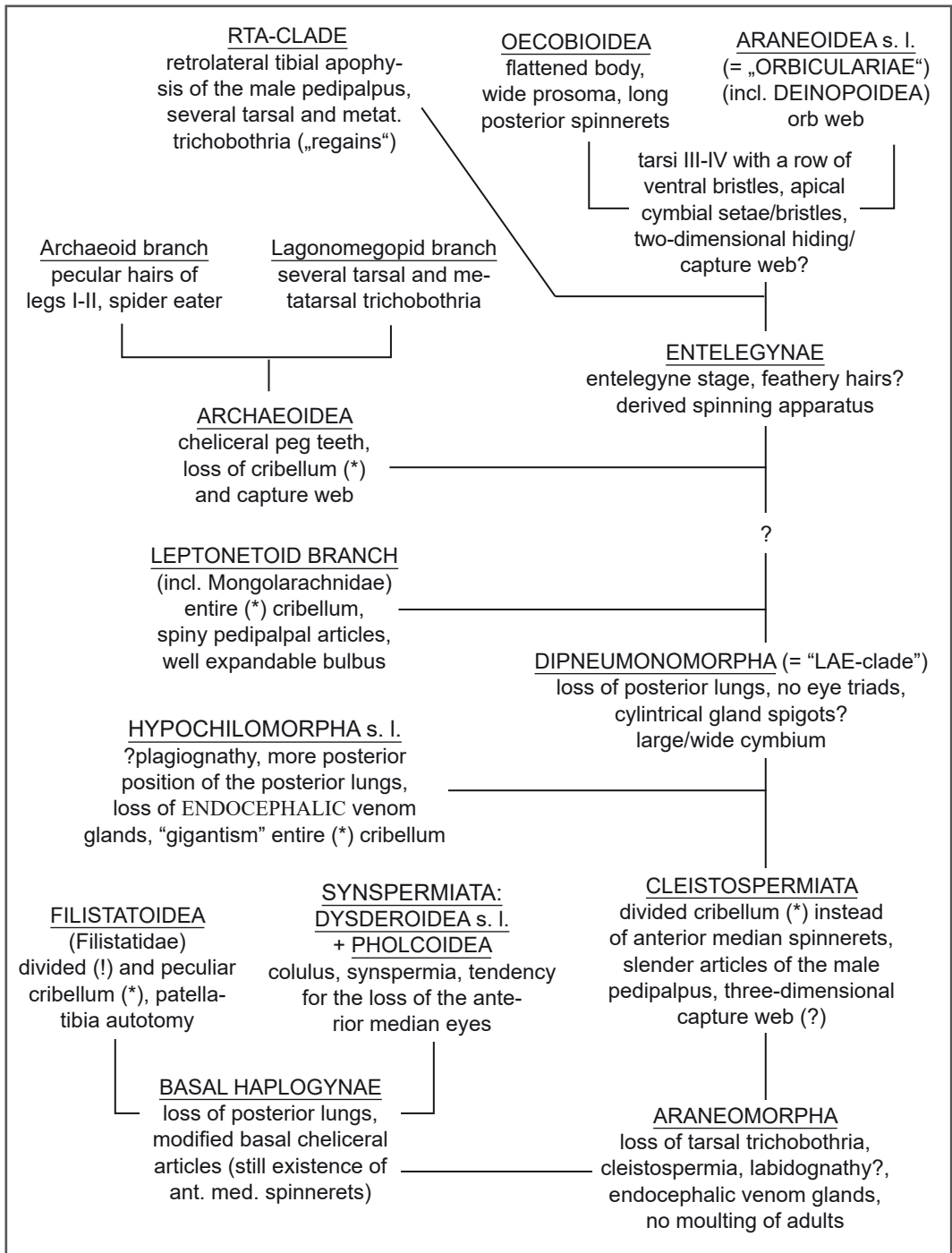
(\*) In most cribellate spiders a capture web exists but in few families exist signal lines originating from the entrance of a funnel (e. g. in the haplogyne Filistatidae) or a hiding web (in the Oecobiidae). Probably sticky cribellate threads originated with the Opisthothelae from the entrance of a funnel/retreat in a similar kind, and developed in a second step to a three-dimensional capture web, so probably in the Hypochilidae or its relatives for the first time.

(13) **The new introduced LAE-clade**, the Leptonetoid-Archaeoid-Entelegynae-clade includes the huge branch Entelegynae as well as the haplogyne superfamilies Leptonetoidea (which are capture web dwellers) and the Archaeoidea (= Palpimanoidea) (in which a capture web is absent and which are – at least the extant spiders – mainly sit-and-wait predators of spiders; the existence of cylindrical gland spigots is unknown to me). The ancestor of this clade lost the posterior pair of lungs and the triad eye position; it was cribellate in my opinion (the cribellum is lost in the Archaeoidea), and developed additional structures of the bulbus convergently to certain taxa of the modified chelicerae branch like Pholcidae and Dysderidae.

NOTES: (1) In the haploid superfamilies Leptonetoidea and Archaeoidea (= Palpimanoidea) the chelicerae are free, a cheliceral lamina and distal lobe are absent, the articles of the male pedipalpus are slender or fairly slender (certain Archaeoidea), and the ventral tibial and metatarsal I-II bristles (they may be absent) stand out from their article in contrast to members of the Dysderoidea in which the position of these leg bristles in the usual position is close to their article. Both taxa appear more derived in some respect than the Dysderoidea and Pholcoidea in which basically a paired tracheal opening, tube/funnel-dwelling, as well as thick articles of the male pedipalpus exist. Therefore these superfamilies are not included here in the branch of Dysderoidea + Pholcoidea, see Fig. F, and compare fig. G.

(2) In the Leptonetidae (Archoleptonetinae, Leptonetinae and Palaeoleptonetinae; all are six-eyed) a small alveolus still exists in contrast to the eight-eyed Praeterleptonetidae, Pholcochyroceridae and Mongolarachnidae (the eye number in the Mongolarachninae is unknown). Probably the small alveolus regains in the Leptonetidae, or – based on this character – this family is the member of a less derived branch besides the more evolved branch of Praeterleptonetidae + Pholcochyroceridae.

(3) The existence of feathery hairs (= brachiate hairs) already in the Hypochilomorpha has been published e. g. by LEHTINEN (1967: 283, fig. 1) but I did not find such hairs in this taxon, and I suppose that the origin of these hairs happened two steps later than shown in fig. 3 by LEHTINEN. In my opinion fig. 148 D in GRISWOLD et al. (2005) shows feathery bristles/spines but not hairs. So probably feathery hairs originated first with the Entelegynae.



**Fig. G.** Alternative suggestion of the suprafamilial branchings of the Araneomorpha, based on few important characters which were selected subjectively. See the cladogram presented by ESKOV & ZONSHTEIN (1990: 135 (fig. 1) as well as fig. F, and the proposed new classification of the Araneae p. 46. The family Eresidae is not included.

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(\* ) I suppose here that the cribellum evolved twice (in the Filistatidae and in the precursor of the Hypochilomorpha (of the Cleistospermiata n. taxon), see below as well as the cladogram presented by ESKOV & ZONSHTEIN (1990: 135, fig. 1), and LEHTINEN (2013). The cribellum should have been divided at its origin (because evolved from a PAIR of spinnerets) but entire in certain derived taxa. – I can not agree with the derived position of the Mesothelae in the cladogram p. 135 and also not with the position of the Filistatidae as sister group of the more „primitive“ Mygalomorpha; see fig. G. I suppose here that the anterior median spinnerets were replaced several times: (a) in the Synspermiata by a colulus, (b) by a cribellum: in the Filistatoidea and (c) by a cribellum in the Cleistospermiata. The name “divided cribellum clade” in the sense of certain authors is not justified for “higher” spider taxa. The eye tubercle of the Filistatidae is similar to certain Mygalomorpha and exists also in the family Hersiliidae. I do not want to exclude with certainty that the branch “Basal Haplogynae” may be diphyletic. Probably plagiognathy evolved in the Hypochilomorpha.

Note: The family Filistatidae was placed with/near the Mygalomorpha already in the 19th Century by WALCKENAER and C. KOCH, see SIMON (1892: 255)

#### Further discussion:

(1) I suggest the following plesiomorphic characters of the Araneomorpha which are treated here (apomorphic characters: see above, fig. G; labidognathy appears not quite sure to me):

- two pairs of lungs,
- four pairs of spinnerets (cribellum and colulus absent),
- eye triads,
- haplogyne stage,
- coenospermia,
- thick articles of the male pedipalpus,
- tube dwelling,
- no capture web (?).

(2) Most important – unbelievable? impossible? – in this cladogram are ...

(a) the derived position of the Hypochilomorpha in contrast to traditional cladograms.  
– Remark: According to my hypothesis the Hypochilomorpha (s. str.!) lost the ENDOCEPHALIC part of their venom glands. This loss may be connected with the existence of large basal chelical articles of this branch.

(b) The quite basal position of a particular branch of haplogyne spiders: a „Microorder“ which I call „Basal Haplogynae“. Its precursor never had a cribellum: in my opinion its anterior median spinnerets changed directly to a colulus: in the Synspermiata (= Dysderoidea s. l. + Pholcoidea) resp. to a cribellum: in the Filistatoidea. – See ESKOV & ZONSHTEIN (1990). – Mesothelae and Mygalomorpha possess Coenospermia. The existence of coenospermia also in the Filistatidae is regarded by MICHALIK & RAMIREZ

(2014) as a regain but it appears more likely to me that this form of sperm transfer is a plesiomorphic character of the Filistatidae and chanced two times: (a) in the Synspermiata sensu MICHALIK & RAMIREZ – Dysderoidea + Pholcoidea –, and (b) in the Cleistospermiata (which is not identical with the Entelegynae sensu MICHALIK & RAMIREZ).

(3) I assume twice the origion of a cribellum and twice the loss of the posterior pair of lungs (a third loss exists in certain Hypochiloidea s. l.: *Austrochilus* and *Thaïda*).

(4) In the quite important step to the Cleistospermiata **n. taxon** the anterior median spinnerets were replaced by a cribellum.

(5) Regains (like of tarsal trichobothria) and of convergences: See the discussion above.

(6) I do not think that the Archaeoidea (= Palpimanoidea) is basically an entelegyne taxon; see HUBER (2004). Members of the advanced Cretaceous lagonomegopid branch possessed tarsal trichobothria and a ~ retroapical tibial apophysis of the male pedipalpus; some of their taxa had furthermore strong leg scopulae which hairs are different from the flattened scopula hairs of the Palpimanoidae, see above. An unknown extinct member of – or a cribellate member near to – the „lagonomegopid branch“ may be identical with the still enigmatic root of the RTA-clade.

## ENTELEGYNAE

### Superfamily uncertain:

Family **BURMASCUTIDAE** WUNDERLICH 2008

See WUNDERLICH (2008: 624-627, figs. 93-106, photos 99-103) and (2012: 210).

Type taxon (the only known one) in Burmite: *Burmascutum aenigma* WUNDERLICH 2008.



**Diagnostic characters** (♂♀): Spinnerets in an anterior position, opisthosoma strongly armoured, 8 eyes in two wide rows, no (♂) or only few thin leg bristles, tarsal claws probably toothless, large anal tubercle bearing strong basal bristles, epigyne with a sclerotized plate, bulbus with one or two apophyses and a long questionable conductor.

The **relationships**: are quite unsure, see WUNDERLICH (2008: 624-625); really a member of the Entelegynae?

**Distribution**: Mid Cretaceous amber forest of Myanmar (Burma).

## SUPERFAMILY OECOBIOIDEA

Mesozoic Oecobioidea have been rarely reported but regarding their well-known Cretaceous taxa – which are mainly known in Burmite – this superfamily was quite diverse at that time, and probably even one or two undescribed extinct families existed, see the tab. below, the new oecobiid subfamily Retrooecobiinae and the dubious relationships of the genus *Zhizhu* SELDEN et al. 2015.

Two well diagnosed families – regarding their posterior spinnerets, the shape of their clypeus, their anal tubercle and their metatarsal trichobothria, but see below – are known from this superfamily: Hersiliidae and Oecobiidae; Oecobiidae is much more diverse than Hersiliidae.

## Phylogenetics

### Fossils may teach us ...

(1) About the origin and the sequence of „diagnostic family characters“ – which evolved STEP BY STEP – as well as about LOSSES and CHANGES of characters within a long phylogenetic history (\*), see WUNDERLICH (2004: 835), and below.

Remarkably LOSSES OF CHARACTERS are frequent, and more losses exist than noted below: The cribellum became lost within the Oecobiidae in the Mizaliinae, Retrooecobiinae and Urocteini, a large anal tubercle – and probably the median spinnerets – have been lost in the Retrooecobiinae n. subfam., large posterior spinnerets are reduced in the Retrooecobiinae. The changes of the kind of leg autotomy are problematical and dif-

difficult to interpret, see WUNDERLICH (2004: 837); a coxa-trochanter autotomy appears now likely to me as a plesiomorphic character of the superfamily.

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(\*) Besides the Leptonetoidea (see above) and the Uloboridae (see below) the taxa of the Oecobioidea – especially the Oecobiidae – may be the best taxon for a study in this respect.

(2) About **different family diagnoses** if fossil taxa are included:

A diagnosis should be based – if possible – on apomorphic characters mainly. Further typical characters have to be used which are different from related/similar taxa. – Oecobiidae: Two of the typical characters of extant Oecobiidae are absent in the new extinct subfamily Retrooecobiinae: The quite large and hairy anal tubercle and the long posterior spinnerets. Therefore the nose-shaped protruding clypeus and the quite weak basal cheliceral articles are the main and best usable diagnostic characters of extant AND extinct members of the family Oecobiidae, see the list of its apomorphic characters below.

At the beginning of this reflection it has to be decided: Which characters are symplesiomorphies or synapomorphies of the two families in question; compare certain differences to the cladogram given by WUNDERLICH (2004: 835).

Symplesiomorphies: The existence of feathery hairs, a cribellum, ventral tarsal/ metatarsal III-IV bristles, – probably – a coxa-trochanter leg autotomy, a relatively short leg III, at least one metatarsal trichobothrium (several trichobothria probably as a „regain“ in the Hersiliidae) in a distal position (figs. 328-329), thick/stout articles of the male pedipalpus (mainly patella and tibia), a median apophysis, two pairs of receptacula seminis, and – probably! – a three-dimensional capture web (known from primitive extant species of the Hersiliidae as a reversal?).

The synapomorphic characters of the superfamily may be:

- a flattened body,
- a wide prosoma (ca. as wide as long, fig. 300; but see *Retrooecobius*),
- a mediograde position of the legs,
- quite long posterior spinnerets (photos) (but see figs. 318-319 of *Retrooecobius*),
- a large anal tubercle (figs. 298, 305) (small in *Retrooecobius*),
- existence of apical cymbial bristles (lost e. g. in Mizaliinae and Retrooecobiinae),
- a „sit-and-wait“ predatory life style in extant taxa,
- prey fixing by rapid circling in extant taxa.

Furthermore the apomorphic characters/losses of these families should be listed/ discussed:

(1) Apomorphic characters of the Hersiliidae:

- extremely long posterior spinnerets (photos),
- raised eye field with strongly recurved posterior eye row,

- loss of the cribellum,
- patella-tibia leg autotomy? (\*). Apparently convergently evolved in certain taxa of the Oecobioidea. In four Cretaceous Hersiliidae specimens I found no leg autotomy (!).

## (2) Apomorphic characters of the Oecobiidae:

- existence of a ventrally protruding, usually even „nose-shaped“ clypeus (figs. 300, 313),
- small (slender AND short) basal cheliceral articles (fig. 322),
- a large anal tubercle which bears a fringe of long hairs (figs. 298, 305); both are reduced in the Cretaceous Retroecobiinae n. subfam. (figs. 318-319) but well developed/large, and hairs furthermore divided longitudinally (only!) in the extant taxa,
- loss of feathery hairs,
- relatively long leg III,
- loss of cheliceral teeth (?) (\*),
- probably small/reduced body size (compared to the related Hersiliidae) but secondary „gigantism“ in the Oecobiinae: Urocteini as a „reversal“,
- plate-shaped and more or less sclerotized epigyne (\*),
- only a single pair of – thin-walled – receptacula seminis (\*),
- (loss of a three-dimensional capture web?); development of a flat, tent-shaped hiding web consisting of two layers and surrounded by signal lines (\*).

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 (\*) Unknown in fossil taxa.

## **Family OECOBIIDAE BLACKWALL 1862 Family key no. 22**

Diagnostic apomorphic and plesiomorphic characters: See above.

Interestingly the family diagnosis has to be strongly modified if extinct (Mesozoic) taxa are included:

The most typical/apomorphic characters of extinct AND extant members of the family Oecobiidae are the prolonged anterior-ventral margin of the clypeus (figs. 300, 313) which even may be „nose-shaped“, the weakly developed basal cheliceral articles, and the relatively long legs III (photos), see above.

Members of this diverse family are cribellate or cribellate; the calamistrum may be one or double-rowed, and may be strongly reduced in the male sex like the median spinnerets, too. In the Eocene and Cretaceous Mizaliinae a huge structure may be a large colulus – or probably a functionless „pseudocribellum“ (fig. 298)? The leg autotomy is quite variable within this family but constant within each subfamily, see WUNDERLICH (2004: 836-837). In extant taxa a patella-tibia leg autotomy exists but in the extinct Mizaliinae a leg autotomy may be absent, and in the Retroecobiinae n. subfam. a

coxa-trochanter autotomy exists. A large anal tubercle bearing a fringe of long hairs as well as large (lateral) posterior spinnerets are absent in this Cretaceous new subfamily (the anterior spinnerets are largest).

Remark: Because of their rareness – and usually more or less decomposed bad/ incomplete preservation – the diagnoses and the relationships of most Cretaceous higher taxa are only insufficiently known.

Selected characters of the Cretaceous subfamilies of the Oecobiidae and a questionable member of the Oecobiioidea:

See also below: Oecobiidae indet., ♂ in Burmite, F2737/BU/CJW, Oecobiidae indet. sensu PENNEY (2002), and the genus *Zhizhu* SELDEN et al. below (Deinopoidea?).

	Oecobiidae: Mizaliinae	Oecobiidae: Lebanoecobiinae	family?	Oecobiidae: Retroecobiinae
taxa	<i>Zamilia</i>	<i>Lebanoecobius schleei</i> (♂) WUNDERLICH 2004	?Oecobiioidea indet. (♂), F2006/JB/CJW	<i>Retroecobius</i> (*)
distribution	Burmite	Lebanon amber	Jordan. amber	Burmite
cribellum/ calamistrum	-- (**)	+ single-rowed	-- (?)	--
leg autotomy	absent?	patella-tibia	?	coxatrochanter

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 (\*) The only oecobioid taxon with the prosoma distinctly dome-shaped (fig. 314, photo), and the small anal tubercle bears only rather short hairs.

(\*\*) Existence of a very wide colulus – or functionless pseudocribellum? – (♂), similar to *Mizalia* (Mizaliinae) in European Eocene ambers.

(a) A spider in **Jordanian amber**:

?Oecobioidea indet.

2008 Oecobioidea indet., -- WUNDERLICH, Beitr. Araneol., 5: 566, 623, 668: Figs. 90-92 (♂).

Material: 1♂ in Early Cretaceous amber from Jordan, F2006/JB/CJW.

The relationships of this taxon remain unsure, see the tab above. Metatarsus IV is straight, a calamistrum – and thus a cribellum – are most probably absent, apical cymbial bristles are absent in contrast to *Lebanoecobius* and extant *Oecobius*. In contrast to my previous statement feathery (two-dimensional) hairs are apparently absent in the holotype, the only known specimen of this taxon; the order of the legs is I/II/IV/III.

(b) A spider in **Lebanese amber**:

*Lebanoecobius schleei* WUNDERLICH 2004 (Lebanoecobiinae WUNDERLICH 2004)

See WUNDERLICH (2004: 827-830, figs. 26-31) and the tab. above.

In this cribellate taxon the position of the posterior spinnerets is divergent, a patella-tibia autotomy exists like in extant Oecobiidae (!), the cymbium bears apical bristles like in extant Oecobiidae (!); the structures of the bulbos are simple.

(c) A spider in **amber from New Jersey**:

PENNEY (2002: 714-716, fig. 4, pl. 2 fig. 2) described under ?*Oecobius* sp. an incompletely preserved female. The shape of opisthosoma and legs appear similar to the genus *Zamilia* (see directly below) but a well developed calamistrum exists. Cretaceous

spiders – and even spiders from the Paleogene – are completely unknown and the legs appear more spiny in the female in question than in *Oecobius*. Therefore I prefer this taxon to list under Oecobiinae indet. but not under ?*Oecobius* sp. but I do not want to exclude that it may be a member of the Mizaliinae.

(d) Spiders in **amber from Myanmar** (Burma):

***Zamilia*** WUNDERLICH 2008: See below (relationships).  
See also above (c) and below: 1♂ ?*Zamilia* sp. indet and 1♂ Oecobiidae indet.

**Key** to the species (♂):

- 1 Body length 3.5 mm. . . . . ?*Z. sp.* (F2672)
- Body length 1.5 mm. Metatarsus and tarsus IV bear numerous short ventral spines (figs. 296-297), the embolus describes ca. one loop (fig. 299). . . . . *aculeopectens*
- Body length 2.5-2.6 mm. No numerous short spines on leg IV. . . . . 2
- 2(1) Leg IV bears few long bristles, including ventral metatarsal and tarsal ones (fig. 303). The embolus describes two wide loops (figs. 309). . . . . *quattuormammillae*
- Leg IV bears several long bristles, including metatarsal and tarsal ones, see WUNDERLICH (2008: 668, fig. 86). . . . . *antecessor*

***Zamilia aculeopectens* n. sp.** (figs. 295-299) photos 145-146

Etymology: The species name refers to the comb-shaped (pecten lat. = comb) ventral spines (lat. aculeus) of some leg articles.

**Material**: Holotype ♂ in Mid Cretaceous amber from N-Myanmar (Burma) and two separated pieces of amber, F2715/BU/CJW.

**Preservation and syninclusions:** The spider is completely and fairly well preserved in a clear yellow piece of amber, body and pedipalpi are strongly deformed, the spinnerets are well preserved, a fissure within the amber runs through the prosoma in a transverse position and disappeared in most parts after the use of benzylbenzoat. – **Syninclusions:** Spider's threads, few Acari, a winged insect, a larger larva of a questionable Grylloidea, numerous Collembola, plant hairs and particles of detritus.

**Diagnosis** (♂; ♀ unknown): Tarsi and metatarsi bear short ventral spines (figs. 296-297); pedipalpus (fig. 299): A large median apophysis exists; the deformed embolus describes almost one loop. Body length only 1.5 mm.

**Description** (♂):

Measurements (in mm): Body length 1.5, prosomal length ca. 0.7; leg I: Femur 0.9, patella 0.3, tibia 0.75, metatarsus 0.7, tarsus 0.4, tibia II 0.7, tibia III ca. 0.6, tibia IV ca. 0.7. Colour medium brown.

Prosoma strongly deformed, wide, 8 eyes in two rows, basal cheliceral articles stout, fangs short. – Legs (figs. 295-297) mediograde, order probably IV/I/II/III, III relatively long, hairs not distinct, bristles numerous and partly long, existing from femora to metatarsi, exact number difficult to observe, a longer distal bristle of tibia I is too small for a „clasping spine“, metatarsus I with short ventral spines besides longer basal bristles, metatarsus and tarsus IV with numerous ventral spines, metatarsal IV calamistrum and preening comb absent, position of the metatarsal III trichobothrium in more than 0.9, tarsal trichobothria absent. – Opisthosoma (fig. 298) dorsally strongly deformed but ventrally distally well preserved, colulus („pseudocribellum“) large, anterior spinnerets largest but not longest, fairly stout and widely spaced, median spinnerets well developed and slender, posterior spinnerets slender, anal tubercle large, two-segmented and bearing long hairs. – Pedipalpus (fig. 299) (it is strongly deformed; bulbus and embolus have originally probably been more circular): Bulbus bearing a large median apophysis, conductor small and funnel-shaped at the tip of the embolus which describes almost one loop.

**Relationships:** See the key.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

***Zamia quattuormammillae* n. sp.** (figs. 300-309) photo 147

Etymology of the species name: quattuor (lat. = four) for the existence of probably only four spinnerets (mammillae).

**Material:** Holotype ♂ in Mid Cretaceous amber from Myanmar (Burma), F2554/BU/CJW.



**Preservation and syninclusions:** The spider is well and almost completely preserved (only the retrobasal part of the right metatarsus IV is cut off) in a yellow piece of amber, a fissure of the amber runs longitudinally through the body, the opisthosoma is dorsally artificially depressed. A posterior prosomal depression (fig.) may be artificial; its position is just in front of the opisthosomal depression. – A thin spider's thread runs sideward from the left legs of the spider. Just in front of the spider remains of a quite long-legged parasitic mite (Erythraeidae?) are preserved; a second apparently conspecific and better preserved mite has been separated from the piece of amber, F2563/BU/CJW. A Diptera and 2 tiny wingless insects are also preserved.

**Diagnosis** (♂; ♀ unknown): Leg I > II (photo), median spinnerets probably strongly reduced or even absent (fig. 305); pedipalpus (figs. 306-309): Cymbium with a transverse rim, the embolus describes probably two wide loops.

**Description** (♂):

Measurements (in mm): Body length 2.6, prosoma: Length 1.1, width 1.2; Leg I: Femur 1.25, patella 0.5, tibia ca. 1.0, metatarsus 1.0, tarsus 0.6; femur II 1.2, femur III 1.2, femur IV 1.15.

Colour dark brown, legs not annulated.

Prosoma (fig. 300, photo) slightly wider than long, smooth, a posterior depression may be artificial, clypeus nose-shaped ventrally, 8 eyes in two rows, the laterals distinctly spaced from each other, basal cheliceral articles weakly developed, other mouth parts hidden, coxae IV not widely spaced from each other. – Legs (figs 301-304, photo) only fairly long, position mediograde, feathery hairs absent, I longest, IV about the same length, III not distinctly shortest, hairs short, bristle long and fairly thick, on femora, patellae, tibiae, metatarsi and tarsis IV ventrally; leg I: Femur 4, patella 2 dorsally and 1 prolaterally, tibia 7, metatarsus few ventral spines, tarsus IV with 4 ventral bristles; metatarsus IV straight, calamistrum absent, tarsal trichobothria absent, metatarsi with a trichobothrium near its end, paired tarsal claws with long teeth, unpaired claw stout. – Opisthosoma (fig. 305, photo) 1.75 times longer than wide, covered with short hairs. Anterior spinnerets short, widely spaced, not converging, two-segmented, median spinnerets apparently strongly reduced or even absent, posterior spinnerets long, slender, widely spaced and two-segmented, colulus (or functionless „pseudocribellum“) wide, apparently partly hidden by a fold, anal tubercle very large, bearing long hairs. – Pedipalpus (figs. 306-309) with slender femur and patella, globular tibia and a wide cymbium which bears no apical bristles but a transverse rim; bulbus large, bearing a longer tegular apophysis and a bent median apophysis (these terms are provisional), embolus long, describing at least a single – but more likely two – wide loops.

**Relationships:** See the key above.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

Zamilia sp. indet.

**Material:** 1♂ in Mid Cretaceous amber from Myanmar (Burma), F2736/BU/CJW.

The male is only fairly well preserved in a yellow piece of amber, apparently partly decomposed, the dorsal part of the opisthosoma is cut/broken off, the structures of the bulbus are deformed. Measurements (in mm): Body length 1.8, prosoma: Length 0.85, width 0.8, femur I 1.0.

?Zamilia sp. indet.

**Material:** 1♂ in Mid Cretaceous amber from Myanmar (Burma), F2564/BU/CJW.

The male is incompletely badly preserved, partly pyretized and darkened, 2.9 mm long. Mainly according to its relatively long and slender posterior spinnerets and its habitus it is most probably a member of the genus *Zamilia*.

? Zamilia sp. indet. (photo 148)

**Material:** 1♂ in Burmite and 3 separated pieces of amber, F2672/BU/CJW.

The spider is completely preserved and strongly pyritized, the body length is 3.5 mm, its femora are stretched to the side but the remaining leg articles are bent below the body. This is the largest known oecobiid specimen in Burmite. I do not want to exclude that it is a member of the genus *Zamilia* WUNDERLICH 2008.

Oecobiidae indet. (figs. 310-313)

**Material:** 1♂ and articles of four legs of a probably conspecific female as well as a separated piece of amber in Mid Cretaceous Burmite, F2737/BU/CJW.

**Preservation and syninclusions:** The male and the loose leg articles are preserved in a muddy piece of amber which contains numerous tiny brown droplets. The right patellae I-II as well as the distal parts of the femora and the basal parts of the tibiae of these legs are cut off, the prosoma, the spinnerets and the pedipalpi are deformed, the eyes and the mouth parts are not observable. – Left below and behind of the male some articles of four legs are preserved, quite spiny and hairy, which may be remains of a conspecific female which is cut off. In the separated piece of amber a small insect is preserved.

**Diagnosis** (♂; ♀ unknown): Legs with numerous long bristles. Pedipalpus (figs. 311-312): Tibia with a dorsal outgrowth. Larger spiders, body length 5 mm.

**Description** (♂):

Measurements (in mm): Body length 5.0, prosomal length 2.1, femur IV ca. 2.1.

Colour light to medium brown.

Prosoma longer than wide, legs not very long, III relatively long, hairy, bristles numerous and long, opisthosoma distinctly longer than wide, spinnerets strongly deformed, hair brush of the large anal tubercle well developed.

**Relationships:**

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma), and probably Upper Cretaceous amber of New Jersey, see above.

**RETROOECOBIIINAE n. subfam.**

Etymology: From (1) „retro-„ (lat.) = back, retour; according to the short posterior spinnerets which are regarded as a regain of the ancient condition of the ancestor of the superfamily Oecobiioidea, and (2) from the family name Oecobiidae.

Type genus (by monotypy): *Retrooecobius* n. gen.

**Diagnosis:** Anterior spinnerets longest, distinctly longer than the posterior spinnerets (figs. 318-319), anal tubercle small, its hairs rather short; prosoma (figs. 313-314, 322.) strongly domed in the middle, distinctly longer than wide.

Further characters: Cribellum, feathery hairs and apical cymbial bristles (figs. 320-321) absent, median spinnerets strongly reduced or even absent (figs. 318-319), 8 eyes in two almost parallel rows, anterior median eyes largest (figs. 313, 322), a single metatarsal trichobothrium exists near the end of the article (figs. 316, 324), coxa-trochanter leg autotomy (photo), colulus unknown, cymbium slender (fig. 320).

**Relationships:** The weak basal cheliceral articles, the „nose-shaped“ clypeus (distinct in the male, fig. 313) and the ventral tarsal bristles are comparable to other members of the family Oecobiidae. – In all remaining taxa of the Oecobiidae the POSTERIOR spinnerets are the largest (like in the Hersiliidae), the anal tubercle is large and bears long hairs (fig. 305), and the prosoma is not domed in the middle. According to the absence of a cribellum and the existence of a coxa-trochanter leg autotomy the Eocene subfamily Mizaliinae THORELL may be most related; in the Mizaliinae the posterior spin-

nerets are largest, the anal tubercle is large and bears long hairs, and a large colulus (or a „pseudocribellum“?) exists. – With some hesitation I regard the small posterior spinnerets and the small anal tubercle – both are unique within the superfamily – as regains („reversals“) of the Retroecobiinae. If these structures are basical (plesiomorphic) characters of the Retroecobiinae this taxon has to be elevated to family rank and regarded as sister group of Hersiliidae + Oecobiidae.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

**Retroecobius n. gen.**

Etymology: See above.

The gender is masculine.

Type species: *Retroecobius chomskyi* n. sp.

**Diagnosis, relationships and distribution:** See above.

***Retroecobius chomskyi* n. gen. n. sp. (figs. 313-321) photo 149-153**

Derivatio nominis: This peculiar spider species is named in honour to NOAM CHOMSKY, who – according to the NEW YORK TIMES – is probably the most important and influential living intellectual human and an excellent social critic. In my opinion CHOMSKY's view of anarchism makes sense in a world full of corrupt, inhuman and criminal political, economic and religious leaders

Is it not a shame that inhuman and horrible political leaders like HENRY KISSINGER and BARACK OBAMA – whose machinations caused so many killings – got the Nobel Peace Prize? CHOMSKY has the courage to expose inhuman acts of the US-American administrations like lies, killing civilians by bombs, mines and poison, as well as stirring wars in Central and South America and in South East Asia. The number of killed humans runs into millions. In contrast murderers of single persons are imprisoned .... – Few of CHOMSKY's numerous books have been recently translated into German by SVEN WUNDERLICH – LOWELL FACTORY BOOKS –, for example „Der Schutzschirm der Amerikanischen Macht – die Widersprüche der US-Politik zur Allgemeinen Erklärung der Menschenrechte“ („The Umbrella of U.S. Power – The Universal Declaration of Human Rights and the Contradictions of U.S. Policy“).

This many-sided author compared also excellently the evolution of languages with the evolution of animals.

**Material:** Holotype ♂ in Mid Cretaceous amber from North Myanmar (Burma), F2653/BU/CJW.

**Preservation and syninclusions:** The spider is very well preserved in a clear yellow piece of amber, both bulbi are strongly deformed, a „fluid“ comes out in front of the anterior spinnerets (figs. 318-319), the right legs III and IV are lost beyond the coxa by autotomy, the left leg I is cut off through the tibia, the right leg I is cut off through the metatarsus, small bubbles exist on articles of the left legs III and IV. – Three insect's larvae (probably related to Gryllidae) are preserved on the left above and on the left below the spider. Insects excrement, detritus and plant hairs are also preserved.

**Diagnosis** (♂; ♀ unknown): Leg bristle numerous (figs. 315-316), the deformed pedipalpus is shown in the figs. 320-321, the cymbium is slender, apical bristles are absent.

### **Description** (♂):

Measurements (in mm): Body length 3.5, prosoma: Length 1.7, width ca. 1.3, opisthosoma: Length 1.6, width 1.3; tibia I ca. 1.4, tibia III ca. 1.0, leg IV: Tibia 1.4, metatarsus 1.3, tarsus ca. 0.85.

Colour medium to dark grey.

Prosoma (figs. 313-314, photos): distinctly longer than wide, strongly domed, highest in the middle, hairs short and indistinct, fovea large/deep, 8 eyes in two rows, posterior row straight, anterior median eyes largest, posterior median eyes spaced by at least their diameter, clypeus long, „nose-shaped“ protruding ventrally, basal cheliceral articles weak, mouth parts hidden, sternum longer than wide, coxae IV spaced by less than half of their diameter. – Legs (figs. 315-317, photos): Position probably medio-grade, fairly stout, III shortest, spines long and numerous, metatarsal preening comb and calamistrum absent, metatarsal trichobothria near the end of the articles, unpaired tarsal claws well developed, paired claws with 5 or more long teeth, coxa-trochanter autotomy. – Opisthosoma (figs. 318-319, photo) oval, 1.23 times longer than wide, hairs short and numerous, anal tubercle short, hairs rather short, colulus unknown probably hidden or small, median spinnerets strongly reduced or even absent, anterior spinnerets largest, fairly slender and distinctly separated, posterior spinnerets distinctly shorter. – Pedipalpus (figs. 320-321): Femur fairly slender, patella and tibia stout, cymbium fairly slender, apical cymbial bristles absent, bulbus distinctly deformed, its structures partly hidden, bearing a large questionable conductor and probably a long embolus.

**Relationships:** In *R. convexus* n. sp. the prosoma is domed, too, but the number of leg bristles is much lower, a „clypeal nose“ is absent (probably because of the deformed prosoma) in the single known female.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

**Material:** Holotype ♀ (originally probably egg-bearing) in Mid Cretaceous amber from N-Myanmar (Burma), F2553/BU/ CJW.

**Preservation and syninclusions:** The spider is incompletely and only fairly well preserved in a yellow piece of amber, it is deformed, strongly darkened and apparently partly pyritized; the right side of the opisthosoma including the spinnerets and the genital area are cut off within the amber, the opisthosoma is hollow. The left patellae I-III are cut off, parts of the right legs III and IV are lost. – A small and strongly deformed juvenile Araneae indet., a Collembola, 2 Coleoptera, few Acari and Diptera, remains of plants and detritus are also preserved.

**Diagnosis** (♀; ♂ unknown): Leg bristles not numerous, partly long (figs. 223-225), clypeus – it is deformed – probably not „nose-shaped“ (fig. 322).

**Description** (♀, apparently egg-bearing):

Measurements (in mm): Body length 5.0, prosomal length ca. 1.8, opisthosoma: Length 3.7, height 2.6; leg II: Femur 1.6, patella 0.7, tibia 1.15, metatarsus 1.0, tarsus 0.7, tibia I 1.0, tibia III 0.9, tibia IV 1.0.

Colour: Prosoma and legs strongly darkened and apparently pyritized, opisthosoma light grey, translucent.

Prosoma (fig. 322, photo) (deformed) probably longer than wide, hairy, distinctly domed, posteriorly depressed, 8 eyes in two almost parallel rows, lateral eyes distinctly spaced from each other, clypeus ventrally protruding but apparently not „nose-shaped“, basal cheliceral articles small, other mouth parts hidden. – Pedipalpus with large and stout articles, tarsal claw large, bearing several long teeth. – Legs (figs. 323-325, photo) deformed, stout, III slightly the shortest, feathery hairs absent, bristles not numerous, existing on femora, patellae, tibiae, metatarsi and (at least some) tarsi, femora with ca. 3 stronger dorsal bristles, patellae with 2 thin dorsal bristles, tibiae with 2 long and thin dorsal bristles which are stronger on III-IV, ventral tarsal II bristles existing, ventral tarsal III-IV bristles hidden, rubbed off or probably absent, tarsal trichobothria absent, position of the metatarsal I trichobothrium in ca. 0.85, unpaired tarsal claw well developed, paired claws large, bearing 5 or more long teeth. – Opisthosoma (fig. 322, photo) quite large, oval, originally probably egg-bearing (now hollow), covered with short hairs; spinnerets and genital area are cut off.

**Relationships:** See *R. chomskyi* n. sp.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

The mainly tropical members of the family Hersiliidae are easily recognizable by the existence of extremely long posterior spinnerets (photos), and 2-8 metatarsal trichobothria in the distal half (figs. 328-329) which easily may be overlooked in fossil specimens; see also the lists of characters above. Frequently the legs are quite long, and the metatarsi I, II and IV are divided in several taxa (photo, fig. 333).

Certain Hersiliidae live under stones, few build capture webs, numerous members are found on the bark of trees as sit-and-wait predators, which capture their prey by rapid encircling and fixing them with the help of threads.

Several fossil taxa have been reported from Eocene European amber forests, see WUNDERLICH (2004: 814-821). The first Cretaceous Hersiliidae – *Burmesiola cretacea* WUNDERLICH 2011 (: 551-552) was only recently described, based on a single juvenile. The two Cretaceous taxa treated here are quite different regarding the relative length and the structures of their legs. The existence of a well developed metatarsal „preening comb“ (fig. 229) contradicts the use of a capture web in the short-legged (photo) members of *Burmesiola*. The existence of a tibial I „clasping spine“ – used for fixing the mating couple – in the long-legged male (photo) of the second genus – *Spinasilia* n. gen. – (fig. 331) is a unique structure in this family and the whole superfamily Oecobioidae. What is the explanation for the existence of this unusual clasping spur/spine in this entelegyne (\*) taxon? In my opinion it well may be a REGAIN of an ancient structure in this genus, which is known e. g. in haplogyne members of the Plectreuridae and Segestriidae: Ariadninae in a similar proventral apical position. (See also the mating spurs/ bristles of the male anterior tibia in mygalomorph spiders like Dipluridae or Nemesiidae).

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(\*) Clasping spines of the male anterior leg are also known, e. g., in extant and fossil members of the entelegyne superfamily Aranezoidea: In the families Anapidae, Cyatholipidae and Mysmenidae, see WUNDERLICH (2004: E. g. 177f, figs. 1f, 1094, fig. 48, 11-7-1108, figs. 122, 129). Shape and position of their clasping spines are quite different from the clasping spine in *Spinasilia* which are similar to those in most Ariadninae and Plectreuridae. Such structures in the Anapidae, Cyatholipidae and Mysmenidae each have evolved separately (convergently).

***Burmesiola*** WUNDERLICH 2011: 551

**Revised diagnostic characters** (?juv.): Clypeus shorter than the field of the median eyes (fig. 327), posterior median eyes largest, anterior median eyes small but larger than the anterior lateral eyes, all metatarsi undivided (figs. 228-229), legs relatively short, metatarsus III (fig. 329) bears 5 long trichobothria in the distal half, flexible tarsal



and metatarsal zones absent, posterior spinnerets at least as long as 2/3 of the opisthosomal length, their apical article at least as long as the basal article.

**Relationships:** In *Hersiliola* THORELL 1870 (extant, Mediterranean to Afghanistan), which I regard as related, the legs are similar but the posterior spinnerets are distinctly stouter, the clypeus is much longer and the posterior median eyes are larger. – In the second hersiliid genus in Burmite – based on a male – the legs are much longer and the metatarsi (except III) are divided.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

*Burmesiola daviesi* n. sp. (figs. 326-330) photos 140-142

Derivatio nominis: With pleasure I name this nice species after SCOTT DAVIES in Bangkok/Thailand, who selected important spiders in Burmite for my investigation.

**Material:** Holotype ?juv. ♀ in Mid Cretaceous Burmite, F2646/BU/CJW.

**Preservation and syninclusions:** The spider is well preserved near the surface of a red-orange piece of amber which was rolled and which consists of more than 20 layers within a diameter of 1 cm. Most parts of the spider are preserved, half of the left patella and tibia II are cut off, most parts of the left leg IV, the right metatarsi and tarsi II and III are also cut off. – Spiders threads – part of a capture web? – are preserved e. g. right behind the spider, 1 Coleoptera, 1 Psocoptera, two tiny winged insects and some plant hairs are also preserved.

**Diagnosis** (?juv. ♀): Posterior median eyes only fairly large (figs. 226-227), opisthosoma 1.15 times wider than long (photo).

**Description** (?juv. ♀):

Measurements (in mm): Body length 2.2, prosoma length and width ca. 1.1; opisthosoma: Length ca. 1.25, width 1.1; leg I: Femur 2.1, patella 0.5, tibia 1.9, metatarsus 2.3, tarsus 1.8; femur II 2.1, femur III 1.0, femur IV ca. 1.5.

Colour mainly light brown, some leg articles probably slightly annulated.

Prosoma (figs. 226-227, photo) about as long as wide, foveal depression well developed, cephalic part weakly raised, thoracal part distinctly raised, with a pair of „shoulders“, both prosomal parts separated by a depression, eye field wide, posterior row recurved, all eyes of similar size, clypeus ca. as long as 1 ½ diameters of the anterior median eyes, basal cheliceral articles slender, fangs, cheliceral teeth and mouth parts hidden. – Pedipalpus with long and slender articles. – Legs (figs. 228-230, photo) fairly long and slender, order I/II/IV/III, I and II distinctly longest, III distinctly shortest, feathery hairs existing, all metatarsi undivided, tarsi short, bristles slender and numerous, leg I: Femur 4 dorsally and 2 prolaterally, patella 2 dorsally, tibia and metatarsus at least 5 ones each. Metatarsal preening comb III well developed. Metatarsal trichoboth-

ria long and numerous in the distal half, on I at least 8, on III at least 5. Three tarsal claws. – Opisthosoma (photo) ca. 1.15 times longer than wide, not densely covered with thin hairs of medium length. Three pairs of spinnerets, the posteriors as long as the opisthosoma, their distal articles about the same length, anal tubercle relatively large and hairy.

**Relationships:** In *B. cretacea* WUNDERLICH 2011 the posterior median eyes are distinctly larger and the opisthosoma is as wide as long (but the shape of the opisthosoma may be variable in these species).

**Ecology:** The well developed metatarsal preening comb indicates that members of this species were not capture web dwellers, so the threads near the spider are not part of its capture web.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

### **Spinasilia n. gen.**

**Etymology:** Spina (lat.) = thorn, according to the tibial „clasping spine“ of the holotype; silia is part of the family name Hersiliidae.

The gender of the name is feminine.

**Type species** (by monotypy): *Spinasilia dissoluta* n. sp.

**Diagnosis** (♂; ♀ unknown; prosoma and opisthosoma deformed, eyes hidden): Tibia I with a „clasping spine“ (fig. 331), metatarsi I, II and IV divided (fig. 333), opisthosoma (photo) long, not widened, posterior spinnerets (they are not well preserved and deformed) very long, the apical article much longer than the basal one, cymbial bristles absent, shape of the bulbus almost circular (fig. 334), kind of autotomy unknown.

**Further characters:** Metatarsal preening comb and – apparently – ventral metatarsal and tarsal IV bristles absent.

**Relationships:** A tibial „clasping spine“ is unique in this family and may be a regain from ancestors like the Segestriidae. A close extant taxon is unknown to me.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

***Spinasilia dissoluta* n. gen. n. sp.** (figs. 331-334) photos 143-144

Etymology of the species name: From *dissolutum* (lat.) = dissected, according to the partly dissected body and legs of the holotype.

**Material:** Holotype ♂ in Mid Cretaceous Burmite, F2647/BU/CJW.

**Preservation and syninclusions:** The spider is almost completely preserved but dissected and apparently decomposed, preserved in a larger redbrown and muddy piece of amber, darkened by natural heating and pressure. Three of the anterior legs are bent below the body, prosoma and opisthosoma are strongly deformed, the position of the eyes and the shape of the prosoma are unknown. – Some thin spider's threads, a tiny Acari (above the left tibia II), numerous hyphae, large remains of leaves and several plant hairs are also preserved.

**Diagnosis:** See above.

**Description** (♂):

Measurements (in mm): Body length 4.0, prosomal length ca. 2.0, opisthosomal length ca. 2.3, length of the posterior spinnerets ca. 3.0, femur II ca. 4.5, leg IV ca. 13.0.

Colour dark brown (darkened by natural heating and pressure).

Prosoma (photo) strongly deformed. – Legs (most articles are more or less deformed) (figs. 331-333, photo) bearing short hairs and numerous bristles; tibia I bears ventrally near its end a strong „clasping spine“. Trichobothria are hard to detect, metatarsus I bears at least two ones near the end of the article. Metatarsal preening comb IV absent (III is hidden), ventral bristles on the tarsi – and apparently on the metatarsi – absent (III is hidden). Feathery hairs existing. Three tarsal claws. – Opisthosoma (it is decomposed) probably slightly longer than wide. – Pedipalpus (fig. 334) with stout articles, cymbium short, apical bristle most probably absent, tegulum flat, its shape almost circular, the distal part of the questionable embolus thin, the central parts of the tegulum are not recognizable with the help of a light microscope.

**Habitat:** According to the long legs and the long spinnerets the members of this species may have had an arborical life style.

**Relationships:** See above.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

**Further material – Hersiliidae indet. – in Burmite:**

1♀, F2673/BU/CJW: The spider is strongly deformed, 4 mm long, preserved together with a juv. female of the Lagonomegopidae indet. and a female of the family Tetrablemmidae indet.

1 probably adult ♀, F2738/BU/CJW: The spider is incompletely and deformed preserved in a yellow-orange piece of amber, together with 6 Diptera, remains of a Coleoptera and plant hairs. Four of the small eyes, the mouth parts and the right leg I beyond the coxa (autotomy) are lost. The spinnerets are deformed and incompletely preserved. Prosoma and opisthosoma are wider than long. The legs are distinctly annulated, all metatarsi are undivided, metatarsus III bears at least 3 long trichobothria in the distal half, the leg bristles are fairly short. – Measurements (in mm): Body length 3.5, prosoma: Length ca. 1.7, width 1.85, opisthosoma: Length 1.85, width 2.0; legs: Tibia I 2.2, II: Femur ca. 2.2, patella 0.6, tibia 2.3, metatarsus 2.7, tarsus 0.8; tibia III 0.8, tibia IV 1.9.

**Relationships:** I do not want to exclude that the female may be a member of *Burmesiola daviesi* n. sp. in which the legs are not (distinctly) annulated; the annulation is probably not preserved in the single known specimen of *B. daviesi*.

## **SUPERFAMILY ARANEOIDEA s. l. (= „Orbiculariae“)**

Remark: Recently – based on molecular genetic studies – HORMIGA (2014) doubted the monophyly of this branch – and even strong relationships of the two main branches of the „Orbiculariae“ which are considered by most authors: The ecribellate Araneoidea s. str. and the cribellate Deinopoidea s. str., and he also doubted the monophyly of the orb web but see above (phylogenetics).

**Diagnostic characters:** Members of this entelegyne and three-clawed superfamily (in the wide sense) basically build an ORB WEB. This kind of capture web is strongly modified in numerous taxa (e. g. in the Deinopidae and certain Araneidae) or absent (lost) (e. g. in the Mimetidae and some Theridiidae). – Also other characters of this branch vary remarkably: A pair of lungs (and lung covers) exists in most families but are reduced or even absent in or within some families of the Araneoidea s. str. (some taxa of the theridiosomatid branch). The cuticula is usually scale-shaped (rarely smooth) in the araneoid branch and usually furrowed in the deinopoid branch (but see *Burmadictyna*). Tarsal trichobothria are absent, the metatarsi (at least I-II) bear a single trichobothrium (they are frequently absent on IV, in certain Theridiidae even on III); femoral trichobothria exist in most Uloboridae (not in all fossil taxa, see the tab. below), in several Tetragnathidae, and in a single genus of the Linyphiidae: *Orsonwelles* HORMIGA 2002. Leg bristles are frequent and exist usually on femora and/or patellae and/or tibiae and/or

metatarsi, and – in most Deinopoidea s. str. – even ventrally on the tarsi. In few taxa – like certain Theridiidae – leg bristles are completely absent. Cribellum and calamistrum exist usually in the deinopoid branch (but may be strongly reduced in the male sex), and are absent in the araneoid branch. A colulus exists usually in the araneoid branch but has been lost e. g. in certain Theridiidae. 3 pairs of short spinnerets exist: In a rosette-shaped position in the ecribellate araneoid branch; the anterior spinnerets are basally widely spaced and usually strongly converging in the cribellate deinopoid branch. Feathery hairs may exist: In most members of the deinopoid branch, absent e. g. in *Burmadictyna*, see the tab. below. Accessory apical hairs of tarsus IV exist usually. Most often exist 8 eyes, rarely 6, e. g. in the Anapidae and certain Theridiidae or 4, in few Uloboridae (*Miagrammopes*).

A retrolateral – usually retroapical – pedipalpal tibial apophysis exists in numerous members of the araneoid branch (e. g. in most members of the Linyphiidae: Erigoninae and certain Tetragnathidae). (It exists also in members of the RTA-clade and in certain taxa of the extinct family Lagonomegopidae (Arachaeoidea). A retrobasal paracymbium and a – usually distinctly sclerotized – epigyne (and/or an epigynal scape) exist in most members of the araneoids (the Araneoidea s. str.) (a retrobasal paracymbium is absent/lost in the Theridiidae in which also an epigynal scape is usually absent), a non-sclerotized epigynal outgrowth exists in numerous deinopoids. A colulus exists in most members of the araneoid branch in which the spinnerets have a rosette-shaped position, and a triad of spinules exists on the posterior spinnerets. An epigynal plug or broken (parts of the) embolus – which may avoid sperm competition – exists in several families of both branches; it is first reported here from a fossil taxon, the genus *Burmadictyna* of the extinct family Salticoidae, see below.

FORSTER (1970) – see HARVEY (1995: 282) – suggested that „the affinities of the NICODAMIDAE are with the Araneoidea“ but FORSTER was not able to identify the sister group of the Nicodamidae which are still completely unknown from fossils. The trichobothriotaxy of Araneoidea and Nicodamidae is quite similar.

Araneoidea s. l. is – in the geological sense – a very (more than 200 million years) old branch, known already from the Triassic. The advanced ecribellate subbranch, the Araneoidea s. str., is the most diverse high taxon of spiders today (and already in the Eocene), but it was much less diverse in the Mesozoicum in which haplogyne spiders (as well as certain entelegyne members of the cribellate deinopoid branch like Uloboridae). Most extant – and most probably mesozoic – species of both araneoid branches are dwellers of higher strata of the vegetation, and thus they are not rarely preserved in most kinds of amber worldwide, in contrast to mainly ground-living spiders like Mygalomorpha and most members of the araneoid subfamily Erigoninae of the Linyphiidae which is a „young“ taxon and even not reported from the Eocene Baltic amber, see WUNDERLICH (2004).

# **(1) The DEINOPOID branch** (the cribellate araneoid branch) (= „Deinopoidea“)

Three families have been reported: Deinopidae (Eocene up to now), Uloboridae (Mesozoicum – Jurassic – up to now) and Salticoididae (Mesozoicum). Here I transfer the extinct Salticoididae to the deinopoid branch, include the genus *Burmadietna* in this family, and transfer the genus *Palaeomicromenueus* from the Deinopidae (\*) to this family.

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(\*) Alleged Deinopidae: The – in my opinion, see below – erroneous and unique report of the only named mesozoic taxon of the family Deinopidae, the genus *Palaeomicromenueus* PENNEY 2003 (preserved in Lebanese amber) is now considered by me as a member of the Salticoididae. Furthermore I now regard two juvenile questionable deinopid spiders in Burmese amber – see WUNDERLICH (2008: 631) – not as members of the Deinopidae but probably – at least one of these – as member(s) of the family Uloboridae. Therefore Deinopidae has to be removed from the list of Mesozoic spider families.

Note during printing of this paper: SELDEN et al. (2015, in press, J. Syst. Palaeontology) described two species of the new cribellate genus *Zhizhu* in stone from the Middle Jurassic of China (in Liaoning the spiders were very frequent, eudominant!), and regarded it as a member of the Deinopoidea. In my opinion the relationships of this genus are quite unsure. The thickened articles of the male pedipalpus and the (sclerotized?) epigyne are similar to the superfamily Oecobioidea but the depressed and concave metatarsus IV is similar to the family Uloboridae – a „first step“ to the Uloboridae? On the other hand I do not want to exclude relationships to the extinct cribellate family Mongolarachnidae, see above. *Zhizhu* has been regarded by SELDEN as a member of the Entelegyne by its „complex male pedipalpus“ but the bulbus structures of numerous Haplogynae are quite complex, see DEELEMEN-REINHOLD (1995) and this paper! In my opinion *Zhizhu* is more likely a member of the Haplogynae, see above: the family Mongolarachnidae.

## **Key to the fossil and extant families of the deinopoid branch:**

Notes: See above: the intrafamilial variability. – In certain taxa of all the three families the embolus possesses a spiral position (extremely developed in the extant Deinopidae, fig. 336, and in *Burmadietna* of the Cretaceous Salticoididae, fig. 351. The coiled embolus may be a plesiomorphic character of the branch. In males of certain Uloboridae cribellum and calamistrum may be strongly reduced.

1 Eyes (fig. 335) in a unique position of three rows, posterior median eyes very large to huge, distinctly the largest eyes and DIRECTED FORWARD, anterior median eyes smallest, anterior lateral eyes situated on large tubercles on the extreme anterior-lateral margin of the clypeus and directed side- and downwards. Legs I AND II very long, used to hold an expandable unique web for active capturing arthropods from the air. Metatarsus IV straight and not compressed. Embolus long, in a flat spiral (fig. 336). Poison glands existing. Largest members of the Deinopoidea s. str. („gigantism“), body length ca. 6-20 mm. Eocene (Baltic amber) to extant. . . . . Deinopidae

- Eye position different: Posterior median eyes never so large, position of the anterior lateral eyes never on LARGE tubercles at the extreme anterior-lateral margin of the clypeus. Leg II frequently distinctly smaller/shorter than I. Metatarsus IV and embolus similar or different. Body length 0.9-10 mm. . . . . 2

2(1) Position of the eyes frequently in a long field with anterior and posterior eyes distinctly to widely spaced (figs. 367-368), at least posterior median eyes frequently situated on humps, posterior eye row frequently strongly recurved. Femoral trichobothria (fig. 387) – which are usually stronger developed on III-IV – exist in all extant taxa but are absent in few extinct taxa (\*), see the tab. below. Metatarsus IV dorsally concave and laterally compressed (e. g. figs. 360-361) in the extant and usually in the fossil taxa. Poison glands absent at least in the extant taxa. Jurassic to extant. . . . . Uloboridae

- Position of the eyes (figs. 338, 340, 343) in two short and almost parallel rows, lateral eyes CLOSE TOGETHER, EYES NOT SITUATED ON HUMPS. Femoral trichobothria absent. Metatarsus IV straight and not compressed. Existence of poison glands unknown. Creaceous (probably older). . . . . Salticoididae

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 (\*) Absent in *Bicalamistrum* which is only based on juv. males and in *Burmuloborus*. In *Microuloborus* the number of femoral trichobothria is apparently strongly reduced. In the dubious genus *Zhizhu* (see above) femoral trichobothria are absent.

## Family SALTICOIDIDAE WUNDERLICH 2008    Family key nos. 17, 21

Type genus: *Salticoididus* WUNDERLICH 2008 in Jordanian amber.

Further genera: *Palaeomicromenneus* PENNEY 2003 in Lebanese amber, *Burmadictyna* in Burmite and probably additionally an unnamed taxon in amber from New Jersey (under Dictynidae gen. et sp. indet. sensu PENNEY (2002: 717-720)), see above, the chapter on erroneous determinations; in this species the calamistrum is quite short and the cephalic part bears numerous long and strong setae.



**Emended diagnostic characters** after the inclusion of the genera *Palaeomicromeneus* and *Burmadictyna*; see also the characters of the deinopoid branch and the additional characters below: Femoral trichobothria absent, metatarsus IV straight and not compressed laterally, two wide but not long rows of eyes which all are not placed on humps, anterior and posterior lateral eyes close together (figs. 340, 342), embolus spirally, fairly to very long (figs. 339, 341, 351).

Further/basic characters and further intrafamilial variability: Cribellate (fig. 346), unpaired tarsal claw existing, entelegyne, clypeus (fig. 343) short, fangs small/slender (fig. 343), gnathocoxae not converging, labium free and not rebordered (fig. 344), leg I strongly elongated (and much longer than II in *Palaeomicromeneus*), leg bristles numerous, short ventral bristles of tarsus IV usually existing, feathery hairs existing (in *Salticoididus*) or absent (absent in *Burmadictyna*; they are reported from *Palaeomicromeneus* but not figured), position of its single metatarsal trichobothrium in the distal half (fig. 345). The anterior median eyes are quite large in *Salticoididus*, see WUNDERLICH (2008: 670: figs. 107-108). Anal tubercle at least in *Burmadictyna* (fig. 346) quite large and bearing long hairs in an undivided group. Embolus in a spiral position, describing about 2 or 3 loops in *Palaeomicromeneus* (fig. 339) and *Salticoididus* or even a dozen narrow spirals which build a cylindrical form in *Burmadictyna* in which a complicated distal structure exists (figs. 350-352) which apparently functioned as a mating plug. The existence of this structure is absent in *Palaeomicromeneus* and unknown in *Salticoididus*. KRAUS (1956: Fig. 5) figured the modified tip of the embolus of an extant Deinopidae (*Deinopis diabolica*) which probably functioned as a „mating plug“. See also HERBERSTEIN et al. (2012) and UHL et al. (2009).

#### **Relationships** (see the key above):

In the original description of the type genus *Salticoididus* WUNDERLICH 2008 of the Salticoididae I found morphological relationships to the Araneoidea and to the Oecobioidea. Cribellum/calamistrum were not reported. According to its characters – see above –, after the discovery of new members of the apparently related cribellate genus *Burmadictyna*, and the revision of the genus *Palaeomicromeneus* I now regard the Salticoididae as a family of the deinopoid branch of the superfamily Araneoidea s. l., probably it is the most primitive known family of the superfamily Araneoidea s. l..

I consider the following characters of this family as primitive (plesiomorphic) of the deinopoid branch:

- the absence of femoral trichobothria,
- an unmodified metatarsus IV (straight and not compressed laterally),
- unmodified characters of the eyes: No humps, no enlarged or reduced eye lenses,
- no strongly recurved posterior row, lateral eyes close together.

Deinopidae may be the most related family: Femoral trichobothria are absent like in the Salticoididae and metatarsus IV is not modified – two plesiomorphic characters are shared by these families. In connection with its nocturnal life style and its special capturing behaviour the Deinopidae evolved huge posterior median eyes which are directed forward (fig. 335) as well as a long leg II (besides the also elongated leg I). Both characters are different in the Salticoididae. A strongly coiled embolus evolved – in my opinion convergently – in the Deinopidae and in *Burmadictyna*. A modified distal part of the embolus – which bears two barbets and apparently functioned as a mating plug

in *Burmadictyna excavata* (figs. 350-352) – has also been described from a member of the family Deinopidae (the genus *Deinopsis*) in which it possesses a similar shape, see fig. 337. The most derived Deinopidae is probably the youngest one of the three families in question: The oldest report dates from the Eocene Baltic amber, see WUNDERLICH (2004).

The trichobothriotaxy and the modifications of the eyes as well as of metatarsus IV are more derived in the Uloboridae compared with the remaining two families.

**Ecology and behaviour:** Fossils of this family have been found in amber of tropical forests; in such forests also live most of the extant deinopoids. The existence of well developed accessory tarsal hairs („claws“), the relatively long legs I as well as the short legs III may indicate that the Cretaceous Salticoididae were orb-web weavers like extant relatives. The not strongly elongated leg II – or even legs I AND II – contradict a peculiar prey capture behaviour like in the Deinopidae. See SELDEN (1990: 281). Nothing is known about the existence/absence of poison glands of the Salticoididae (they are absent at least in the extant members of the Uloboridae) or its probably modified orb web. The not strongly enlarged median eyes contradict a nocturnal life style of these spiders. Breakable mating plug of the embolus: See *Burmadictyna excavata*.

**Distribution** wide in space and time: Mid Cretaceous amber forest of Myanmar (Burma) (*Burmadictyna*), Early Cretaceous ambers from Lebanon (*Palaeomicromenneus*) and Jordan (*Salticoidides*), and probably Upper Cretaceous amber of New Jersey, an unnamed taxon, see the chapter on erroneous determinations above.

### Key to the genera of the family Salticoididae:

An unnamed and probably confamiliar taxon in Cretaceous amber of New Jersey (see above) is not included.

2(1) Feathery hairs absent. Embolus very long, describing about a dozen narrow loops in a cylindrical structure, bearing a harpoon-shaped structure (mating plug) at its end (figs. 350-352). Burmite. . . . . *Burmadictyna*

- Feathery hairs (see fig. 389) existing. Anterior median eyes (fig. 340) distinctly the largest eyes. Embolus (fig. 341) describing 2-3 loops. Jordanian amber. . . *Salticoidides*

- Feathery hairs existing. Anterior median eyes (fig. 338) not enlarged. Embolus describing 2-3 loops. Lebanese amber. . . . . *Palaeomicromenneus*

Type species (by monotypy): *Salticoididus kaddummiorum* WUNDERLICH 2008.

**Main diagnostic characters**, see above and WUNDERLICH (2008: 628) (♂; ♀ unknown): Anterior median eyes (fig. 340) enlarged, embolus (fig. 341) describing two or three loops.

**Relationships**: See the key to the genera and the characters of the family Salticoididae.

**Distribution**: Lower Cretaceous amber forest of Jordan.

**Palaeomicromenneus** PENNEY 2003 (described in the family Deinopidae) (figs. 338-339) (**n. relat.**)

Type species (by monotypy): *Palaeomicromenneus lebanensis* PENNEY 2003.

Remark: I did not get the opportunity to study the generotype which is kept in the MNHP.

**Diagnostic characters** (♂; ♀ unknown) of the genus are the wide and not modified eye field (fig. 338) with not enlarged median eyes, and the long embolus which describes two or three wide loops (fig. 339). Femoral trichobothria are absent, metatarsus IV is not modified.

**Relationships**: As I pointed out previously – see WUNDERLICH (2008: 631-632) – no sure proof of the family Deinopidae from the Mesozoic period exists, although the present taxon was assigned to this family by PENNEY (2003).

I still doubt the deinopid relationships of *Palaeomicromenneus* for the following reasons:

(a) The position and the size of the eyes – the shape and the position of the (small!) posterior median eyes and the position of the anterior eyes – are completely different from all Deinopidae, see fig. 335. The assignation of *Palaeomicromenneus* to the family Deinopidae is already excluded from this character alone. The highly developed eye position of this genus may be a pre-condition for the special kind of prey capturing which is a typical character of this family.

Remarks: (1) PENNEY regarded the deinopid genus *Avellopsis* as having a less developed eye position but this genus actually possesses a well developed deinopid eye position.

(2) Confusion/discrepancy exists regarding the description of the eye position of *Palaeomicromenneus lebanensis* by PENNEY and the figure of these eyes. This author writes on p. 571: „Eight eyes: posterior median eyes separated by 0.14, directed forwards and subequal to pos-

terior lateral eyes, which are slightly wider apart, posterior row distinctly recurved (Fig. 3).“ See fig. 338. Actually in fig. 3 the posterior median eyes are not directed forwards (but upwards), and the posterior eye row is distinctly PROcurved in fig. 3! Is the text correct or the figure? PENNEY (person. commun. in XI 2013) was unable to answer this question.

(b) Leg II of *Palaeomicromenneus* is distinctly shorter than leg I in contrast to extant Deinopidae which need a long leg II while holding their web for prey capturing.

(c) PENNEY (person. commun. in XI 2013) identified the holotype of *P. lebanensis* as a deinopid spider based „on the remarkable similarity of the pedipalp structure.“ Apparently this author regarded the coiled embolus of *Palaeomicromenneus* as a typical deinopid character, but a coiled embolus evolved convergently in several taxa of numerous spider families like Hersiliidae, Salticoidae, Uloboridae, Theridiidae, Thomisidae and Salticidae besides the Deinopidae.

(d) A dorsal outgrowth of the pedipalpal patella was not reported by PENNEY (2003); it is probably absent in this taxon or hidden or it was overlooked by the author.

Conclusions: Taking together all these findings *Palaeomicromenneus* is surely not a member of the family Deinopidae but most likely of the family Salticoidae (**n. relat.**) which possessed still (?) an unmodified eye field and – compared with leg I – relatively short legs II. Therefore Deinopidae has to remove from the list of Mesozoic spider families.

**Distribution:** Lower Cretaceous Lebanese amber forest.

### ***Burmadiictyna* WUNDERLICH 2008 (**n. relat.**)**

Type species (by monotypy): *Burmadiictyna pecten* WUNDERLICH 2008 (♀).

Further species: *Burmadiictyna excavata* n. sp. (♂) and *B. clava* n. sp. (♂).

**Diagnosis:** Male: Embolus (figs. 350-352) very long, describing about a dozen narrow loops in a cylindrical structure, bearing distally a modified and breakable part which apparently functioned as a mating plug. – Female (see WUNDERLICH (2008: 648-649); the unknown introductory ducts of the female should be quite long and coiled, corresponding to the embolus.

Further important characters: Cribellum entire (well recognizable in the generotype), wide eye field (figs. 340–343), legs annulated, metatarsus IV straight and not compressed laterally (deformed in the generotype), anal tubercle (fig. 346) quite large and setose, undivided. (The strong posterior prosomal incision of *B. excavata*, fig. 342, is apparently caused by the preservation). Body length 2.5 mm (♂) – 3.6 mm (♀).

The MODIFIED EMBOLUS (fig. 350-352, 355) exist in all the three known males of this genus. It has about a dozen loops in a narrow position in a long cylindrical structure. I estimate the length of the embolus 3 ½ times of the body length of the male, ca. 9.6 mm. It bears distally a complicated harpoon-shaped and stronger sclerotized structure which is constricted at its base. The sperm duct is observable and terminates with a pointed tip. Dorsally it bears two barbs and basally apparently (in my opinion) a breaking line at the constriction where the seam of the embolus terminates. The pointed tips of these barbs are directed backwards and may hinder so the retraction of this stick after copulation. This structure may well have functioned as a mating plug. A modified structure at the end of the embolus has also been described from another taxon of the same superfamily, from an extant member of the family Deinopidae – the genus *Deinopsis*, figs. 336-337 – in which it possesses a similar shape but only a single and not distinctly pointed barb. The function of this structure in the extant species as a breakable mating plug appears likely to me; it was not specified in this sense by KRAUS (1956), and not mentioned by UHL et al. (2010).

A long and coiled embolus exists in numerous spider families, see the similar spiral embolus of a species of the genus *Neosparassus* (Sparassidae), JÄGER (2006: fig. 2), and the discussion on lengthening of embolus and copulatory duct in the family Sparassidae in the same paper. – In numerous taxa of – mainly entelegyne – spider families, after mating, the male deposits a breakable part of the embolus (or even the whole embolus) as “mating plug” within the female copulatory organ to prevent the intromission of sperm by other males. “Plugs can be considered as male adaptations to avoid sperm competition.” (UHL et al. (2010)). Examples for such a male genital self-mutilation are the genus *Latrodectus* (Theridiidae) and several members of the family Araneidae like *Argyope*, see HERBERSTEIN et al. (2012). The only taxa of the superfamily Deinopoidea in which mating plugs have been reported are two extant members of the family Uloboridae: of the genera *Philoponella* and *Uloborus*, see UHL et al. (2010: 87). In both taxa the mating plug is formed by amorphous material (originated from the male pedipalpal bulb) but not by genital self-mutilation of the male as it is suggested by me in *Burmadictyna*. The existence of such a structure in all the three males of *Burmadictyna* indicates that highly specialized mating plugs and male genital self-mutilation existed in spiders already in the Mid Cretaceous, a hundred million years ago.

**Relationships:** See the key to the genera. The extremely long embolus and the modified distal part of the embolus are unique within the family Salticoididae.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

***Burmadictyna excavata* n. sp.** (figs. 342-352) photos 156-159

**Etymology:** The name refers to the – apparently artificially – posteriorly excavated prosoma, from (lat.) excava = excavate.

**Material:** 2♂ in Mid Cretaceous amber from Myanmar (Burma); holotype F2725/BU/CJW, a piece of amber with an Acari: Ixodidae has been separated as no. 2724/BU/CJW; probably conspecific ♂ and two separated pieces of amber F2765/ BU/CJW.

**Preservation and syninclusions:** Holotype: The spider is excellently and completely preserved in an orange piece of amber. Longitudinal prosomal – including lateral cheliceral – furrows are caused by the preservation, the eyes are partly covered with emulsions or small bubbles. – Few plant hairs are also preserved; a mite larva: See above (material). – The probably conspecific male is completely but only fairly well preserved in an orange piece of amber between gas/water bubbles, the prosoma is strongly deformed, most parts of the pedipalpi are hidden. – 2 tiny Acari and ½ small insect are preserved in the same piece of amber.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (figs. 347-352): Patella bearing a long dorsal bristle on a hump, tibia with a retrolateral hump which bears a row of long hairs.

### **Description** (♂):

Measurements (in mm): Holotype: Body length 2.8, prosoma: Length 1.5, width 0.95; opisthosoma: Length 1.8, height 0.9; leg I: Femur 1.45, patella 0.5, tibia 1.3, metatarsus 1.35, tarsus 0.85, tibia II 1.25, tibia III 0.7, tibia IV 0.85. – Probably conspecific ♂: Body length 2.0, prosomal length 1.0, opisthosoma: Length 1.35, width 0.8; tibia I 1.0, tibia IV 0.75.

Colour: Prosoma and legs medium brown, legs annulated (more distinctly in the paratype), opisthosoma grey brown.

Prosoma (figs. 342-344, photos) 1.6 times longer than wide, not raised, dorsally bearing artificially longitudinal furrows which apparently are caused by the preservation, anteriorly distinctly narrowed, posteriorly – most probably caused by the preservation – strongly inclined, fovea low, hairs indistinct, feathery hairs absent, cuticula almost smooth, 8 eyes in a wide field, posterior row slightly recurved, lateral eyes close together, anterior median eyes largest, posterior median eyes spaced by ca. 1 ½ of their diameter, clypeus short, basal cheliceral articles stout, bearing 3 teeth on the anterior margin of the fang furrow, fangs slender, labium free, wider than long, not rebordered, gnathocoxae not converging, sternum not elongated between the coxae IV. – Legs (fig. 345, photos) only fairly long and slender, order I/II/IV/III, I not distinctly the longest, III distinctly the shortest, hairs only fairly long, metatarsus IV straight and not compressed laterally, calamistrum not well developed, probably ca. 0.6 of the metatarsal length. Bristles numerous and partly long, existing on femora (6 on I), patellae (a thin dorsal-apical one on III-IV, a retrolateral one on I-II), tibia I-II 2 ventral pairs, 2 pro- and retrolaterally, and apicals, tibia IV additionally with a dorsal-distal bristle, all metatarsi with several bristles, tarsi without trichobothria nor (III-IV) with well developed ventral bristles, position of the single metatarsal I trichobothrium in ca. 0.76, feathery hairs and metatarsal IV comb absent, 3 tarsal claws, paired claws with long teeth, accessory hairs existing. – Opisthosoma (fig. 346, photo) ca. 1.7 times longer than wide, hairs fairly short, cribellum hidden (apparently wide), 3 pairs of spinnerets, the anteriors basally widely spaced, converging, anal tubercle quite large and hairy, a single group. – Pedipalpus (figs. 349-352, photo 158) with slender articles, patella short, bearing a long dorsal bristle on a hump, tibia with a retrolateral hump which bears a row of long hairs, cymbium large, bearing a probasal blunt outgrowth, median apophysis short, blunt and not sclerotized, embolus bearing a wide seam, forming a cylindrical spiral of



a dozen loops which are close together, at its end a stronger sclerotized complicated harpoon-shaped structure which bears two barbs and basally apparently a breaking line. The sperm duct ends at the pointed tip of the embolus. This complicated structure functioned probably as a mating plug to hold off spermatozoa from other males, see above. The pedipalpus of the second – smaller – male is not well preserved and may be identical.

**Relationships:** See *B. clava* n. sp.

**Ecology:** See above, the family Salticoididae.

**Distribution:** See above.

***Burmadictyna clava* n. sp.** (figs. 353-356) photo 155

**Entymology:** The species name refers to the club-shaped dorsal pedipalpal patellar apophysis/outgrowth, from *clava* (lat.) = club.

**Material:** Holotype ♂ in Mid Cretaceous amber from Myanmar (Burma) and a separated piece of amber, F2770/BU/CJW.

**Preservation and syninclusions:** The spider is only fairly well preserved in a clear yellow-orange piece of amber, partly deformed (e. g. the spiral of the left embolus); except the tarsus II the right legs are complete, most articles of the left legs are cut off, the left leg I is partly complete but basal parts are retrolaterally cut off. – Numerous tiny bubbles and decomposed parts of plants (leaves) are preserved in both pieces of amber.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (figs. 354-356): Patella with a large erect and club-shaped outgrowth, distal part of the embolus modified to a mating plug (see above) which bears two barbets.

**Description** (♂):

Measurements (in mm): Body length ca. 2.5; prosomal length 1.3; femur I 1.85, leg II: Femur 1.75, patella 0.55, tibia 1.55.

Colour: Prosoma dark brown, legs distinctly annulated.

Prosoma setose, fovea deep, feathery hairs absent, cephalic part higher than the thoracic part, mouth parts hidden. – Legs (fig. 353, photo) only fairly long, setose, I not thickened and not distinctly longer than II or IV, feathery hairs absent, bristles numerous and partly long, existing on femora, patellae (few thin ones dorsally-apically), tibiae, metatarsi and tarsi, some apical metatarsal bristles may form a comb, tarsi III-IV bear ventrally a single or few hair-shaped bristles, position of a questionable metatarsal trichobothrium on III in 0.3. The right tibia III bears at least half a dozen of long trichobothria in two rows. Metatarsus IV straight, not compressed laterally, calamistrum



reaching almost 2/3 of the metatarsal length. Three tarsal claws, paired claws with long teeth, unpaired claw well developed. – Most parts of the opisthosoma are not preserved. – Pedipalpus (figs. 354-356): See the diagnosis. The deformed embolus describes at least ten loops. The two mating plugs appear quite different in different aspects; the left one seems more deformed, it bears two barbs.

**Relationships:** In *excavata* n. sp. the patellar outgrowth of the pedipalpus is distinctly smaller and bears a strong bristle.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

?*Burmadictyna* sp., ?ad ♀ in Burmite, F2771/BU/CJW: The spider is difficult to study because it is preserved in a muddy piece of amber, the prosoma is deformed. Its body length is ca. 2.5 mm, tibia I is 0.9 mm long, the legs are indistinctly annulated, the clypeus is short, the eyes are insufficiently observable, the basal cheliceral articles are large, the legs are fairly stout, metatarsus IV is straight, the calamistrum is well developed.

**Family ULOBORIDAE** THORELL 1869    Figs. 367-389, photos 160-170  
Family key nos. 9, 29

Members of this old cribellate family are dwellers of higher strata of the vegetation; they were very diverse in the Cretaceous amber forest of Myanmar (Burma) (six genera), a single one has been reported from from New Jersey amber (a questionable one from the Jurassic):

- *Burmuloborus parvus*, *Paramiagrammopes cretaceus* and *P. resica*:  
WUNDERLICH (2008: 632-639, figs. 115-126, photos 105-110);
- *Jerseyuloborus longisoma* (North American amber from New Jersey):  
WUNDERLICH (2011: 552-553, figs. 10-17, photos 54 a-b);
- *Ocululoborus curvatus*: WUNDERLICH (2012: 211-212, figs. 54-55, photos 27-29).

Further new taxa: See the tab. below. – The dubious genus *Huergina* SELDEN & PENNEY: See below: Nephilidae.

The discovery of new Cretaceous taxa indicate a striking infrafamilial variability of certain characters, and lead to a new/emended diagnosis of the family Uloboridae:

Provisional list of **diagnostic characters** of the family Uloboridae including the fossil taxa:

- Poison glands absent at least in the extant taxa (unknown in the fossil taxa);
- cribellum (photo 167) usually existing (probably absent in the Eocene genus *Opellianus* WUNDERLICH 2004), undivided; calamistrum (\*) usually existing, too; it may be indistinct or even absent in the male sex of extant spiders and is absent in fossil males of *Opellianus*;
- metatarsus IV concave dorsally and compressed laterally (figs. 360, 372, 375, 384) in the extant taxa but metatarsus straight and not compressed e. g. in the tiny extinct genus *Microuloborus* (fig. 380);
- femoral trichobothria (figs. 379, 387) exist in the extant taxa but are absent in certain fossil taxa (*Bicalamistrum*, *Burmuloborus*), see the tab. below;
- ventral bristles of tarsus III-IV (figs. 366, 373-374) existing in the extant taxa but absent in certain fossil taxa, see the tab. below;
- feathery hairs (fig. 389) existing in most extant taxa but absent in several fossil taxa, see the tab. below;
- basically exist no evidence of leg autotomy in the Uloboridae and other Deinopoidea, see ROTH & ROTH (1984: 142) ;
- basically orb weavers (see below: „Further characters“).

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(\*) It seems usually uniseriate but an additional row of short setae exists and „betrays the double nature of the calamistrum.“ See OPELL (1979: 470). Is the calamistrum double row a plesiomorphic character of cribellate spiders? See below, the genus *Bicalamistrum* n. gen. in which a well developed TWOseriate calamistrum exists.

Further characters (see JOCQUE & DIPPENAAR-SCHOEMAN (2007: 266) for further characters of extant taxa): Eye field most often wide and long, eyes frequently on humps, so most often the posterior lateral ones (figs. 367, 377). Opisthosoma elongated in certain taxa, even beyond the spinnerets (figs. 362, 367), see the tab. below. The pedipalpal femur bears a ventral tubercle or hump (fig. 389) in certain taxa. The spiders construct complete orb webs or quite modified/reduced capture webs. Body length 0.9 (in certain fossils) up to 10 mm in extant females.

**Relationships:** See the key to the families above. Deinopidae + Salticoididae may be the sister group.

**Distribution:** Cosmopolitical, mainly tropical.

Genus	femoral trichobothria	long opisthosoma	anterior spinnerets position	feathery hairs	ventral tarsal IV bristles	metatarsus IV compressed & dors. convace
<i>Bicalamistrum</i> *	--	--	--	--	+	+ (fig.361)
<i>Burmuloborus</i>	--	--	+ (fig. 367)	--	--	+(-)
<i>Jerseyuloborus</i>	+	+	+	--	+	+
<i>Microuloborus</i>	+	--	--	-?	--	--
<i>Ocululoborus</i>	?	?	?	?	?	+
<i>Palaeomiagrammopes</i>	+	+	(+)	-(?)	+	+(?)
<i>Palaeouloborus</i>	+	--	(+)	--	--	+
<i>Paramiagrammopes</i>	+ (fig. 387)	+	--	+ (fig. 389)	+ (fig. 384)	+

Tab.: Selected characters of the Mesozoic genera of the family Uloboridae.

Remarks: (+) indicate weakly developed characters.

- Based on additional material certain characters may have to be corrected in the future.
- The Jurassic genus *Talbragaraneus* SELDEN & BEATTIE 2013 – described in stone from Australia as a questionable taxon of the family Uloboridae, see below – is not included in this tab. Femoral trichobothria are not reported from the single known juvenile or female specimen. Is it really an entelegyne taxon?
- *Palaeouloborus* SELDEN 1990 (= *Macryphantes* SELDEN 1990, n. syn.) is known in in both sexes in stone of Lower Cretaceous of Spain.
- *Jerseyuloborus* WUNDERLICH 2011 is based on a juv. female in Upper Cretaceous amber from New Jersey.
- \* – *Bicalamistrum* is the only genus in which a BISERiate calamistrum (figs. 360-361 exists, consisting of NARROW rows. This genus is only known from subad. males in Burmite. See *Burmuloborus*.
- The remaining taxa are based on adult males in Mid Cretaceous Burmese amber, only *Palaeomiagrammopes* on the female sex.

**Key** to the genera of the family Uloboridae in Burmite:

The remaining Mesozoic genera like *Palaeouloborus*: See the tab. above.

1 Tiniest species, body length of the single male 0.9 mm. Femur I quite spiny (fig. 378). Femoral trichobothria apparently strongly reduced (fig. 379). ♂-Pedipalpus: Figs. 381-382. .... *Microuloborus*

- Body length usually 1.8-4.5 mm, in *Paramiagrammopes cretaceus* 1.2 mm. Femur I usually not spiny, metatarsi usually not very setose. .... 2
- 2(1) Posterior lateral eyes huge, see WUNDERLICH (2012: 229, fig. 54). ♀ *Ocululoborus*
  - Posterior lateral eyes not huge. ♂♀. .... 3
- 3(2) Femoral trichobothria existing (fig. 387). .... 4
  - Femoral trichobothria absent. .... 5
- 4(3) Terminal position of the spinnerets. ♂-Pedipalpus (fig. 389) with a large erect dorsal patellar apophysis. Body length 1.2-2.2 mm. .... *Paramiagrammopes*
  - More anterior position of the spinnerets, see WUNDERLICH (2008: 632, 672, fig. 124). ♂ unknown. .... *Palaeomiagrammopes*
- 5(3) Anterior position of the spinnerets (fig. 362, photos 161-163). Body length at least 1.8 mm. Calamistrum uniseriate (figs. 365, 372). .... *Burmuloborus*
  - Terminal position of the spinnerets. Body length 3 mm. Calamistrum biseriate (figs. 360-361) in quite narrow rows. .... *Bicalamistrum*

### **Intrafamilial evolution of three characters:**

(1) Femoral trichobothria (see the tab. above): It is unknown if the absence or the existence (and losses) (or both?) of femoral trichobothria is a plesiomorphic character of the family Uloboridae. In the tiny specimen of *Microuloborus* the number of femoral trichobothria is apparently strongly reduced. One may compare the family Tetragnathidae in this matter: Femoral trichobothria exist in the advanced subfamily Tetragnathinae but are absent e. g. in more ancient Eocene genera in Baltic amber, see WUNDERLICH (2004).

(2) Number and pattern of the eyes (see WUNDERLICH (2008: 556-558, figs. A-C)): The figs. A-C in that paper show a „row of reduction“ as well as a change of the shape of the prosoma and of the position of the eyes during 100 million years in three genera which I regards as related. (Fig. C. shows the pattern in the genus *Palaeomiagrammopes* which is quite similar in the genus *Paramiagrammopes*). I regard the Eocene genus *Eomiagrammopes* WUNDERLICH 2004 as the model of a „missing link“.

### (3) The body size:

The body length is...

in males in Cretaceous Burmite 0.9-3.2 mm, in average almost 3 mm,

in males on Eocene Baltic amber 1.4-5.7 mm,

in extant spiders 3-10 mm (♂♀; see JOCQUE & DIPPENAARE-SCHOEMAN (2007:266).

I estimate the average of more than 4 mm in the male sex of today's spiders.

Most probably larger spiders were captured less frequent in the fossil resins than small spiders. Results – if focused on the tiniest species which were captured most easy in the fossil resins –: The body length of such tiniest Eocene males is more than 150 % compared with the Cretaceous males, the body length of tiniest today's males is more than 200 % compared with Eocene males and even more than 300% of the Cretaceous males.

More fossil – and probably extant – material is needed for definitive conclusions about the increasing of the body length in the family Uloboridae during the last hundred million years.

## **Description of the taxa**

### **Bicalamistrum n. gen.**

Etymology: The name refers to the biseriate calamistrum; bi- (lat.) = double.

The gender of the name is neuter.

**Type species** (by monotypy): *Bicalamistrum mixtum* n. sp.

**Diagnosis** (subad. ♂): Femoral trichobothria and feathery hairs absent. Calamistrum consisting of TWO narrow (close together), long and well developed rows of setae (figs. 360-361) (unique in the family Uloboridae) (but see fig. 372!).

Further characters: Basal cheliceral articles strongly developed (fig. 357), ventral tarsal IV bristles existing.

**Relationships**: According to the shape of metatarsus IV and the eye field I regard *Bicalamistrum* as a member of the family Uloboridae although femoral trichobothria are absent. The basically double nature of the calamistrum of the family Uloboridae has been pointed out by OPELL (1979: 470) but in all extant taxa of this family only a single row of calamistrum setae is well developed and long. A study of the bulbus of the unknown adult male is needed to find out closer relationships of the new genus.

Note: A biseriate calamistrum (but not a dorsally concave metatarsus IV) exists also in certain members of the family Oecobiidae, in the family Hypochilidae, and certain members of the family Amaurobiidae.

**Distribution**: Mid Cretaceous amber forest of Myanmar (Burma).

**Etymology:** The species name refers to its characters which are mixed from different taxa, from *mixtura* (lat.) = mixture.

**Material:** 2 subad. ♂ in Mid Cretaceous amber from Myanmar (Burma); holotype and a separated piece of amber F2763/BU/CJW, paratype and a separated piece of amber F2764/BU/CJW.

**Preservation and syninclusions:** The holotype is excellently and almost completely preserved in a clear yellow-orange piece of amber; only the retrolateral part of the left patella II is cut off within the amber, the right leg I is strongly raised, see the photo. A white emulsion and probably Bacteria cover the dorsal side of the opisthosoma. – Some spider threads exist just below the spider on a layer within the amber, several tiny bubbles of water/air and tiny particles of detritus are also preserved. – The paratype is incompletely preserved and deformed apparently by the preservation, most parts of the opisthosoma are lost or translucent and injured, a particle of detritus exist in the original position of the opisthosoma, the left leg II is cut off through the metatarsus. The spider has probably been a prey. – The female pedipalpus of a spider, ½ tiny Diptera (at the surface of the amber), 2 Collembola, numerous plant hairs, particles of detritus and some pear-shaped grey „bubbles“ at the surface of the amber exist in the same piece.

**Diagnosis, relationships and distribution:** See the new genus.

**Description** (subad. ♂; mainly based on the holotype):

Measurements (in mm): Holotype: Body length 3.0, prosomal length ca. 1.3, opisthosoma: Length 2.0, width 1.2; leg I: Femur 2.1, patella 0.6, tibia 2.0, metatarsus 2.25, tarsus 0.85; tibia II 1.1, tibia III 0.55, tibia IV ca. 0.8; pedipalpus: Femur 1.0, patella 0.35, tibia 0.5, tarsus 0.55. – Paratype Body length ca. 3.0, metatarsus I 1.9.

Colour: Prosoma and legs medium brown, legs apparently not annulated, opisthosoma light grey brown.

Prosoma (figs. 357-358, photo) (it is deformed and partly hidden) fairly stout, most hairs short, 8 eyes in a very wide field, posterior row recurved, lateral eyes on humps, anterior median eyes spaced by probably their diameter, posterior median eyes largest, clypeus short, basal cheliceral articles large, fangs slender. – Pedipalpus (photo): Articles long and slender, tibia with few dorsal trichobothria and a dorsal-distal bristle, tarsus spiny and thick, with a large apical claw which bears long teeth. – Legs (figs. 359-361, photo) fairly long and slender, order I/II/IV/III, I distinctly the longest, III distinctly the shortest, hairs short and indistinct, bristles numerous and short, usually not much longer than the diameter of the article (seemingly longer on the shrunk legs of the paratype), existing ventrally, dorsally and laterally on the femora as well as existing on patellae, tibiae, metatarsi and tarsi (few ventral ones). Metatarsus IV distinctly concave dorsally, distinctly compressed laterally, bearing two long and narrow rows of calamistral setae. Trichobothria absent on femora and tarsi, some long ones exist in the basal third of tibia I, position of the metatarsal I trichobothrium in 0.22. Feathery hairs absent. Paired tarsal claws with long teeth, unpaired claw fairly large. – Opist-

hosoma (photo) oval, 1.6 times longer than wide, bearing short hairs and two pairs of tiny sigilla (observable in the holotype). Anal tubercle and spinnerets short, cribellum short, wide and entire.

**Burmuloborus** WUNDERLICH 2008

Type species (by monotypy): *Burmulobous parvus* WUNDERLICH 2008 (?ad. ♀).

See WUNDERLICH (2008: 634).

Most probably femoral trichobothria and ventral bristles on tarsus III-IV are absent in this genus, see the tab. below.

Here I describe two species based on female which are probably congeneric.

***Burmulobous antefixus* n. sp.** (figs. 362-366) photo 161

Etymology of the species name: From antefixus (lat.) = fixed anteriorly, based on the anterior position of the spinnerets.

**Material:** Holotype ♀ in Mir Cretaceous Burmite, F2485/BU/CJW.

**Preservation and syninclusions:** The spider is completely and well preserved in a yellow (slightly green) piece of amber, parts of the body and legs are fairly deformed, e. g. the left metatarsus IV bears a „furrow“ which I regard as an artefact, the eyes, the eye field and the spinnerets are deformed, the cribellum is hidden by a bubble. A questionable cribellate thread – including questionable axial fibers – is preserved just above the left calamistrum and runs to the spinnerets. – A six-legged larva of a tick, body length 0.55 mm, is preserved just right of the left leg I, a tiny deformed Diptera, a larger claw which may originate from a vertebrate animal, numerous particles of insect's excrement, several plant hairs and few hardened particles of fossil resin are also preserved.

**Diagnosis** (♀; ♂ unknown): Spinnerets (fig. 362, photo) in an advanced position on the long opisthosoma, legs (figs. 364-366) long and slender (photo), bearing numerous thin bristles, femur I as long as the body.

**Description** (♀):

Measurements (in mm): Body length 3.2, prosomal length 1.0; opisthosoma: Length 2.3, height 0.8; leg I: Femur 3.2, patella 0.5, tibia 3.0, metatarsus 2.8, tarsus 1.4, tibia II 1.3, tibia III ca. 0.75, tibia IV ca. 1.15.

Colour medium brown, legs not annulated.



Prosoma (photo) longer than wide, fairly low, smooth, fovea well developed, 8 large eyes in two wide and almost parallel rows (the field is deformed), clypeus not protruding, ca. as long as the eye field, basal cheliceral articles fairly large, lateral files absent, teeth of the fang furrows hidden or absent, fangs large, gnathocoxae stout, not converging and widely spaced by the labium which is probably fused to the sternum, sternum slender, distinctly longer than wide, coxae IV not widely spaced. – The pedipalpal tarsus (fig. 363) bears a long and toothless claw. – Legs (figs. 364-366) long and slender, order I/IV/II/III, I distinctly the longest, III distinctly the shortest, hairs indistinct and simple, bristles numerous, short and very thin (some almost hair-shaped), existing on femora, patellae, tibiae and metatarsi, ventral tibial and metatarsal bristles absent; leg I (some bristles may be broken off): Femur dorsally 5, prodorsally 2 like on the remaining legs, patella and tibia dorsally 2 like on the remaining legs and tibia retrolaterally 2, metatarsi apparently 3 very thin bristles. Most bristle of the remaining legs may be rubbed off. Trichobothria absent on femora and tarsi, a single trichobothrium exists at least on the metatarsi I-III, their position in ca. 0.15. Metatarsus IV dorsally concave (this is not well observable in the position of fig. 365), distinctly compressed laterally, the hairs of the calamistrum occupy ca. 40% of the metatarsal length. Three larger tarsal claws which all may be smooth, few thin ventral bristles on tarsus IV. – Opisthosoma (fig. 362, photo) almost three times longer than high, soft, hairs tiny and indistinct, epigaster not protruding, epigyne absent, tracheal spiracle apparently near the large spinnerets which are set forward, the anterior pair widely spaced and converging, cribellum hidden, anal tubercle small.

**Relationships:** See ?*B. prolongatus* n. sp. *B. parvus* is distinctly smaller, body length 1.8 mm, and the opisthosoma is stout, see WUNDERLICH (2008: 671, fig. 117).

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

?*Burmuloborus prolongatus* n. sp. (figs. 367-368) photos 162-163

**Etymology:** The species name refers to the long opisthosoma which is distinctly prolonged beyond the spinnerets, from (new lat.) prolongare = prolongate.

**Material:** Holotype juv. ♀ and two separated pieces of amber in Mid Cretaceous Burmite, F2775/BU/CJW. This piece was separated from a larger piece of amber, F2774/BU/CJW, in which a second juv. Uloboridae indet. and two juv. Lagonomegopidae indet. are preserved.

**Preservation and syninclusions:** The spider is excellently and completely preserved in a clear yellow piece of amber, the prosoma is dorsally somewhat depressed, the sternum is somewhat compressed laterally. – Below the labium a particle of insect's excrement is preserved. In the smaller separated piece is an Acari: Erythraeidae preserved, in the larger piece few plant hairs. See also above (Material).

**Diagnosis** (juv. ♀): Opisthosoma (fig. 367, photo) widely prolonged posteriorly beyond the spinnerets, femoral trichobothria and leg bristles apparently absent. Eyes as in figs. 367-368

**Description** (juv. ♀):

Measurements (in mm): Body length 2.3, prosoma: Length 0.7, width 0.5; opisthosoma: Length 1.6, width 0.6; leg I: Femur 0.85, patella 0.27, tibia 0.47, metatarsus 0.7, tarsus 0.3, tibia II 0.22, tibia III 0.18, tibia IV 0.5.

Colour light brown, legs annulated.

Prosoma (figs. 367-368, photo) 1.4 times longer than wide, hairs indistinct, feathery hairs absent, thoracic fissure indistinct, eyes in a wide field, fairly large, anterior and posterior laterals on indistinct humps, posterior distinctly recurved, median eyes widely spaced, clypeus long, basal cheliceral articles fairly large, bearing a long thin bristle in the basal half, anterior margin of the fang furrow bearing 2 or 3 teeth, fangs long and thin (needle-shaped), labium apparently long, gnathocoxae strongly converging, sternum not elongated posteriorly. – Pedipalpus long and slender. – Legs only fairly long and slender, order I/IV/II/III, IV almost as long as I, III shortest, II also short, hairs indistinct, bristles absent (probably rubbed off), ventral tarsal IV bristles absent, metatarsus IV bent, concave dorsally, calamistrum well developed, length more than half of the metatarsal length. Femoral trichobothria absent, metatarsal trichobothria unknown, tarsal claws small. – Opisthosoma (fig. 367, photo) 2.7 times longer than wide, anteriorly distinctly inclined, hairs short, cribellum hidden, anterior spinnerets large and strongly converging, anal tubercle large.

**Relationships:** In ?*B. antefixus* the legs are distinctly shorter, leg bristles are absent (or rubbed off?), the opisthosoma is not inclined anteriorly, the spinnerets are in a more posterior position, the position of the eyes is different. When knowing the unknown male we may decide if prolongation is probably the member of a separate genus.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

?*Burmuloborus* sp. indet. (figs. 369-373) photo 164

**Material:** ♀-exuvia in Mid Cretaceous amber from Myanmar (Burma), F2448/BU/ CJW. According to its long and slender legs the exuvia did not originate from a young spider but probably from a subadult specimen.

**Remark:** According to the position of the legs (see the photos and below), the preserved peltidium, the slender pedipalpi, and the small and hairy remains of the opisthosoma as well as remains of gas in the basal cheliceral articles and in some leg articles I conclude that the holotype is a female exuvia.

**Preservation and syninclusions:** The exuvia is incompletely, partly hidden, decomposed, and badly preserved near the corner of a mainly clear yellow-orange piece of amber which is 3 cm long; parts of the prosoma are deformed and anteriorly covered with a bubble, e. g. parts of the eye field, the distal parts (tarsi, parts of the metatarsi) of legs I and II are cut off, only hairy remains exist of the crumbled opisthosoma, the chelicerae and most legs including the calamistra are well preserved, the legs are stretched strongly ventrally (which is typical for exuviae), see the photos. – **Syninclusions** are numerous and mostly decomposed, remains of detritus and insects like several Diptera as well as loose wings, legs and excrements, 3 larvae of cicads, a Thysanoptera; a tiny mite and a tiny lump of questionable Bacteria are preserved near the margin of the piece of amber, small remains of plants like hairs and wood are also preserved.

**Diagnosis** (♀-exuvia): Femoral trichobothria absent, legs with numerous bristles (figs. 372-373), position of the metatarsal II trichobothrium in ca. 0.15 (fig. 373), metatarsus IV with a long and deep depression (fig. 372).

**Description** (♀-exuvia):

Measurements (in mm): Body length ca. 3.0, prosomal length 1.6; length of the pedipalpus ca. 1.4; leg s: I: Femur ca. 2.8, patella 0.8, tibia 2.3; II: Tibia ca. 1.3, metatarsus 1.6; III: Tibia 0.65, metatarsus 0.75, tarsus 0.55; tibia IV ca. 1.0.

Colour orangebrown, legs not annulated.

Prosoma (figs. 369-371; parts are hidden or deformed) probably low, hairs indistinct, cuticula smooth, eyes large, the field wide, triads existing, the laterals widely spaced from each other, posterior row strongly recurved. Fovea unknown, clypeus short, not protruding. Basal cheliceral articles large, in a vertical position, with a strong basal-medial sclerite, medial depressions and lateral files absent, fang furrow large, anterior margin with 3 teeth, posterior row with at least 3 small teeth, fangs stout, in an oblique (plagiognath) position. Gnathocoxal serrula apparently a single row. Sternum probably longer than wide. – Legs (figs. 372-373, photo 164) spiny, long and slender, order I/II/IV/III, bristles slender and numerous, on femora, patellae (weak and partly hair-shaped), tibiae, metatarsi and tarsi; leg I (tarsus and distal parts of the metatarsi are cut off): Femur 10 dorsally and prodistally (a single one), patella a long hair-shaped dorsally-apically, tibia 1/1/1 ventrally, prolaterally and retrolaterally, 1 dorsally-distally, metatarsus with about 10 bristles. The metatarsi bear a circle of about 6 apical bristles. Tarsus IV bears 2-3 bristles in the distal half, 2 near the end. Metatarsus IV with a long and deep depression, calamistrum long an additional row of short setae exist on the other side of the depression, position of the metatarsal II trichobothrium in ca. 0.15. Three tarsal claws, paired claws toothed and not dissimilar. – Opisthosoma: Only small hairy remains exist.

**Ecology and behaviour:** The spider lived in the Burmese amber forest, a rain forest. According to the existence of a calamistrum (thus a cribellum existed, too), the long and slender legs with a quite shorter leg III as well as the absence of leg scopulae and „preening combs“ on metatarsi III-IV the spiders of this species built capture webs most

probably in an irregular web which included cribellate threads, and were most probably dwellers of higher strata of the vegetation or between rocks. The prey may have been flying insects like Diptera which are frequent in Burmese amber.

**Relationships:** Metatarsus and calamistrum are similar in *Burmuloborus parvus* which is smaller. Adult spiders are needed to find out the relationships.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

?*Burmuloborus* sp. indet. (figs. 374-376)

**Material:** 1♀ in Mid Cretaceous amber from N-Myanmar (Burma), coll. BEATE STOLZ in Bremen, BU/1/CBS.

**Preservation and syninclusions:** The spider is incompletely preserved, parts are hidden or deformed, the opisthosoma and several leg articles are cut off, the right calamistrum is preserved. – 1 3/4 Gastropoda, a tiny Acari, 1 hairy Diplopoda, 1 Diptera and insect's excrement are preserved in the same piece of amber. Above the right tarsus I remains of an insect (Diptera?) are preserved which probably has been the prey of the spider.

**Diagnosis** (♀; ♂ unknown): Metatarsus I with several short ventral bristles which partly are paired (fig. 374).

### **Description** (♀):

Measurements (in mm): Body length probably about 3.0, prosomal length 1.5; leg I: Femur 1.7 (height 0.35), patella ca. 0.7, tibia 1.45 (height 0.2), metatarsus 1.55 (height 0.1), tarsus ca. 0.7; tibia II 1.4, tibia III 1.2 (tibia IV is deformed), pedipalpal tibia 0.9.

Colour grey brown, legs not annulated.

Prosoma (most dorsal parts are hidden by one of the Gastropoda, most ventral parts are covered with an emulsion) apparently distinctly longer than wide and probably flat, eyes hidden. – Pedipalpus very long, slender, spiny and hairy, tarsal claw existing. – Legs (figs. 374-376) long and slender, order I/II/IV/III, hairs numerous but not long, numerous bristles on femora, patellae, tibiae, metatarsi and tarsi; leg I: Femur: several bristles mainly dorsally, patella: 2 thin dorsally, tibia: 2 thin dorsally and 2 ventral pairs besides an apical pair, metatarsus: several ventrals, some are paired, tarsus: few short ventral ones in the distal half. Short ventral tarsal bristles are recognizable on I-II and thus most probably existing on III-IV although not observable. Tarsi protruding (pointing) ventrally-apically and bearing „auxiliary hairs“, 3 claws, the paired ones are toothed, the unpaired one is smooth and stout. Metatarsus IV bears a seemingly double-rowed calamistrum of short hairs besides the basal third and the distal part; the rows of hairs include a quite distinct field. Feathery hairs absent, metatarsal trichobothria unknown, femoral and tarsal trichobothria absent. – Opisthosoma cut off except the most basal part; it may be flattened dorso-ventrally.

**Relationships:** According to the absence of femoral trichobothria and shape of the metatarsus IV as well its calamistrum this specimen may well be a member of the genus *Burmuloborus*.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

**Microuloborus n. gen.**

Etymology: The name refers to the tiny body, from *micro* (gr.) small and to the type genus *Uloborus* of the family Uloboridae.

The gender of the name is masculine.

**Type species** (by monotypy): *Microuloborus birmanicus* n. sp.

**Diagnosis** (♂; ♀ unknown): Body length only 0.9 mm (smallest known member of the family Uloboridae), wide eye field (fig. 377), posterior median eyes widely spaced, femoral trichobothria apparently strongly reduced (fig. 379), bristles of femur I as in fig. 378, metatarsus IV straight, pedipalpus (figs. 381-382) with a long embolus which describes half a circle.

**Relationships** of the unusual taxon: See the tab. above.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

***Microuloborus birmanicus* n. gen. n. sp.** (figs 377-382) photos 165-167

Etymology of the species name: Birma is the oldest name of the country currently named Myanmar.

The gender of the name is masculine.

Material: Holotype ♂ in Mid Cretaceous Burmite, F2767/BU/CJW.

**Preservation and syninclusions:** The spider is almost completely and well preserved (ventrally fairly deformed) in a yellow piece of amber – situated and a bit compressed – between two layers of amber; the right tarsus IV is injured and incompletely preserved. The dorsal part of the prosoma has been cut off inside the amber. – A Diptera: Nematocera, remains of a tiny arthropod, few plant hairs and numerous ?air/water bubbles are preserved in the same piece of amber.

**Diagnosis, relationships and distribution:** See above.

**Description (♂):**

Measurements (in mm): Body length 0.9; prosoma: Length 0.48, width 0.33; opisthosoma: Length 0.55, width 0.42; leg I: Femur ca. 0.45, patella 0.13, tibia 0.32, metatarsus 0.27, tarsus 0.2; tibia II ca. 0.21, tibia III ca. 0.11, tibia IV 0.19.

Colour: Prosoma and legs medium brown, legs not annulated, opisthosoma grey brown.

Prosoma (fig. 367, photo) 1.45 times longer than wide, anteriorly distinctly narrowed, eye field wide, eyes on humps, anterior median eyes largest, posterior median eyes widely spaced, clypeus short, basal cheliceral articles small, fangs slender, gnathocoxae large and converging, serrula very long, labium wide, sternum damaged, bearing long hairs. – Legs (figs. 378-380, photo) fairly short, order I/IV/II/III, anterior femora strongly developed. Leg III distinctly the shortest, hairs indistinct, femur I bears dorsally ca. a dozen long and thin bristles, the remaining femora bear strong/long hairs, metatarsal trichobothria unknown, metatarsus IV straight and not compressed, calamistrum ca. 2/3 as long as the article, ventral tarsal IV bristles probably absent. Femoral trichobothria hard to recognize, at least III and IV bear a long prodorsal one. Three tarsal claws, the paired ones long and slender. – Opisthosoma (photo) (the dorsal part is cut off on a layer in the amber), 1.3 times longer than wide, hairs of medium length, cribellum wide and undivided, anterior spinnerets slender, basally widely spaced, strongly converging, anal tubercle large. – Pedipalpus (figs. 381-382) (its structures are difficult to observe) with slender articles, cymbium large, ebolus long and strongly bent, describing probably half a loop.

**Ocululoborus** WUNDERLICH 2012

Type species (by monotypy): *Ocululoborus curvatus*, see WUNDERLICH (2012: 211, figs. 54-55, photos 27-29). The taxon is based on a decomposed female.

***Palaeomiagrammops*** WUNDERLICH (2008: 632, 672: figs. 123-126, ♂ unknown):

Only *P. vesica* WUNDERLICH 2008. See *Paramiagrammopes* n. gen.

**Palaeouloborus** SELDEN 1990 n. relat. (= *Macryphantes* SELDEN 1990) ( n. syn.)

Based on a probably adult female *Palaeouloborus* has been described in stone of Lower Cretaceous amber from the Sierra de Montsech, North-East Spain.

Type species (by monotypy): *Palaeouloborus lacasae* SELDEN 2002.

**Diagnostic characters** (female; male see below): Femoral trichobothria existing, legs stout, metatarsus IV concave dorsally and calamistrum apparently uniseriate, ventral tarsal IV bristles and feathery hairs ABSENT, opisthosoma not elongated, body length ca. 5.6 mm.

According to SELDEN (1990: 262) „*Palaeouloborus* cannot be included in the family Uloboridae because it has neither feathery hairs nor forth tarsal macrosetae.“ To my knowledge both characters are absent in certain Uloboridae, see the tab. above (feathery hairs are e. g. absent in the Uloborinae). Therefore I regard *Palaeouloborus* as a member of the Uloboridae (**n. relat.**).

*Macryphantes* SELDEN 1990:

Based on two adult males the genus *Macryphantes* has been described under Tetragnathidae (!) (\*) from the same Cretaceous deposit as *Palaeouloborus*. The type species (by monotypy) is *Macryphantes cowdeni* SELDEN 1990. Its body length is probably about 6.5 mm, femoral trichobothria exist, feathery hairs are reported as absent, large basal cheliceral articles or a conductor wrapping the embolus are not reported or absent, the embolus is coiled. According to these characters I regard *Macryphantes* as synonym with *Palaeouloborus* (**n. syn.**), and the family Tetragnathidae has to be removed from the list of the Mesozoic spider fauna. This new synonymy does not touch the species level: *cowdeni* is probably not a synonym of *lacasae*.

I already previously excluded *Macryphantes* from the family Tetragnathidae, see WUNDERLICH (2004: 854).

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(\*) No sure member of the Tetragnathidae has ever been reported from the Cretaceous.

**Paramiagrammops** WUNDERLICH 2008

The genus is well characterized by its male pedipalpus (figs. 385-386, 389) in which the patella bears a long erect dorsal apophysis and the femur bears a ventral outgrowth; metatarsus IV is straight or almost straight and not compressed laterally (fig. 384).

I do not want to exclude that *Palaeomiagrammopes* WUNDERLICH 2008 (♂ unknown) may be synonymous with *Paramiagrammopes*.

Only a single species in Burmite has been described, *P. cretaceus* WUNDERLICH 2008 and a subad. male of *P. sp.* Here I describe two further species from the same kind of amber.

The gender of the name is masculine.



***Paragrammopes longiclypeus* n. sp.** (figs. 383-386)

**Etymology:** The species name refers to the long clypeus, from longus (lat.) = long.

**Material:** Holotype ♂ in Mid Cretaceous Burmite, F2776/BU/CJW.

**Preservation and syninclusions:** The spider is completely but only fairly well preserved; the piece of amber was heated by the preservation. Its left side is in contact to the oxidated surface of the piece of amber which includes a hole to the spider's prosoma; both pedipalpi are apparently dissected/decomposed, the opisthosoma is compressed dorsally. – Some cribellate spider's threads run from the right pedipalpus along the right part of the prosoma. Remains of a tiny Thysanoptera exist, and a tiny (0.8 mm long) decomposed insect – a prey? – is preserved just in front of the spider's pedipalpi.

**Diagnosis** (♂; ♀ unknown): Clypeus (fig. 383) very long and protruding, leg I (photo) distinctly longer than II; pedipalpus (figs. 385-386): Patella bent in a right angle near the tip, bearing a slender apophysis and a tiny additional bristle-shaped apophysis; a femoral apophysis is hidden or absent.

**Description** (♂):

Measurements (in mm): Body length 2.6; prosomal length (including the long clypeus) 0.95; opisthosoma: Length 1.5, width ca. 0.9, height 0.6; leg I: Femur 1.7, patella 0.35, tibia 1.25, metatarsus 1.25, tarsus 0.55, tibia II 0.6, tibia III 0.33, tibia IV 0.62.

Colour medium brown, legs annulated.

Prosoma (fig. 383) (parts are hidden) probably not much longer than wide, fovea large, most probably 8 eyes, clypeus very long and protruding, basal cheliceral articles small, gnathocoxae strongly converging, sternum weakly elongated between the coxae IV. – Legs (fig. 384) partly long, slender, order I/IV/II/III, I distinctly the longest, III distinctly the shortest, hairs indistinct, bristle short and not numerous; femur I 2 dorsals, remaining femora 1 dorsally-distally, patellae with a well developed dorsal-apical bristle, tibia I with 4 bristles in a more or less dorsal position, metatarsus I with a single dorsal bristle, II-IV apparently dorsally bristleless, IV bears a ventral-distal one. Tarsus IV bears 8 short ventral bristles, remaining tarsi bristleless, metatarsus IV concave dorsally, not compressed, calamistrum well developed in the basal third, position of the metatarsal trichobothrium unknown, tarsal claws well developed, unpaired claw at least as long as the paired claws which may be smooth. Femora with few trichobothria which are difficult to observe. – Opisthosoma distinctly longer than wide, hairs short, cribellum hidden, anterior spinnerets widely spaced, anal tubercle well developed. – Pedipalpus (fig. 385-386) (they are not well preserved, parts are hidden): See the diagnosis.

**Relationships:** In the remaining congeneric species the structures of the pedipalpal patella are different.

**Distribution:** Mid Cretaceous amber forest of N-Myanmar (Burma).

***Paramiagrammopes patellidens* n. sp.** (figs. 387-389) photos 168-170

**Etymology:** The spider's name refers to the tooth-like spine of the pedipalpal patella, from dens (lat.) = tooth.

**Material:** Holotype ♂ and a separated piece of amber in Mid Cretaceous Burmite, F2450/BU/CJW.

**Preservation and syninclusions:** The spider is excellently and almost completely preserved in a clear yellow piece of amber, the left tarsus and metatarsus I and the right tarsus I are cut off, the opisthosoma is slightly deformed. – Some irregular and partly clumped spider's threads are preserved near the right tarsus and metatarsus II (probably including an attachment disc) and left behind the spider. Some plant hairs exist in the separated piece of amber.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (fig. 389): Apical patellar apophysis claw-shaped and bent in a right angle, additionally a tooth-like structure retrolaterally in the basal half.

**Further characters:** Feathery hairs existing even on the pedipalpal femur (fig. 389).

**Description** (♂):

**Measurements** (in mm): Body length 2.2, prosomal length 0.8; opisthosoma: Length 1.5, height 0.6; leg I: Femur 1.4, patella 0.3, tibia 1.0, tibia II 0.55, tibia III 0.25, tibia IV 0.55.

**Colour:** Prosoma medium brown, legs light to medium brown, annulated, opisthosoma light grey brwn.

Prosoma (photos) about as wide as long, fovea deep and transverse, apparently most hairs are rubbed off, feathery hairs existing, 8 fairly large eyes in a wide field, posterior row slightly recurved, median eyes not large, anterior median eyes separated by about their diameter, posterior median eyes spaced by ca. two of their diameters, lateral eyes not contiguous, clypeus very long, basal cheliceral articles small, gnathocoxae large and converging, bearing two larger humps and a small one, labium wide and apparently free, sternum unmodified, spacing the coxae IV by about their diameter. – Legs (figs. 387-388, photos) fairly long, order I/II/IV/III, I distinctly the longest, III distinctly the shortest, hairs fairly distinct, bristles numerous: Femur I: 3 prolaterally (2 in the basal half), patellae: I dorsally-apically and additionally a dorsal basal one at least on III, tibia I: 2 in the basal half and 4 distally/apically, metatarsus I few in the distal half/ apically, tarsus III 2 or 3 ventrally, tarsus IV a row of half a dozen ventrally (short). Metatarsal trichobothria unknown, femoral trichobothria long, in an irregular position on II-IV, on IV a row of a dozen and additionally some in an irregular position. Metatarsus IV straight and not compressed laterally, calamistrum indistinct. – Opisthosoma long, cribellum only fairly wide, entire, 3 pairs of spinnerets, the anterior widely spaced and not converging, anal tubercle large. – Pedipalpus (fig. 389): Trochanter long and slender, apically elongated, femur thick, bearing feathery hairs (apparently most of those hairs are rubbed off), a ventral-basal hump and a pointed ventral-distal tooth-shaped apophysis, patella with a basal brush of plumose hairs in a row, a long dorsal bristle, a claw-shaped bristle on a retrolateral hump in the basal half, and a long,

erect, and claw-bearing blunt apophysis. Cymbium wide, with an apical notch but no bristle. Bulbus large, bearing complicated structures including a large median apophysis which bears a strongly bent spur. Embolus long, strong and bent around the spur of the median apophysis.

**Relationships:** In *P. cretaceus* WUNDERLICH 2008 (in Burmite, too) the pedipalpal femoral tooth is more slender, a patellar tooth-like bristle is absent, the tip of the long patellar apophysis is not a claw-shaped bristle, and not bent in a right angle; the structures of the bulbus are quite different.

**Distribution:** Mid Cretaceous amber forest of N-Myanmar (Burma).

### **Uloboridae indet. in Burmite:**

F2772/BU/CJW:

A probably adult ♀ in Mid Cretaceous amber from N-Myanmar. The spider is only fairly well preserved in an almost globular piece of amber which has a boring. Its body is – especially ventrally – covered with a white emulsion, the prosoma is deformed. The left leg I is lost beyond the patella probably by autotomy, the tip of the right tarsus I is cut off. The body length of the spider is ca. 3.6 mm, most eyes are hidden, the calamistrum is well developed on the metatarsi IV which are dorsally concave like in most Uloboridae, not compressed laterally. Parts of a probably cribellate capture web are preserved in the same piece of amber.

### **A questionably taxon of the family Uloboridae from the Jurassic:**

***Talbragaraneus jurassicus* SELDEN & BEATTIE 2013**

A poorly preserved juvenile or female specimen preserved in stone from the Late Jurassic of Australia by SELDEN & BEATTIE (2013). Like in most uloborids the metatarsus IV is concave dorsally and the calamistrum runs almost the full length of the metatarsus IV as in several extant uloborids. The holotype has been „tentatively“ been regarded as a member of the Uloboridae but I am not sure about its relationships – is it really an entelegyne taxon?

## (2) The ARANEOID branch (the ecribellate araneoid branch) (= Araneoidea s. str.)

Characters: See above (Araneoidea s. l.).

Diversity in the Mesozoic: I know mesozoic members of the families Nephilidae, probably (unlikely) Linyphiidae, most probably Theridiidae (a single species), Theridiosomatidae and Zygeliidae. All families are very rarely reported from this era compared with diverse families like Archaeidae, Lagonomegopidae, Praeterleptonetidae or Uloboridae or compared with their high diversity of this branch in the Eocene Baltic amber, see WUNDERLICH (2004).

### Dubious taxa:

See „(?) Araneoidea: Fam. indet.“ in Cretaceous Burmese amber, juv. female sensu WUNDERLICH (2008: 644-645, photo 118) which relationships are quite unsure. Also quite unsure are the relationships of the Jurassic *Mesarania hebeiensis* HONG 1984 from China. – The genus *Seppo*: See below.

Parts of capture webs including threads which bear sticky droplets may originate from members of the Araneoides s. str. and are occasionally preserved in Burmite, e. g. near the holotype of *Cymbiolagonops calcar* n. gen. n. sp. (Archaeoidea: Lagonomegopidae); see also WUNDERLICH (2008: 801, figs. 52-55). Members of the superfamily Archaeoidea do not build capture webs.

### (a) The araneoid subbranch (the ecribellate orb weavers)

I know the families ?Araneidae, Nephilidae and Zygeliidae.

The cribellate family JURARANEIDAE: See the chapter on erroneous determinations and dubious taxa above.

The family TETRAGNATHIDAE has to remove from the list of Cretaceous spiders: The Cretaceous genus *Macryphantes* SELDEN 1990 is regarded here as a member of the family Uloboridae, see the chapter on erroneous determinations above.

Family PROTHERIDIIDAE in Burmite = Leptonetoidea, see above, the chapter on erroneous determinations.

Questionable Araneoidea (Araneidae, Zygiellidae or a related family?):

The Jurassic *Seppo koponensis* SELDEN & DUNLOP 2014 – based on a probably adult female in Jurassic calcit from Germany – has been regarded as a member of the superfamily Archaeoidea (under Palpimanoidea) and not assigned to family level. The authors of this taxon founded their determination mainly on the existence of „peg teeth“ (which really are modified bristles) but their tip is not blunt as in typical peg teeth. Furthermore the existence of numerous leg bristles (they are absent or extremely rare in other fossil and in extant taxa of the Archaeoidea), and a well developed pedipalpal claw (it is absent or strongly reduced in the Archaeoidea) may argue against relationships to the Archaeoidea but more for relationships to the Araneoidea/Deinopidea which usually/frequently possess short legs III and large to powerful legs I as well as large basal cheliceral articles like the present fossil. The transport of a dweller of higher strata of the vegetation – like Araneoidea – on a tree or its branch to a marine deposit appears likely to me. Sure mesozoic ground-living Arachaeoidea are unknown to me but dweller of higher strata of the vegetation were frequent in that era. I do not want to exclude that the fossil in question may be strongly related to the families ARANEIDAE or ZYGIELLIDAE.

## **Family ARANEIDAE**

See the key to the families no. 32 and the Zygiellidae below.

I do not know a sure Cretaceous proof of this family if the family Zygiellidae (see below) is excluded

*Araneus aethus* CHANG 2004, *A. beipiaoensis* CHANG 2004, *A. liaoxiensis* CHANG 2004 and *A. reheensis* CHANG 2004, Cretaceous, in stone from Liaoning in China: The generic and probably even the familiar assignment are unclear, see „Fossils“ (under Araneidae: *Araneus*) in the Spider Catalog by PLATNICK.

The genus *Seppo* SELDEN & DUNLOP 2014: See directly above.

The genus *Mesozygella* PENNEY & ORTUNO 2004: See below, Zygiellidae.

## Family NEPHILIDAE

See the key to the families no.32.

Three species of *Cretaraneus* SELDEN 1990 have been described in stone:

*C. vilaltae* SELDEN 1990 (figs. 390-391), male from Spain,

*C. laoningensis* CHENG et al. in CHENG et al. 2008, male from China and

*C. martensnetoi* MESQUITA 1996, ?juv. ♀ from Brazil.

In my opinion the generic and even the familiar assignments of the latter two species have to check.

*Nephila jurassica* SELDEN et al. 2011 has been described from the Jurassic of China, based on an adult female. SELDEN et al. (2013) transferred the species to the genus *Mongolarachne* of the family Mongolarachnidae, see above.

*Nephila* sp. indet. from Brazil: See DUNLOP & PENNEY 2012: Fig. 93.

In my opinion the generic assignment of these two species has to check.

*Huergina diazromerali* SELDEN & PENNEY 2003 – based on a badly preserved questionable adult female spider in Lower Cretaceous stone from Spain – was placed in the family Nephilidae (under Tetragnathidae: Nephilinae). It „is placed here because of its long, slender legs, lack of tarsal scopulae, elongate abdomen, tightly grouped, short subterminal spinnerets, and lack of distinctive synapomorphies of other superfamilies.“ – According to these characters it appears impossible to assign the taxon to a family level, and I do not want to exclude that it may be a member of the family Uloboridae.

There is no sure report of the family from Burmite. *Geratonephila burmanica* POINAR & BUCKLEY: See above: The chapter on erroneous determinations.

## Family ZYGIELLIDAE

See the key to the families no. 32.

Most recent authors include this taxon as a subfamily in the Araneidae. No distinct sexual size dimorphism exists in contrast to the Araneidae.

According recent studies by GREGORIC et al. (in press; „Abstract Book“ of the Arachnological Congress in Taiwan (2013), p. 66, based on nuclear and mitochondrial data „show that the classical Araneidae is polyphyletic; Zygellidae receives strong support and is not closely related to Araneidae.“.

See above (Araneoidea s. str.), the genus *Seppo* SELDEN & DUNLOP 2014.

The taxon *Mesozygiella dunlopi* PENNEY & ORTUNO 2006 (figs. 392-393) has been described in Lower Cretaceous amber from Alava (Spain), based on the male sex. To my knowledge this is the only sure Mesozoic report of the Zygiellidae.

PENNEY & SELDEN (2002) – see WUNDERLICH (2008: 645) – described the alleged oldest linyphiid (indet.) spider in Lower Cretaceous Lebanese amber, based on an adult female which has a well observable epigynal scape (fig. 394). Number and position of the eyes are unknown. Retrolateral cheliceral stridulatory files – typical for almost all members of the Linyphiidae – are absent, a leg autotomy is absent, too. An epigynal scapus exist in numerous families of the superfamily Araneoidea s. str. In my opinion the stout legs and the partly thick tibial bristles PROBABLY indicate relationships to the families Araneidae and Zygiellidae but not of the Linyphiidae, see below, the family Linyphiidae.

### **Family THERIDIOSOMATIDAE** (figs. 395-397) photos 171-174

See the key to the families no. 35.

The family is best diagnosed by its unique pair of sternal pits (fig. 395) which are openings of sternal glands, see WUNDERLICH (2011: 428; 2012: 213). Unfortunately these pits are usually difficult to identify or even completely hidden in fossil spiders.

Their unpaired tarsal claw is straight or even bent upwards. Quite long and slender leg bristles exist as well as dorsal trichobothria on tibiae III (-IV). The position of the tarsal organs – also very difficult to recognize in fossils – is near the base of the article (in ca. 0.15). Pedipalpus: Patellar or tibial apophyses as well as cymbial spines/bristles absent, paracymbium usually small, bulbus usually large; see figs. 396-397.

Similar fossil spiders: Habitus and leg bristles are quite similar in the ancient extinct family Praeterleptonetidae (Leptonetoidea, see above and the key to the families above) in which the structures of the male pedipalpus are different (the articles are modified, usually the cymbium bears bristles, the bulbus is smaller and the paracymbium is larger), and which Cretaceous members – at least in Burmite – were much more frequent than Theridiosomatidae.

Cretaceous fossils are preserved in Mid Cretaceous Burmite (only *Leviunguis bruckschi* WUNDERLICH 2012) (\*), body length 1.0-1.2 mm, males and a probably congeneric female, in Early Cretaceous clayrock of Russia: *Eocoddingtonia escovi* SELDEN (2010): The largest member of the Theridiosomatidae, body length around 4 mm, both sexes.

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(\* ) A second taxon in Burmite – described under Theridiosomatidae: *Hypertheridiosoma paracymbium* WUNDERLICH 2012: 215 – has turned out to be a member of the family Praeterleptonetidae, see above.



Phylogenetics: This family – and the whole theridiosomatid branch – is very old in the geological sense, the oldest report is the earliest Cretaceous: (*Eocoddingtonia*. According to the described fossil taxa I do not want to exclude that Theridiosomatidae may be even the most ancient known family of the Araneoidea s. str.

***Leviunguis bruckschi*** WUNDERLICH 2012: 213-215, 230: figs. 56-62; photos 30-31. – See the figs. 396-397 and the photos 171-174

This is one of the smallest members of the family Theridiosomatidae, body length 1.0-1.2 mm, pedipalpus figs. 396-397.

Only the male holotype has been known in 2012. In the meantime I got further – questionable – material (remarkably the bulbi of all three males are deformed):

F2711/BU/CJW: A probably juvenile female, body length 1.2 mm, is preserved in the same piece of amber as the male holotype of *Leclercera sexoculata* n. sp. (Psiloderidae).

F2777/BU/CJW and F 2785/BU/CJW: Two males, body length 1.0-1.1 mm. The unpaired tarsal claw is quite long, strongly bent and straight in the distal half. The dorsal part of the prosoma including the eyes are broken off and lost in F2785. Because of the strongly deformed bulbi I am not sure about their conspecificity.

## **(b) The spineless-femur-clade = the theridiid subbranch**

In this subbranch leg bristles exist (at most and usually) only dorsally on tibiae and patellae; they are usually thin/indistinct and in some taxa even completely absent. Like members of the linyphioid subbranch (see below) the spiders build irregular capture webs (in very few taxa a capture web has been lost). Irregular capture webs derived from the ancient/ older araneoid orb web.

See „(?) Araneoidea: Fam. indet.“ in Burmese amber, juv. female sensu WUNDERLICH (2008: 644-645, photo 118) which relationships are quite unsure.

I am sure that *Cretotheridion* is a member of the „spineless-femur-clade“, and rather sure that it is a member of the family Theridiidae in the wide sense (see below). No sure taxon of this subbranch has been reported from the Cretaceous up to now, see above, the chapter „Erroneous determinations“.

## Family THERIDIIDAE SUNDEVALL 1833

See the family key. no. 34.

Theridiidae is one of the most diverse spider families today as well as preserved in Eocene Baltic amber, see WUNDERLICH (2008). In the Mesozoic only a single specimen of a single genus has been found, see below.

The investigation of the ancient Cretaceous genus *Cretotheridion* n. gen. may provide a different and „REDUCED“ revised **diagnosis** of the areneoid family Theridiidae – see WUNDERLICH (2008: 144-145) – if *Cretotheridion* really is a member of this family: Labium (fig. 398) not rebordered, pedipalpal tibia (fig. 405) long, widened distally (plate-shaped) and bearing long ventral-apical bristle-shaped hairs in a transverse row, retro-basal paracymbium absent. (A special irregular theridiid capture web existed probably already in the Cretaceous taxon).

A further character is the long clypeus (in contrast e. g. to the Araneidae); see also the new subfamily.

The Cretaceous taxon *Cretotheridion inopinatum* n. gen. n. sp. may be the first surely known mesozoic member (\*) of the family Theridiidae as well as of the whole „spineless-femur-clade“ within the superfamily Araneoidea which includes the families Cyatholipidae, Nesticidae, Synotaxidae and Theridiidae. Furthermore it might be the first sure proof of a Mesozoic Araneoidea to build irregular capture webs. A Diptera is preserved as the prey of *Cretotheridion tibialis*, see the photos. Members of Diptera are common prey of extant Araneoidea.

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(\*) Only a single – quite doubtful – „?Theridiidae gen. et sp. indet.“ has been published/ listed from/in Upper Cretaceous Canarian amber in MCALPINE & MARTIN (1969). Material for my study was not available.

## CRETOTHERIDIINAE n. subfam.

**Etymology:** „Creto“ from the Mesozoic period Cretaceous, „theridion“ from the type genus *Theridion* of the family Theridiidae.

**Type genus** (by monotypy): *Cretotheridion* n. gen.

**Diagnosis** (♂; ♀ unknown): The new subfamily can be distinguished from other theridiid subfamilies – see WUNDERLICH (2008: 154-157) – by the combination of (a) the absence of teeth of the tarsal claws and (b) the existence of a very long unpaired tarsal claw (fig. 401). See also the fig. below: „Hypothetic relationships of the theridiid subfamily Cretotheridiinae“.

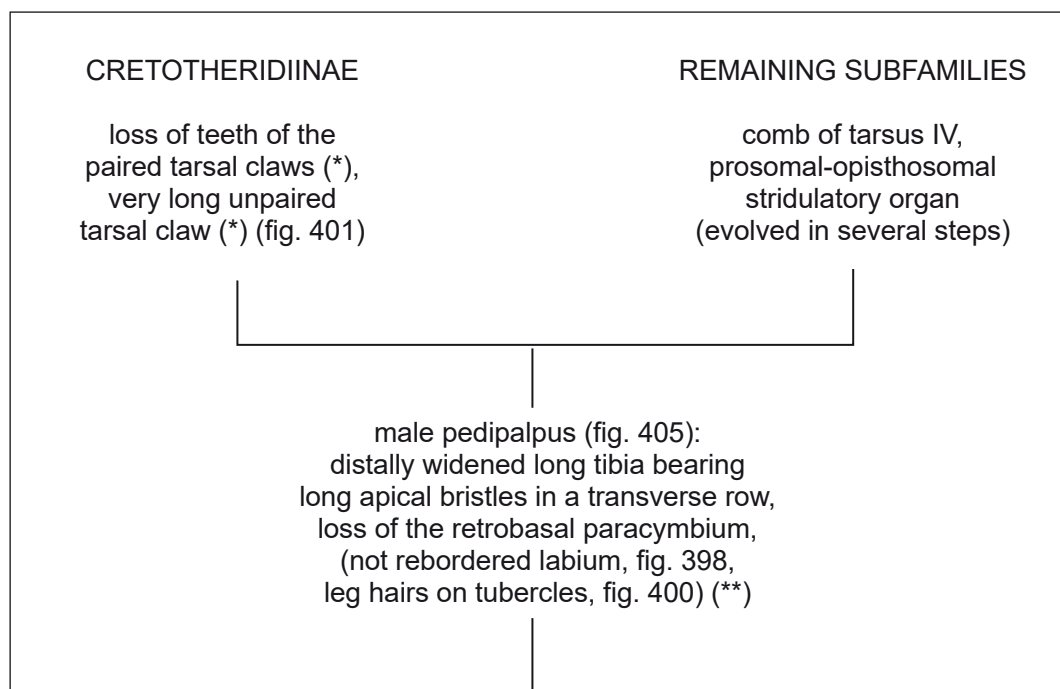
**Further characters:** Comb of tarsus IV and most probably retrodistal paracymbium absent, colulus and (thin) dorsal tibial bristles existing, dorsal and ventral hairs on legs I-II situated on tubercles (fig. 400), opisthosoma soft and egg-shaped (photos), basal cheliceral articles fairly large, pedipalpus (figs. 403-406) with long articles and probably a large theridiid tegular apophysis in a distal position (it is difficult to observe), existence of an internal paracymbium unknown.

**Relationships** (see the fig. below and the paragraph „Hypothetic relationships of the subfamily Cretotheridiinae“):

According to numerous characters which have to be combined – an ecribellate stage, large lung covers, a long clypeus, a rosette-shaped position of the spinnerets, the chaetotaxy, the leg hairs situated on tubercles, the trichobothriotaxy (see above), the slender articles of the pedipalpus, the large/wide cymbium, and the complicated structures of the bulbus (figs. 404-406) (probably a theridiid tegular apophysis exists), – I am rather sure that *Cretotheridion* is a member of the Araneoidea s. str., and furthermore of the „spineless-femur-clade“, and – according to the apically not rebordered (flat) labium (fig. 398) (like in the Synotaxidae which possesses a retrobasal paracymbium), the few and thin leg bristles, the long and distally widened pedipalpal tibia which bears a transverse row of long hairs (fig. 405), as well as the absence of a retrobasal paracymbium – I am fairly sure that it is a member of the family Theridiidae; on the other hand typical characters of certain (!) today's Theridiidae – a comb of tarsus IV and a prosomal-opisthosomal stridulatory organ – are absent. These structures are also absent – lost in my opinion – in some theridiid subfamilies of today, see WUNDERLICH (2008).

The remaining important characters of *Cretotheridion* are a mixture of patterns of different extant subfamilies: the dorsal and ventral tuberculate basis of hairs in legs I-II are e. g. as in the Anelosiminae, the (real?) absence of a retrodistal paracymbium exists in several extant subfamilies like Anelosiminae and Theridiinae, a long unpaired tarsal claw exists in the Argyrodoinae.

**Distribution:** Mid Cretaceous amber forest of N-Myanmar (Burma).



(\*) Convergently developed in certain taxa of the remaining subfamilies like the Argyroderinae.

(\*\*) Probably both plesiomorphic characters.

**Above:** hypothetical relationships of the subfamily Cretotheridiinae

In *Cretotheridion* a comb of tarsus IV as well as a prosomal-opisthosomal stridulatory organ are absent. Is this an old genus of the family Theridiidae which lost two of the main family characters (noted above) of today's and Palaeogene Theridiidae already in the Mid Cretaceous? Or did the two characters in question evolve much later, and *Cretotheridion* is a „primitive“ taxon? The first scenario appears unlikely to me and is in contrast to my hypothesis that Asageninae is the most basal extant theridiid subfamily in which the two characters in question are well developed; see WUNDERLICH (2008: 170).

Does the origin of today's Theridiidae goes much further back than the existence of *Cretotheridion*? There is no fossil proof for this hypothesis up to now. Probably (in my opinion) the ancestor of Palaeogene and today's Theridiidae evolved latest around the CT-event – most probably in different steps – the important characters of advanced Theridiidae: a comb of tarsus IV connected to the wrapping behaviour of prey with threads, and a prosomal-opisthosomal stridulatory organ. Both structures have been lost several times in Palaeogene and extant theridiid taxa, see WUNDERLICH (2008).

If *Cretotheridion* would be a derived taxon certain basal taxa must have existed in the Mid or Early Cretaceous or even in the Triassic, and my previous conclusions would be wrong. More Mesozoic theridiid fossils are needed for a decision of this matter. I do not want to exclude that Cretotheridiinae may be the sister group to all extant Theridiidae. In this case the judgement regarding the level – as a subfamily of the Theridiidae or as a family of its own – might be subjective.

**Cretotheridion n. gen.**

**Type species** (by monotypy): *Cretotheridion inopinatum* n. sp.

**Etymology:** See the new subfamily. The gender is neuter.

**Diagnosis, relationships and distribution:** See above.

***Cretotheridion inopinatum* n. gen. n. sp.** (figs. 398-406) photo 175

**Etymology:** The species name refers to the unexpected find of this taxon in Cretaceous amber; *inopinus* (lat.) = unexpected..

**Material:** Holotype ♂ in Mid Cretaceous amber from N-Myanmar (Burma) and a Diptera as its prey, F2525/BU/CJW.

**Preservation and syninclusions:** The spider is well and completely preserved in a clear yellow and slightly green piece of amber; some fissures in the amber hide parts of the spider, few bubbles incline the opisthosoma dorsally. – A small and distinctly deformed/dissected Diptera (it is not spun in with threads) – apparently a prey of the spider which has been sucked out – is preserved between the chelicerae and the anterior legs. A larger Diptera, a tiny beetle and small remains of plants exist in the same piece of amber. Spider threads are absent. Two pear-shaped bubbles have been cut off from the margin of the amber piece.

**Diagnosis** (♂; ♀ unknown): See the new subfamily. Position of the metatarsal I-II trichobothrium in 0.25, pedipalpus as in figs. 403-406.

**Description (♂):**

Measurements (in mm): Body legs 1.6, prosoma: Length 0.8, width ca. 0.7; leg I: Femur 1.65, patella 0.28, tibia 1.4, metatarsus 1.2, tarsus 0.6, tibia II 0.9, tibia III ca. 0.4, tibia IV 0.6.

Colour: Prosoma and legs medium brown, opisthosoma light grey brown.

Prosoma (certain dorsal parts are hidden) ca. 1.14 times longer than wide, anteriorly distinctly narrowed, smooth, 8 eyes of medium size in a fairly wide field, posterior files apparently absent, clypeus long, basal cheliceral articles long, lateral files absent, teeth hidden, fangs slender, labium (fig. 398) not rebordered, wider than long, fused to the sternum, bearing ca. a dozen short to tiny hairs, gnathocoxae not converging above the labium, sternum about as long as wide, separating the coxae IV at least by their diameter. – Legs (photos) slender, order I/II/IV/III, I and II distinctly longest, hairs fairly short, especially femora, tibiae and metatarsi I-II bear dorsal and ventral hairs which are situated on tubercles which are well developed e. g. in the subfamily Anelosiminae (fig. 400), thin bristles dorsally on patellae and tibiae only, their sequence on the tibiae 2/2/1/2, metatarsal trichobothria unknown on III-IV, their position on I-II in 0.25, tarsal IV comb absent, tarsal claws smooth, unpaired claw about as long as the paired claws and bent in a right angle (fig. 401). – Opisthosoma (photo) egg-shaped, soft, bearing short hairs, epigaster not protruding, lung covers large, tracheal spiracle hidden, spinnerets short and in a rosette-shaped position (\*), the anteriors stout and close together (fig. 402), median spinnerets hidden, colulus small, hairs hidden, anal tubercle large. – Pedipalpus (figs. 403-406) with slender articles, tibia very long, widened distally, and bearing longer apical hairs in a transverse row, cymbium wide, bearing a probasal hook, retrobasal paracymbium absent, retrodistal paracymbium apparently also absent (?), bulbus bearing complicated structures which are difficult to observe and are only provisionally named, apparently with large median, theridiid tegular apophysis, as well as a large and two-partite conductor; the questionable embolus may be long, its position may be almost in a half circle.

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(\*) The anterior spinnerets converging in contrast e. g. to members of the Praeterleptonetidae.

**Relationships:** See above.

**Distribution:** Mid Cretaceous amber forest of N-Myanmar (Burma).

(c) The liniphiid subbranch

On extant and Eocene fossils of this branch: See WUNDERLICH (2008: 117-129).

## Family LINYPHIIDAE

See the family key no. 33.

Eocene taxa: See WUNDERLICH (2004: 1298-1373).

I do not know a sure Cretaceous report of the Linyphiidae or a strongly related family, see above, the chapter on dubious or erroneous determinations and the family Zygiellidae.

A quite dubious member of the family Linyphiidae (gen. & sp. indet.) has been listed in MCALPINE & MARTIN (1969) in Lower Canadian amber.

I do not want to exclude that the single male of an linyphiid indet. male in alleged Cretaceous Ethiopien amber – see in SCHMIDT et al. (2010) – is actually preserved in Cenozoic amber but no recent paper has been published on the age of this amber.

PENNEY (2002: 216-217, t. 2, fig. 3; fig. 5) described a male under Linyphiidae gen. & sp. indet. in Upper New Jersey amber. In my opinion the badly preserved specimen does not allow an assignment to a family, and no indication exists that its paracymbium is a free sclerite.

PENNEY & SELDEN (2002) – see WUNDERLICH (2008: 645) – described the alleged oldest linyphiid (indet.) spider in Lower Cretaceous Lebanese amber, based on an adult female which has a well observable epigynal scape (fig. 294). Number and position of the eyes are unknown. Retrolateral cheliceral stridulatory files – typical for almost all members of the Linyphiidae – are absent, a leg autotomy is absent, too. An epigynal scapus exist in numerous families of the superfamily Araneoidea s. str. In my opinion the stout legs and the partly thick tibial bristles PROBABLY indicate relationships to the families Araneidae and Zygiellidae. Zygiellidae are known from the Cretaceous, see above.

In my opinion – and to the present knowledge – the family Linyphiidae has to be removed from the list of Mesozoic spiders.



# INDEX of most taxa in their main position. See also the list p. 65-81.

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I admire the cooperation of various authors, especially if the number of their names is almost equal (or even longer) than the title of their paper, see e. g. LOPARDO et al. (2004) below. So (a) no one is explicitly responsible for the contents/errors of the paper, and (b) you easily can see who needs money for his scientific work in the future.

The autorship of another paper – see the copy directly below – is quite remarkable and may be regarded as a funny joke: There are 34 authors and the title has 16 words. A dozen of these authors are listed under „acknowledgements“ in this paper – why not all authors?

Could this case be registered in the Guinness Book of Records?

## AMERICAN MUSEUM NOVITATES

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### Tarsal Organ Morphology and the Phylogeny of Goblin Spiders (Araneae, Oonopidae), With Notes on Basal Genera

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Further references: See PENNEY & SELDEN (2011: 114-127) as well as (in the Internet) the chapter on fossil Arachnida by DUNLOP et al. within the World Spider Catalog by PLATNICK which is updated twice a year.

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# THE DRAWINGS

The measurements are given in mm.

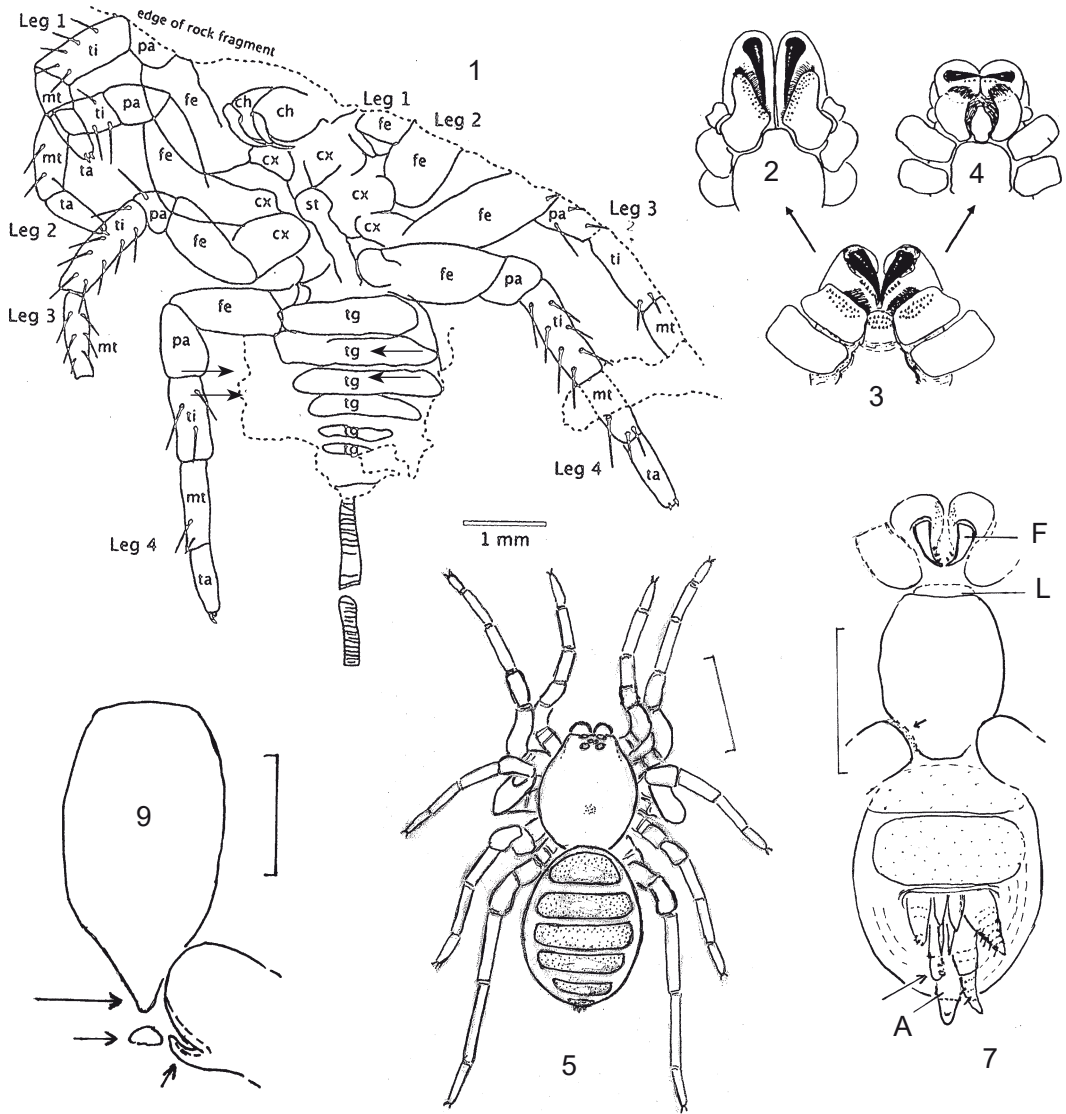
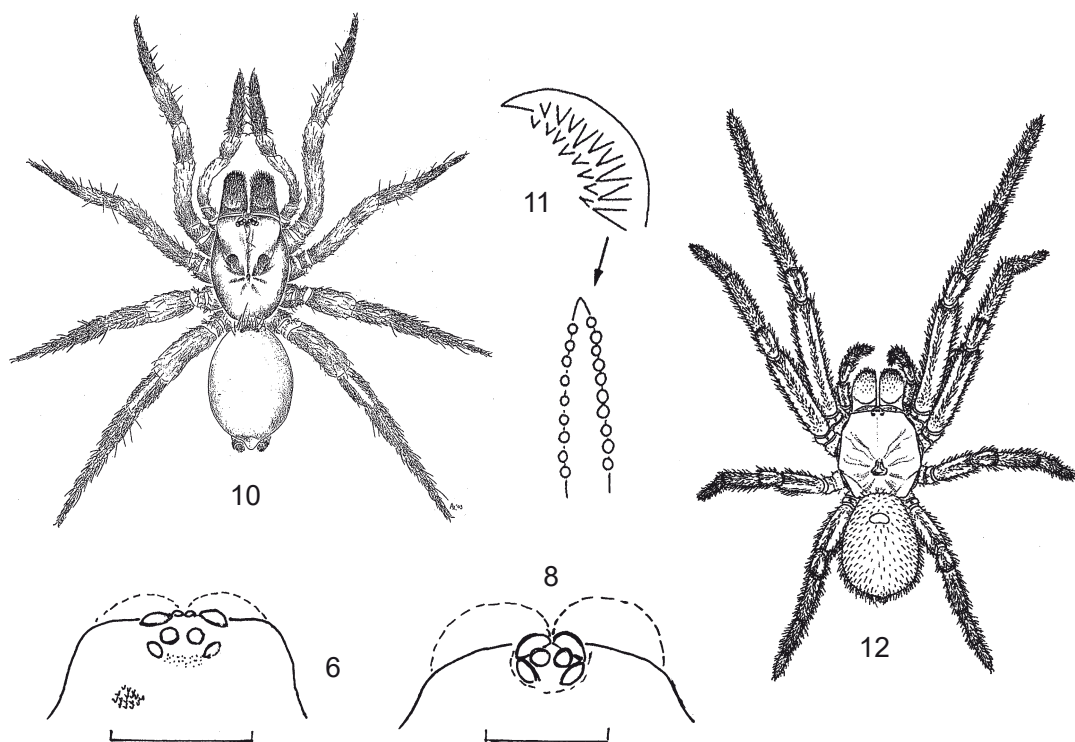


Fig. 1) *Permarachne novokshonovi* ESKOV & SELDEN 2005 (Arachnida: Uraraneida: (PERMARACHNIDAE), holotype, ventral aspect. Devonian of the USA, preserved in stone. Taken from SELDEN et al. (2008).

Figs. 2-4: Position of the fangs in spiders: Orthognathy (fig. 2) and labidognathy (fig. 4) as apomorphic character states derived from plagiognathy (fig. 3). Taken from KRAUS & KRAUS (1993).

Figs. 5-9: Araneae: Fossil and extant Mesothelae.



Figs. 5-7: *Cretaceothele lata* n. gen. n. sp. (LIPHISTIIDAE), juv., 2. or 3. instar, preserved in Mid Cretaceous Burmese amber (Burmite) from N-Myanmar. Hairs and bristles are not drawn. Note the opisthosomal plates (tergites) of this „segmented“ spider; 5) dorsal aspect of the holotype, reconstruction; 6) dorsal aspect of the anterior part of the prosoma. Note the eight eyes and the fine rugose structure of the cuticula; 7) ventral aspect of the body. The right posterior spinneret (long arrow) is deformed, partly retracted or injured. Note the four pairs of spinnerets, the small and slender median pairs, the ventral position of the large anal tubercle and the two large sternites (opercula) which cover the two pairs of book lungs. The small arrow points to the sloping sternum. – A = anal tubercle, F = left fang, L = labium. Scale bars (in mm): 0.5 in figs. 5 and 7, 0.2 in fig. 6.

Figs. 8-9: *Liphistius* sp. indet. (LIPHISTIIDAE), juv., extant, Myanmar (Burma), body length 3.8 mm; 8) dorsal aspect of the anterior part of the prosoma; 9) ventral aspect of the sternum with its posterior elongation (long arrow), the ventral outgrowth of the pedicel (median arrow) and the retrobasal outgrowth of the left coxa IV (short arrow). – Scale bars 0.2 and 0.5.

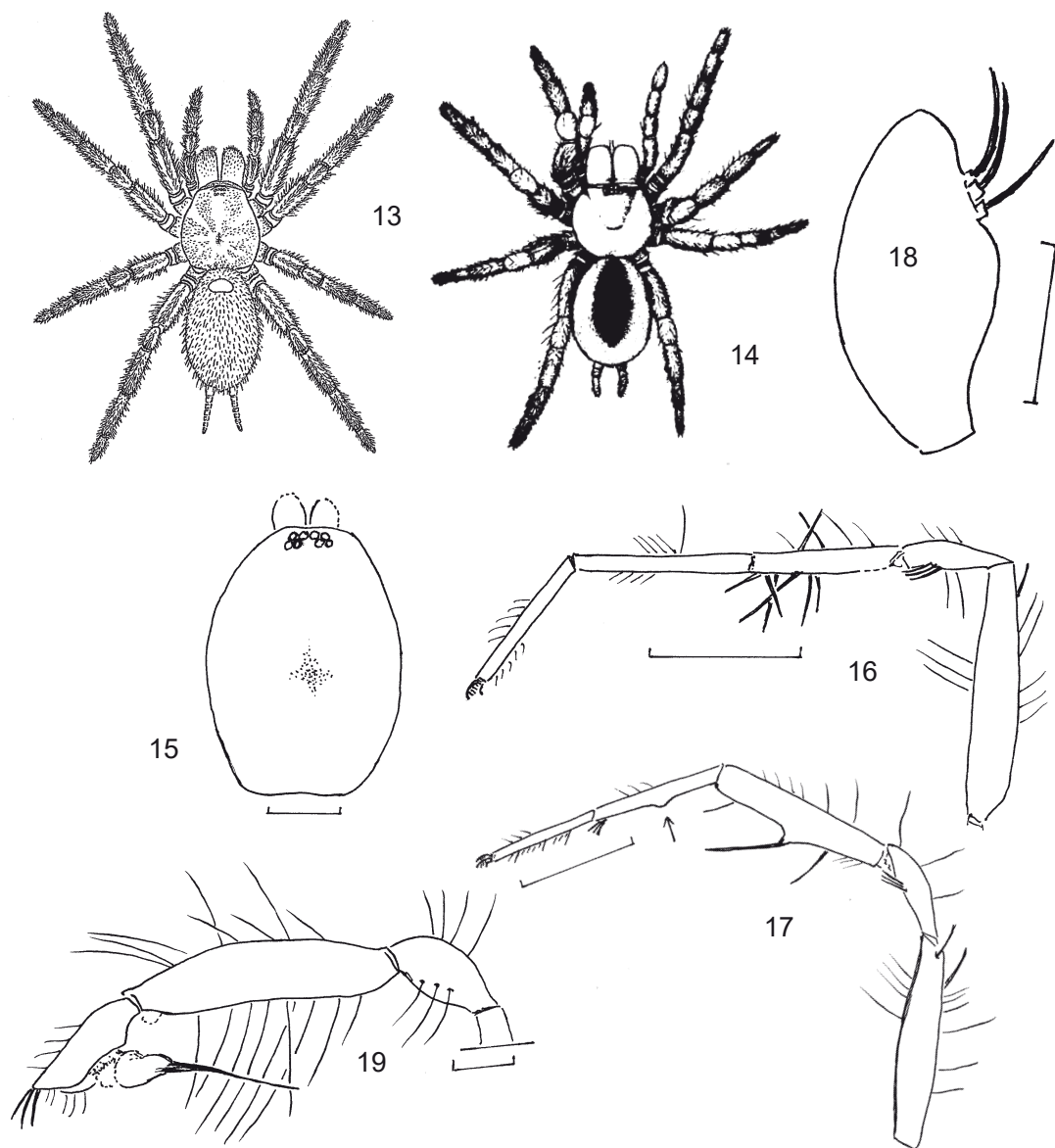
Figs. 10-31: Fossil and few extant Mygalomorpha. Figs. 32ff: Araneomorpha.

10) Extant female of the family ANTRODIAETIDAE, dorsal aspect. –Taken from JOCQUE & DIPPENAAR-SCHOEMAN (2007).

11) Extant specimen of the family NEMESIIDAE: Anaminae Lateral and ventral view of a paired tarsal claw showing two rows of teeth. – Taken from JOCQUE & DIPPENAAR-SCHOEMAN (2007).

12) Female of the Cretaceous genus *Ambortiphagus* (ATYPIDAE: Ambortiphaginae) from Mongolia, dorsal aspect, reconstruction. – Taken from ESKOV & ZONSHTEIN (1990).

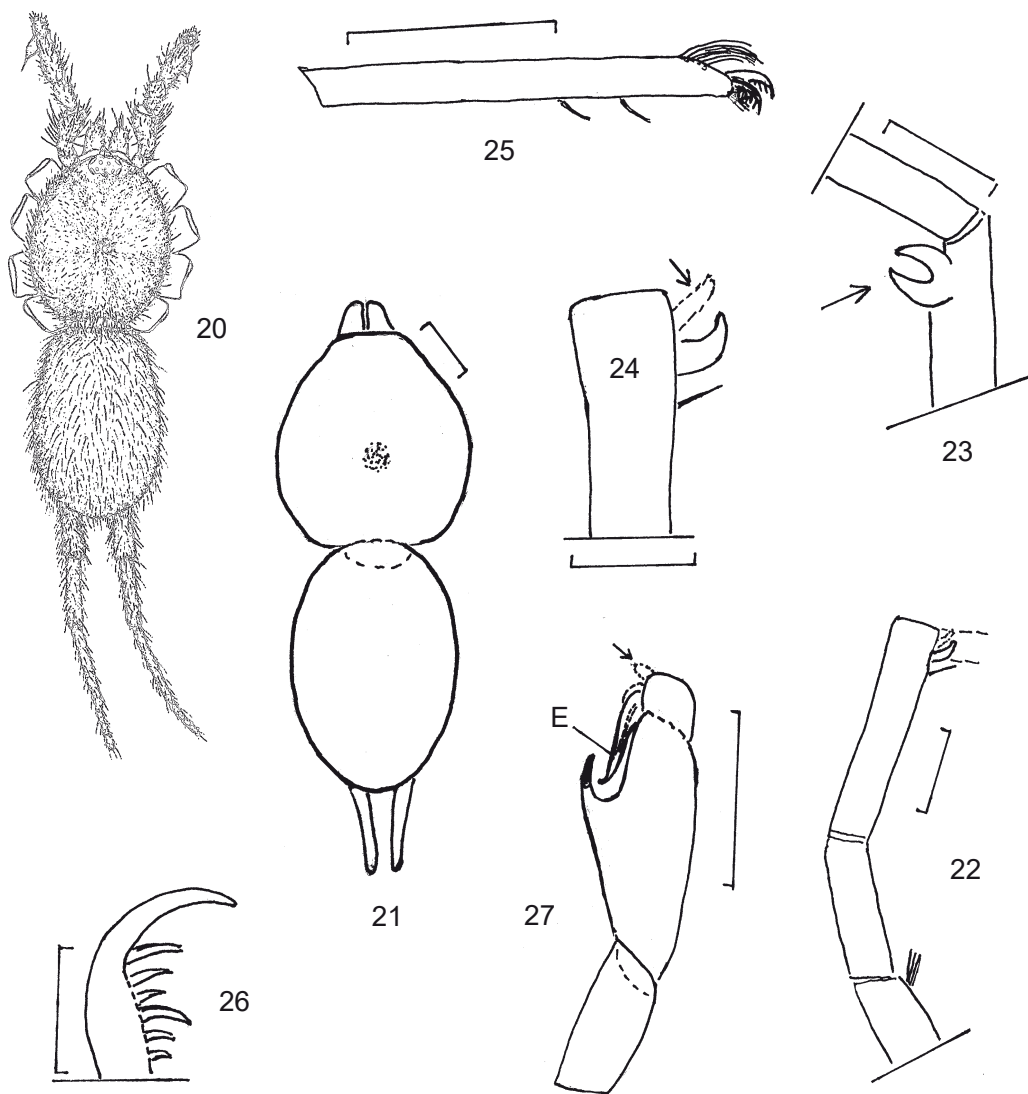




13) Female of the Cretaceous genus *Cretomegahexura* (MECICOBOTHRIDAE) from Mongolia, dorsal aspect, reconstruction. – Taken from ESKOV & ZONSHEIN (1990).

14) Juvenile specimen of the Triassic genus *Rosamygale* (HEXATHELIDAE) from France, dorsal aspect, reconstruction. – Taken from SELDEN & GALL (1992).

Figs. 15-19: *Phyxioschemoides collembole* n. gen. n. sp. (DIPLURIDAE), ♂ in Burmite; 15) dorsal aspect of the prosoma. The fovea is deformed, the eyes are covered with an emulsion; 16) retrolateral aspect of the left leg I; 17) retrolateral aspect of the left leg II. Note the long ventral tibial „clasper“ (bristle). The arrow points to the proventral metatarsal hump; 18) dorsal aspect of the right patella I with bristles. Hairs are not drawn; 19) Retrolateral aspect of the left pedipalpus. Only few hairs are drawn. – Scale bars 0.2 in fig. 18, 0.3 in fig. 17, 0.5 in fig. 15, 1.0 in figs. 15-16.



20) *Phyxioschema huberti* SCHWENDINGER 2009 (DIPLURIDAE), extant ♂ from Thailand, habitus, body length 14.7 mm, dorsal aspect taken from SCHWENDINGER.

Figs. 21-27: *Fossilcalcar praeteritus* n. gen. n. sp. (FOSSILCALCARIDAE) n. fam.), ♂ in Burmese; 21) dorsal aspect of the body, outline. The eyes and the articulation of the spinnerets are hidden; 22) prodorsal aspect of the left leg I: Tibia, patella and distal part of the femur; 23) prodistal aspect of the right tibial clamping outgrowth (arrow); hairs are not drawn; 24) dorsal aspect of the distal part of the left tibia I. The arrow points to a structure which may partly be an artefact or a malformation; 25) retrolateral aspect of the left tarsus IV. Note the dorsal-distal brush of hairs; other hairs are not drawn. Only two ventral bristles are drawn (more bristles may exist); 26) retrolateral and slightly apical aspect of the left retroclaw IV. Most probably not all teeth are observable in this position; 27) dorsal and slightly retrolateral aspect of the left pedipalpus. Hairs are not drawn. The arrow points to a questionable artefact. – E = embolus. Scale bars 0.1 in fig. 26, 1.0 in the remaining figs.

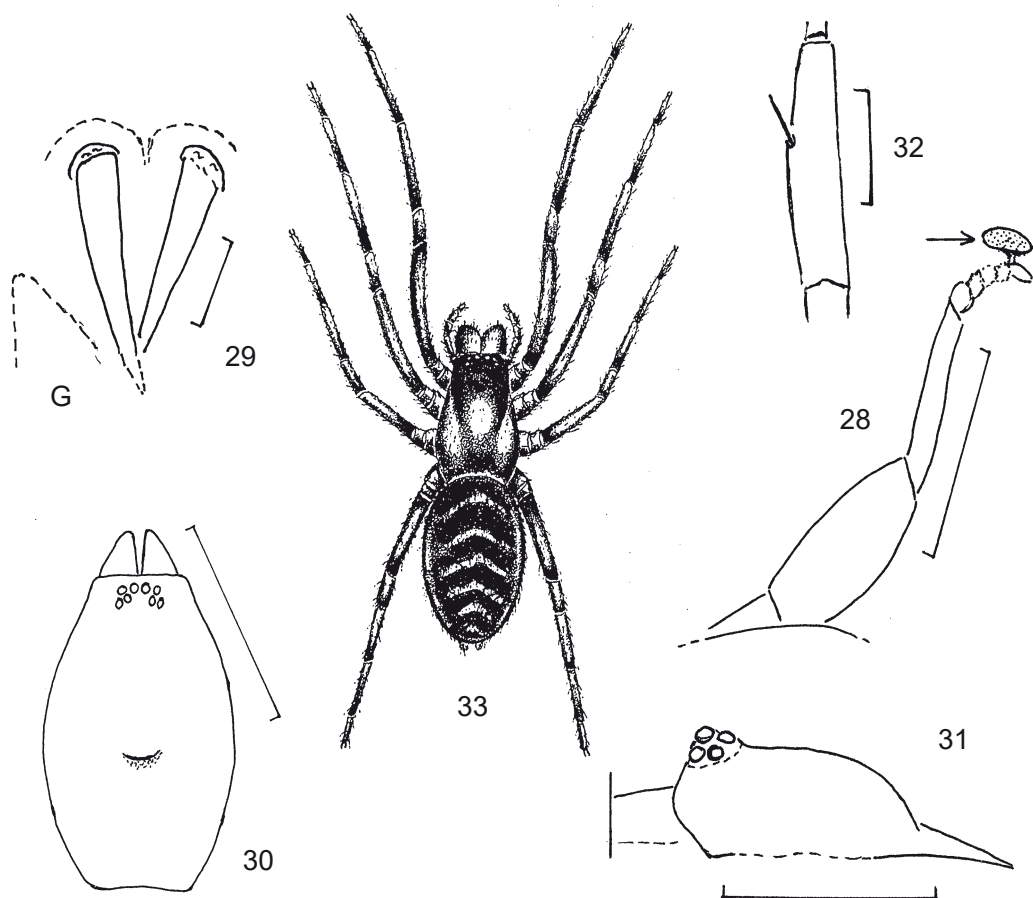


Fig. 28) Insecta: Neuroptera: ?MANTISPIDAE larva in Burmite, prodorsal aspect of the right leg III. The probably parasitic larva is preserved behind a juvenile mygalomorph spider, a questionable member of the family Atypidae, F2608/BU/CJW, see the next drawings. Note the droplet of a questionable secretion (arrow). Scale bar 0.1.

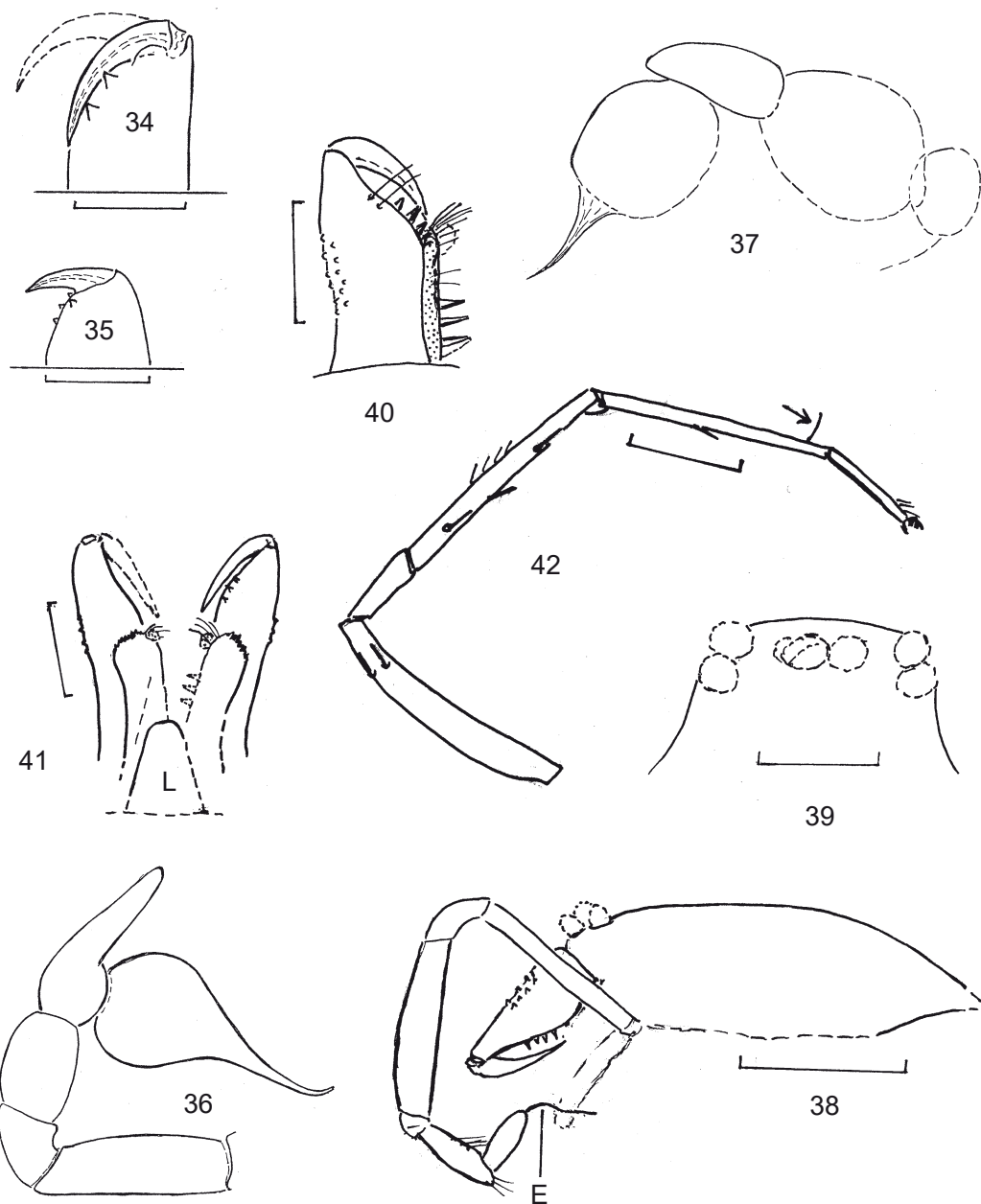
Figs. 29-31: Mygalomorpha indet. in Burmite.

29) ??Atypidae, juvenile specimen, F2608/BU/CJW, ventral aspect of the fangs and possible position of the right gnathocoxa (G); 30-31) indet. sp. 2, F2610/BU/CJW, juvenile specimen, dorsal and lateral aspect of the prosoma. – Scale bars 0.2 in fig. 29, 1.0 in figs. 30-31.

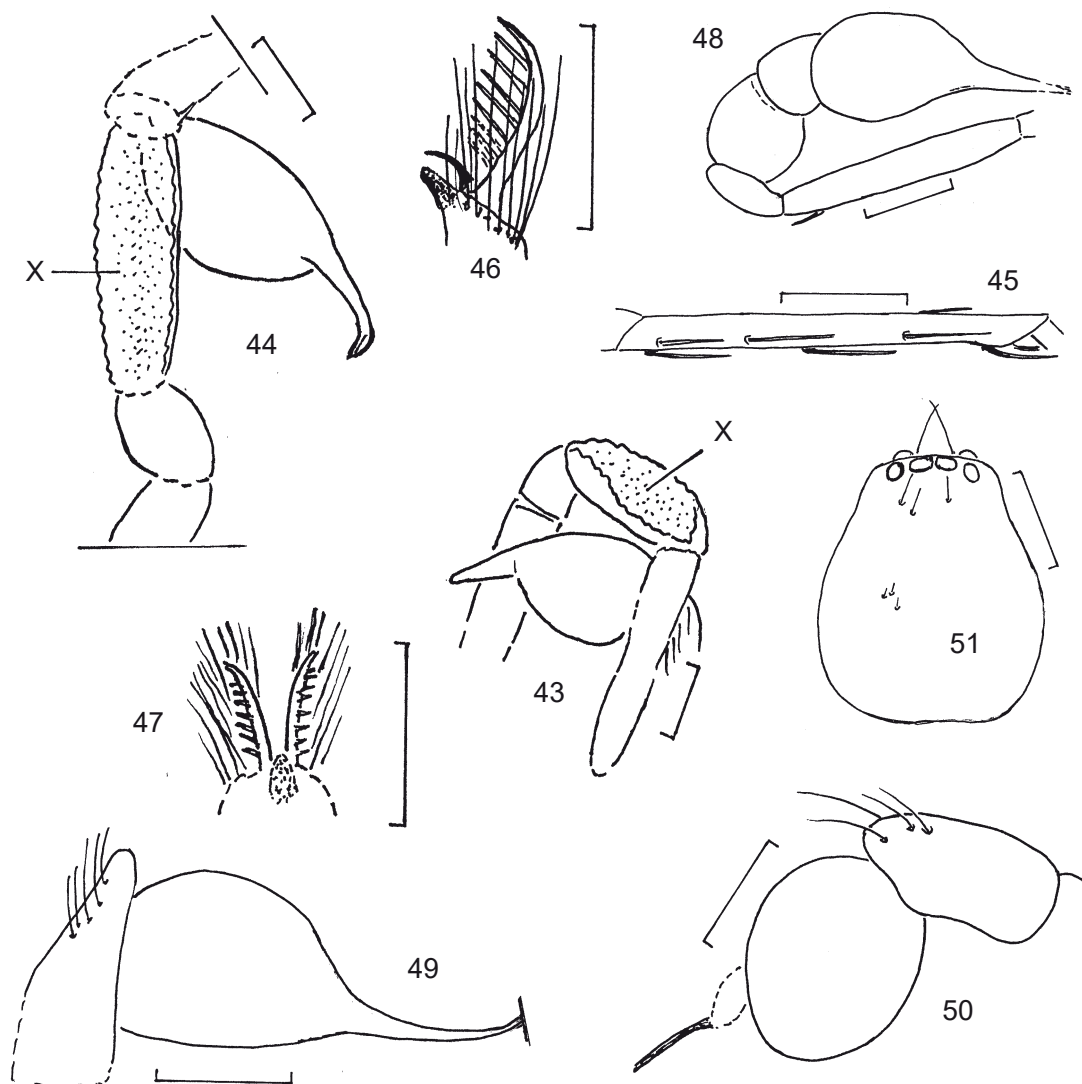
Fig. 32) Eoplectreurys gertschi SELDEN & HUANG 2010 (PLECTREURIDAE), ♂, Jurassic, China, ventral aspect of the right tibia I. – Scale bar 0.5. Taken from SELDEN & HUANG (2010).

Figs. 33-70: Extant (figs. 33-35) and fossil spiders of the family SEGESTRIIDAE.

33) Extant female of the family Segestriidae. Note the position of leg III which points anteriorly, a typical position in this family. Caused by the preservation this leg position may be different in certain fossil spiders. – Taken from JOCQUE & DIPPENAAR-SCHOEMAN (2007); 34) typical left chelicera (ventral aspect of the distal part, the fang is drawn in two different positions) of an extant spider of the subfamily Segestriinae; 35) typical left chelicera (ventral aspect of the distal part) of an extant spider of the subfamily Ariadninae; 36) a typical ♂-pedipalpus of a member of the subfamily Segestriinae; 37) a typical ♂-pedipalpus of a member of the subfamily Ariadninae.



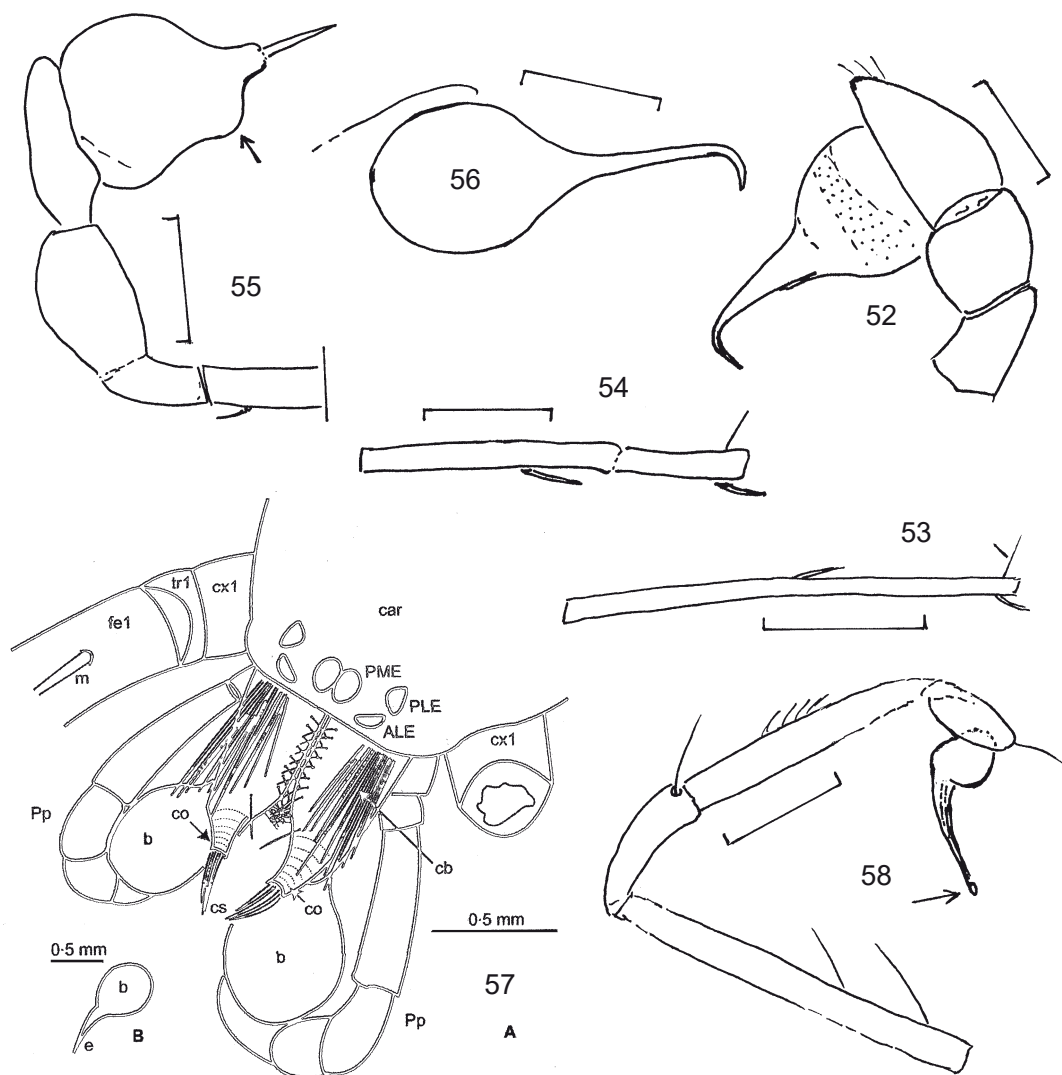
Figs. 38-42: *Denticulsegestria rugosa* n. gen. n. sp. (SEGESTRIIDAE), ♂ in Burmite; 38) left aspect of the prosoma and the left pedipalpus. The eyes are covered with bubbles; 39) dorsal aspect of the anterior part of the prosoma. Bubbles cover the eyes; 40) medio-dorsal aspect of the left chelicera and gnathocoxa (punctuated). Note the three long gnathocoxal teeth (arrow); 41) ventral aspect (outline) of the mouthparts which are fairly deformed and are partly hidden like the labrum; 42) almost prolateral aspect of the left leg I. The arrow points to the metatarsal trichobothrium. In contrast to this leg the right tibia I bears an additional ventral pair of bristles and the right femur bears additional distal bristles. Only few hairs are drawn. – E = embolus, L = labium. Scale bars 0.5 in figs. 38 and 42, 0.2 in figs. 39-41.



Figs. 43-44: *Jordansegestria detruneo* n. sp. (SEGESTRIIDAE), ♂ in Jordanian amber; 43) retrolateral (cymbium retrodorsal) aspect of the right pedipalpus; 44) right pedipalpus with dorsal aspect of the hollow tibia (x) and ventral aspect of the bulbus. - Scale bars 0.2 and 0.1.

Figs. 45-50: *Myansegestria engin* n. gen. n. sp. (SEGESTRIIDAE), ♂ in Burmite; 45) prolateral aspect of the left tibia I. A third ventral pair of bristles is probably broken off. Hairs are not drawn; 46) retrolateral aspect of the tip of the right tarsus IV (the prolateral claw is not drawn); 47) ventral-apical aspect of the tip of the right tarsus II; 48) retrolateral aspect of the right pedipalpus; 49) retroventral aspect of the right pedipalpus. The tip of the embolus is hidden; 50) retrodorsal aspect of the left pedipalpus. The embolus is strongly deformed. Only few hairs are drawn. - Scale bars 0.5 in fig. 45, 0.1 in figs. 46 and 47, 0.2 in the figs. 48-50.

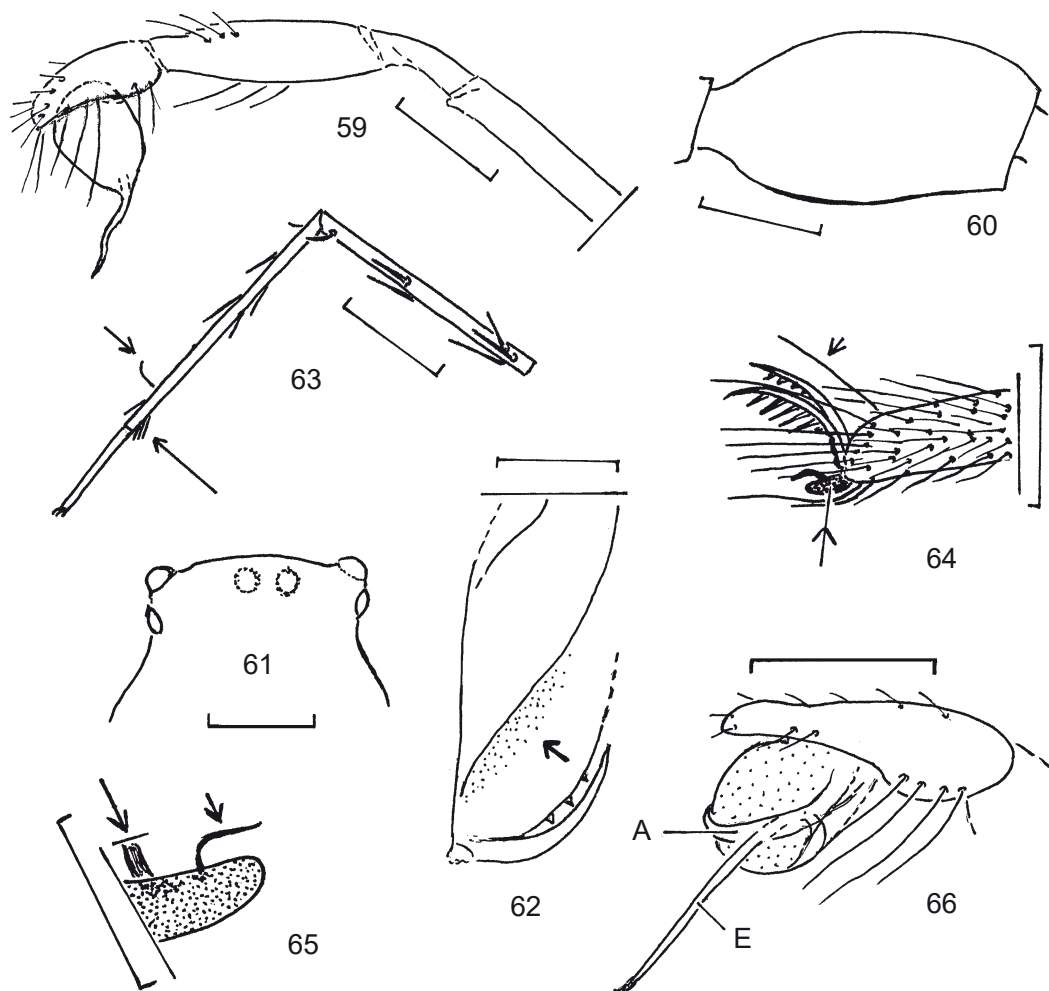
Fig. 51 *Myansegestria ?engin* n. gen. n. sp. (SEGESTRIIDAE), dorsal aspect of the peltidium – preserved near the holotype of *M. engin* – which may be part of the holotype's exuvia. A fovea is absent. Only few hairs are drawn. - Scale bar 0.5.



Figs. 52-56: *Myanseggestria caederens* n. gen. n. sp. (SEGESTRIIDAE), ♂ in Burmite, holotype (fig. 52), paratype (remaining figs.); 52) retrolateral aspect of the left pedipalpus; 53) retrolateral aspect of the right metatarsus I (hairs are not drawn); 54) prolateral aspect of the left metatarsus I which is a „malformation“, probably broken and healed; 55) prolateral aspect of the deformed left pedipalpus. The arrow points to the hump of the bulbus caused by the preservation; 56) prolateral aspect of the left bulbus with embolus. – Scale bars 0.5 in figs. 53-54, 0.2 in the remaining figs.

Fig. 57A-B: *Palaeosegestria luzzii* PENNEY 2004 (SEGESTRIIDAE), ♂ in Upper Cretaceous amber from New Jersey, USA; A) anterior region of the prosoma (car) and pedipalpi (Pp) with the bulbus (b), dorsal aspect; B) bulbus with embolus (e). – Taken from PENNEY (2004).

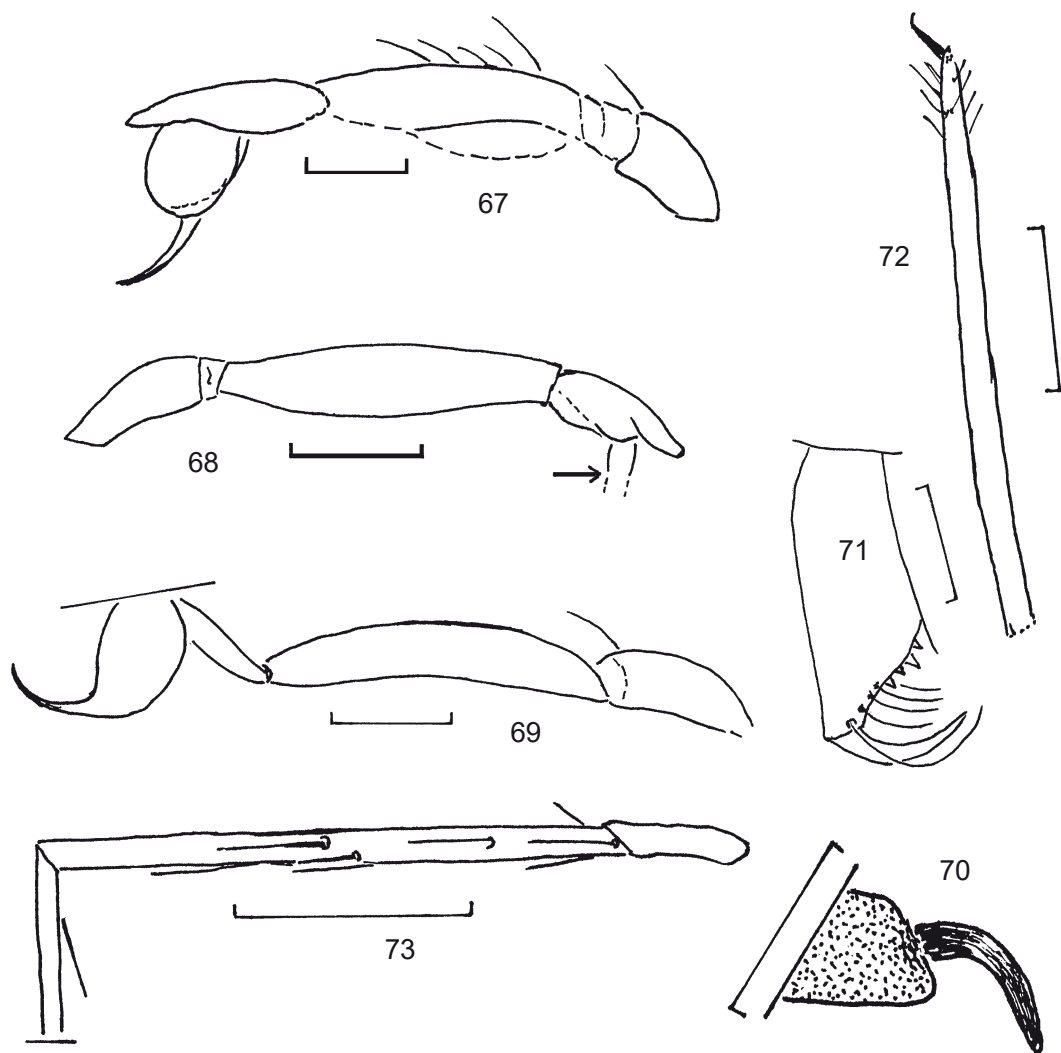
Fig. 58) *Parvosegestria longitibialis* n. gen. n. sp. (SEGESTRIIDAE), ♂ in Burmite, prolateral aspect of the left pedipalpus. Only few hairs are drawn. A tiny droplet is preserved at the tip of the embolus (arrow). – Scale bar 0.2.



Figs. 59-60: *Parvosegestria obscura* **n. gen. n. sp.** (SEGESTRIIDAE), ♂ in Burmite; 59) holotype, prolateral aspect of the right pedipalpus. Only few hairs are drawn; 60) paratype, retrolateral aspect of the right pedipalpal tibia. – Scale bars 0.2 and 0.1.

Figs. 61-66: *Parvosegestria pintgu* **n. gen. n. sp.** (SEGESTRIIDAE), ♂ in Burmite; 61) dorsal aspect of the anterior part of the prosoma; 62) anterior aspect of the right chelicera. I do not want to exclude with certainty that the strong anterior inclination/depression (arrow) is an artefact because it is slightly different in both chelicerae; 63) retrolateral aspect of the right tarsus, metatarsus and tibia IV. The short arrow points to the metatarsal trichobothrium, the long arrow points to the metatarsal preening comb; 64) retrolateral aspect of the tip of the left tarsus IV. The short arrow points to the long and more erect sensory dorsal hair, the long arrow points to the sclerotized apical ventral outgrowth (onychium). The unpaired claw is thicker drawn in this fig. than in reality, see fig. 65. Not all teeth of the paired tarsal claws are drawn; 65) retrolateral aspect of the tip of the right tarsus IV. The short arrow points to the unpaired tarsal claw on the large onychium, the long arrow points to the basal part of the paired retroclaw; 66) prolateral aspect of the right bulbus and embolus. Only few hairs are drawn. – A = possible artefact, E = embolus. Scale bars 0.05 in fig. 65, 0.1 in fig. 64, 0.5 in fig. 63, 0.2 in the remaining figs.

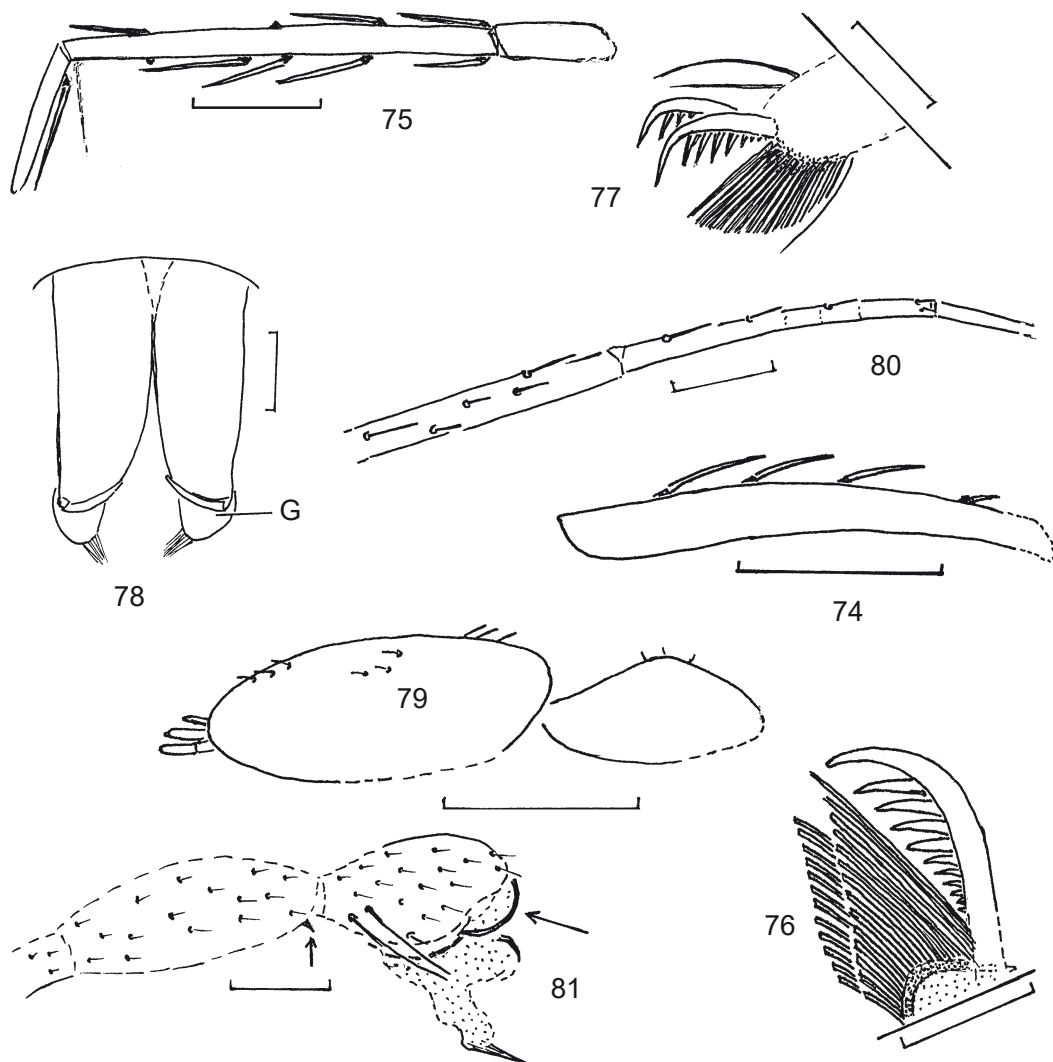




Figs. 67-69: *Parvosegestria triplex* **n. gen. n. sp.** (SEGESTRIIDAE), ♂ in Burmite; holotype figs. 67-68, paratype F2676 fig. 69; 67) prolateral aspect of the right pedipalpus. The ventral swelling of the tibia is most probably caused by the preservation; 68) prolateral aspect of the left pedipalpus which partly is a malformation, see the small bulbus (arrow) of which most parts are hidden. The cymbium is shortened and deformed; 69) retrolateral aspect of the left pedipalpus. – Scale bars 0.2.

Fig. 70) *Ariadna* sp. indet. (extant, Europe) (SEGESTRIIDAE), ♂, retrolateral aspect of the unpaired tarsal claw of the right tarsus II. Note the apical insertion of the claw. – Scale bar 0.1.

Figs. 71-73: *Burmorsolus nonplumosus* **n. gen. n. sp.** (PLUMORSOLIDAE), ?ad. ♀ in Burmite; holotype fig. 72, paratypes fig. 71 (F2733) and 73 (2656); 71) anterior aspect of the right chelicera; 72) prolateral aspect of the left pedipalpal tarsus. Only few hairs are drawn; 73) retrolateral aspect of the left leg I: Patella, tibia and basal part of the metatarsus. – Scale bars 0.2 in figs. 71-72, 1.0 in fig. 73.

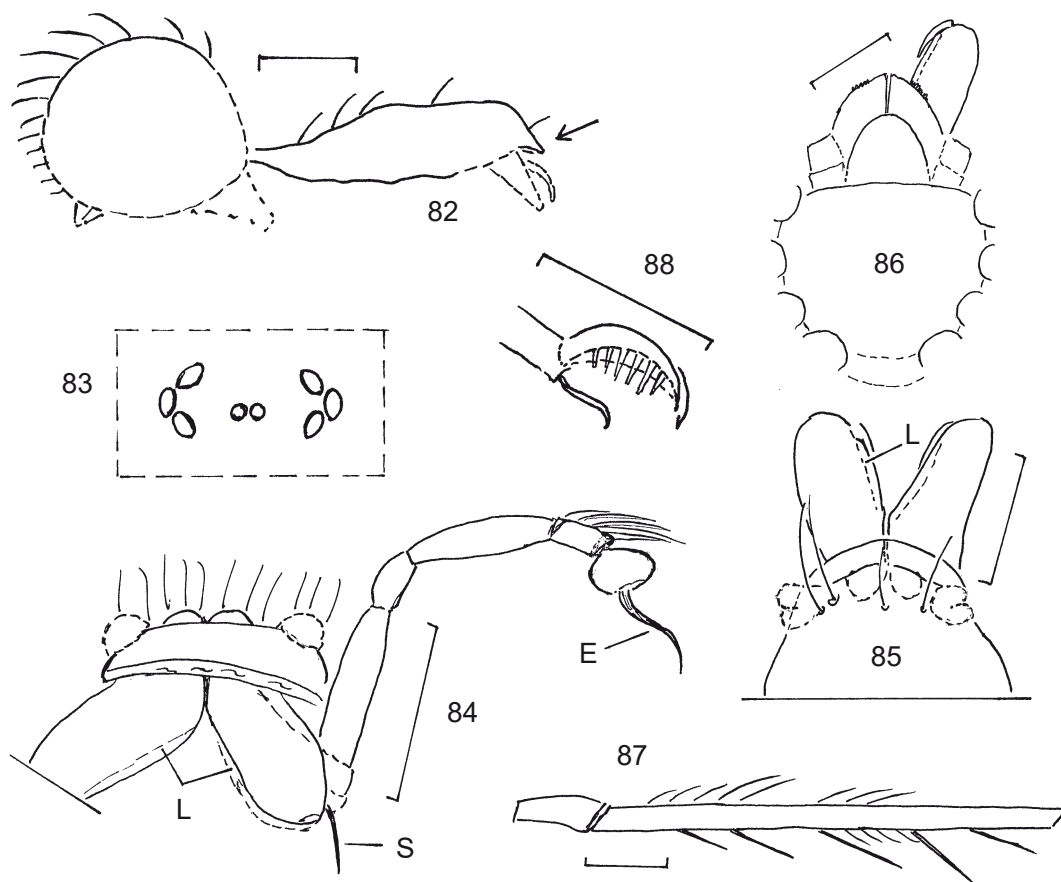


Figs. 74-77: *Burmorsolus crassus* **n. gen. n. sp.** (PLUMORSOLIDAE), ?ad. ♀ in Burmite; 74) prolateral aspect of the left femur IV; 75) retrodorsal aspect of the left leg I: Patella, tibia and basal part of the metatarsus; 76) retrolateral aspect of the tip of the left tarsus I (or II?). The paired retroclaw is drawn and the claw tuft of two distinctly separated rows; 77) retrolateral aspect of the tip of the left tarsus III. Only the retrolateral row of the claws tuft is drawn. – Scale bars 1.0 in figs. 74-75, 0.1 in figs. 76-77.

Fig. 78) *Burmorsolus* sp. indet. (PLUMORSOLIDAE), ?ad. ♀ in Burmite, anterior aspect of the chelicerae and gnathocoxae (G). Probably the chelicerae and gnathocoxae are deformed and in an unnatural position. – Coll. HUANG-HP-B-1277. – Scale bar 0.2.

Fig. 79) *Burmorchestina pulcher* WUNDERLICH 2008 (OONOPIDAE), (F2689/BU/ CJW), outline of the body, lateral aspect. – Scale bar 0.5.

Figs. 80-81: ?Pholcoidea or ?Oecobioidea or Leptonetoidea indet., ♂ in stone from Liaoning, China, F2455/LI/ CJW; 80) (?)proventral aspect of the left leg I: Tibia, metatarsus and part of



the tarsus. The short hairs are not drawn; probably some more bristles exist; 81) (?) prodorsal aspect of the deformed left pedipalpus, the bulbus probably expanded. The short arrow points to the questionable tibial apophysis, the long arrow points to one of the circles of the questionable embolus. Drawings under water. – Scale bars 0.5 and 0.3.

Fig. 82) ?*Pholcoidea* indet., ?ad. ♀ in Burmite (F2633/BU/CJW), outline of the strongly deformed body, lateral aspect. The arrow points to the deformed and protruding anterior margin of the clypeus. – Scale bar 0.2.

Fig. 83) Extant Pholcidae: Typical eye position, anterior aspect. Note the triads which have a characteristic position in this family. The small anterior median eyes are absent in numerous members of the Pholcidae. A Cretaceous proof of this family is absent.

Figs. 84-88: *Eopsiloderces serenitas* n. sp. (EOPSILODERCIDAE), ♂ in Burmite; 84) anterior and slightly ventral aspect of the fairly deformed prosoma and the left pedipalpus. Bubbles cover the eyes. Chelicerae in an artificially diverging position. Only few hairs are drawn; 85) dorsal-anterior aspect of the anterior part of the prosoma. The „clashing spines“ are hidden in this position, the chelicerae have an artificially diverging position, the eyes are covered with bubbles, only few hairs are drawn; 86) ventral aspect of sternum and mouth parts; 87) retrolateral aspect of the right tibia I. Only few hairs are drawn; 88) retrolateral aspect of the tip of the right tarsus II. – E = embolus, L = cheliceral lamella, S = cheliceral „clashing spine“. Scale bars 0.05 in fig. 88, 0.2 in the remaining figs.

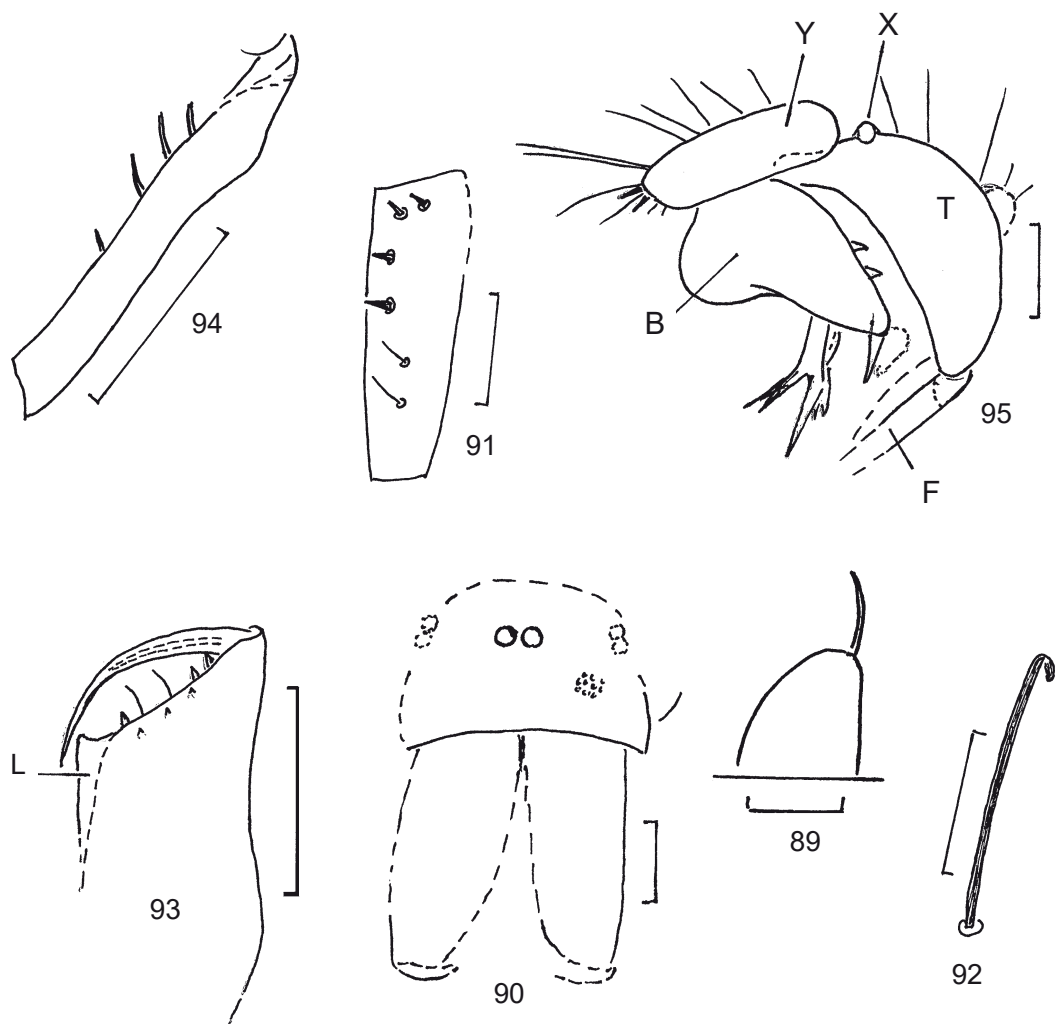


Fig. 89) *Eopsilodermes filiformis* (WUNDERLICH 2012) (EOPSILODERCIDAE), holotype ♂ in Burmite, dorsal-anterior aspect of the right chelicera with its outgrowth („clasping spine“) which is typical for this genus. Scale bar 0.05.

Fig. 90) ?*Eopsilodermes* sp. indet. (EOPSILODERCIDAE), ♀ F2755/BU/CJW in Burmite, anterior aspect (slightly left) of the prosoma (parts are hidden). – Scale bar 0.2.

Figs. 91-92: *Leclercera spicula* WUNDERLICH 2012 (PSILODERCIDAE), ♂ holotype in Burmite; 91) proventral aspect of the femur of the right pedipalpus; 92) almost retrolateral aspect of the long bristle of the left cymbium. – Scale bars 0.1.

Figs. 93-95: *Leclercera ellenbergeri* n. sp. (PSILODERCIDAE), ♂ in Burmite; 93) posterior-distal aspect of the left chelicera (its basal part is hidden); 94) retroventral aspect of the left pedipalpal femur which is slightly deformed; 95) retrolateral aspect of the left pedipalpus. The long cymbial bristle and ventral femoral spines are hidden in this position. Only few hairs are drawn. – B = bulbus, F = femur (strongly deformed), L = lamina, T = tibia, X = questionable sensory organ, Y = cymbium. Scale bars 0.2 in fig. 92, 0.1 in figs. 93 and 95.

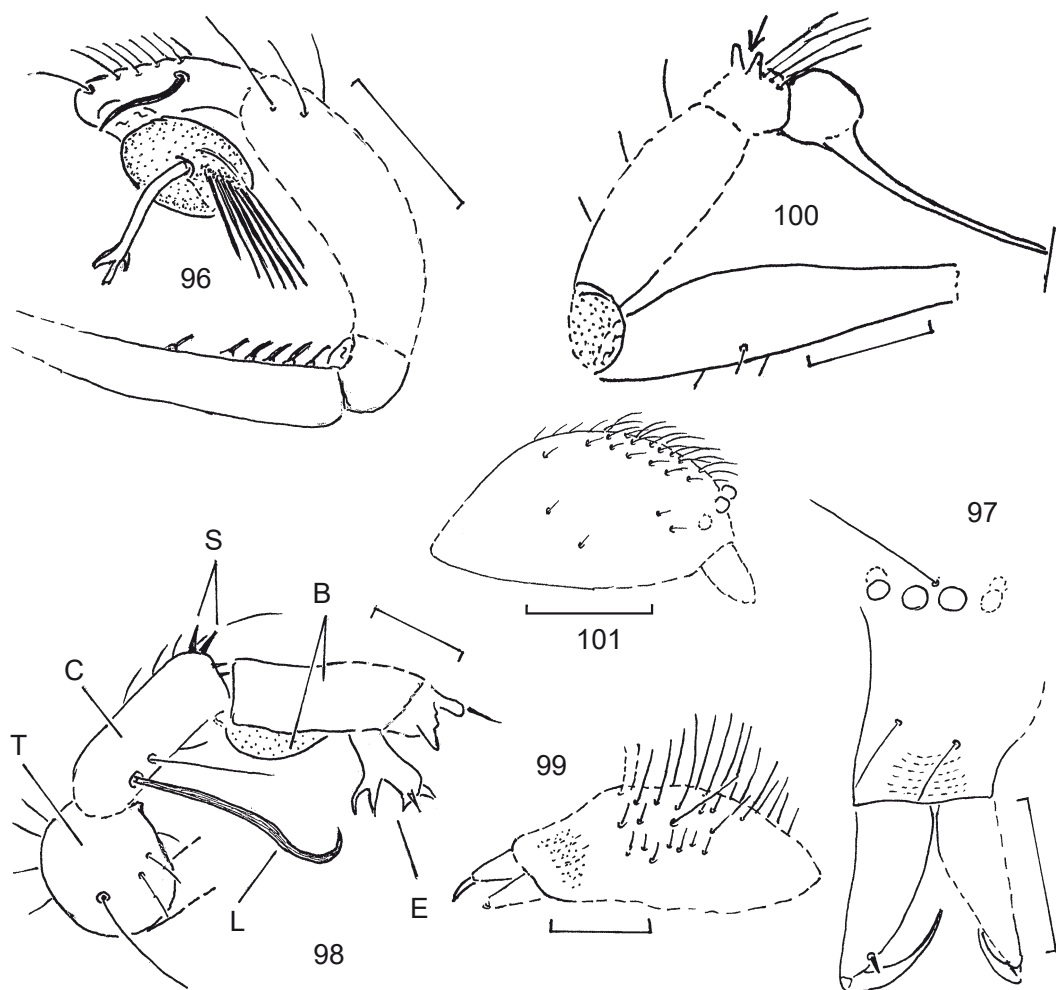


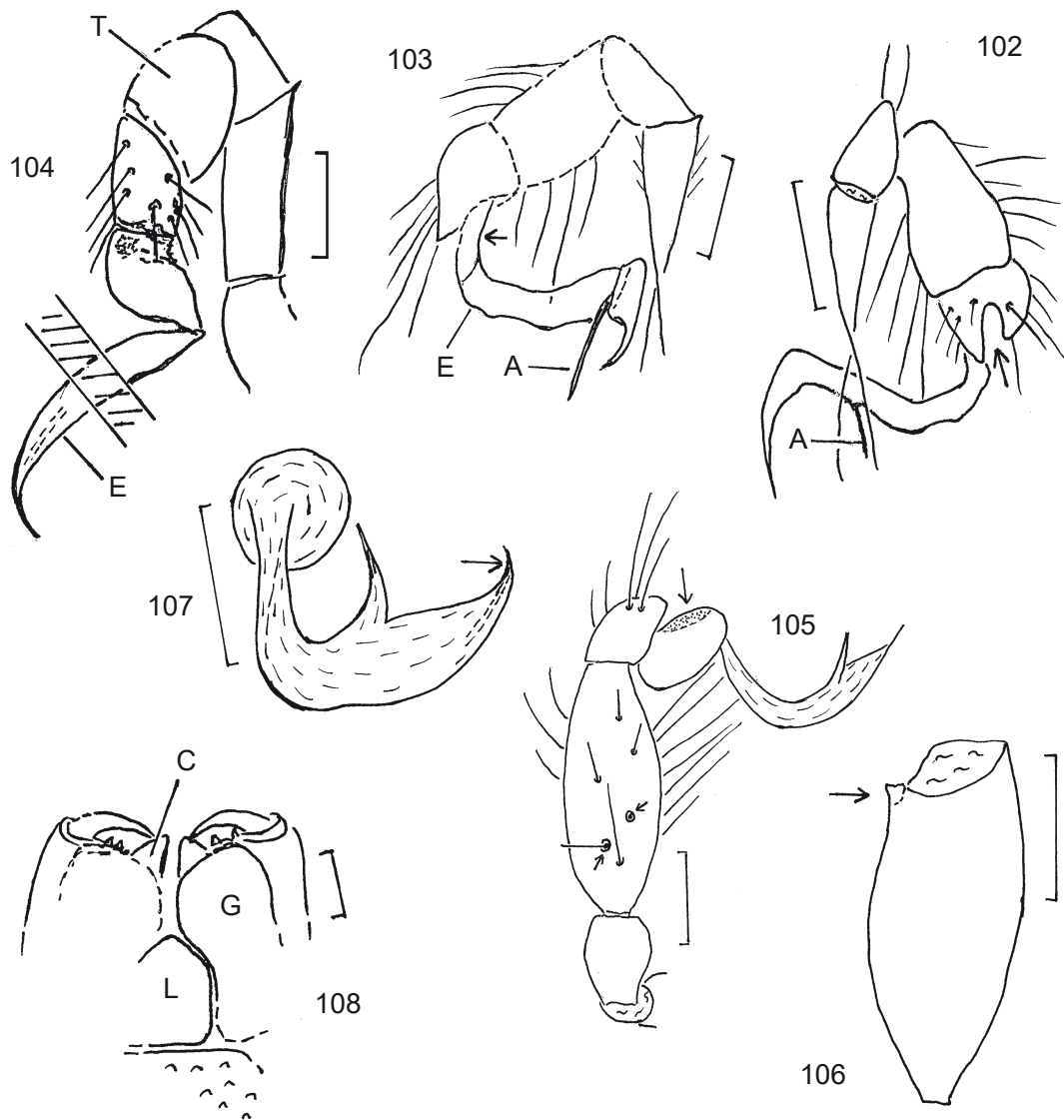
Fig. 96) *Leclercera sexaculeata* **n. sp.** (PSILODERCIDAE), ♂ in Burmite, retrolateral aspect of the left pedipalpus but retroapical aspect of the bulbus. – Scale bar 0.2.

Fig. 97) ?*Leclercera* sp. indet. (PSILODERCIDAE), ♀ F2631/BU/CJW in Burmite, anterior and slightly dorsal aspect of the deformed prosoma. – Scale bar 0.2.

Fig. 98) *Leclercera* sp. indet. (PSILODERCIDAE), ♂ F2632/BU/CJW in Burmite, dorsal aspect of the deformed right pedipalpus. – B = structures of the bulbus, C = cymbium, E = embolus and conductors, L = long cymbial bristle, S = apical cymbial spines, T = tibia. Scale bar 0.1.

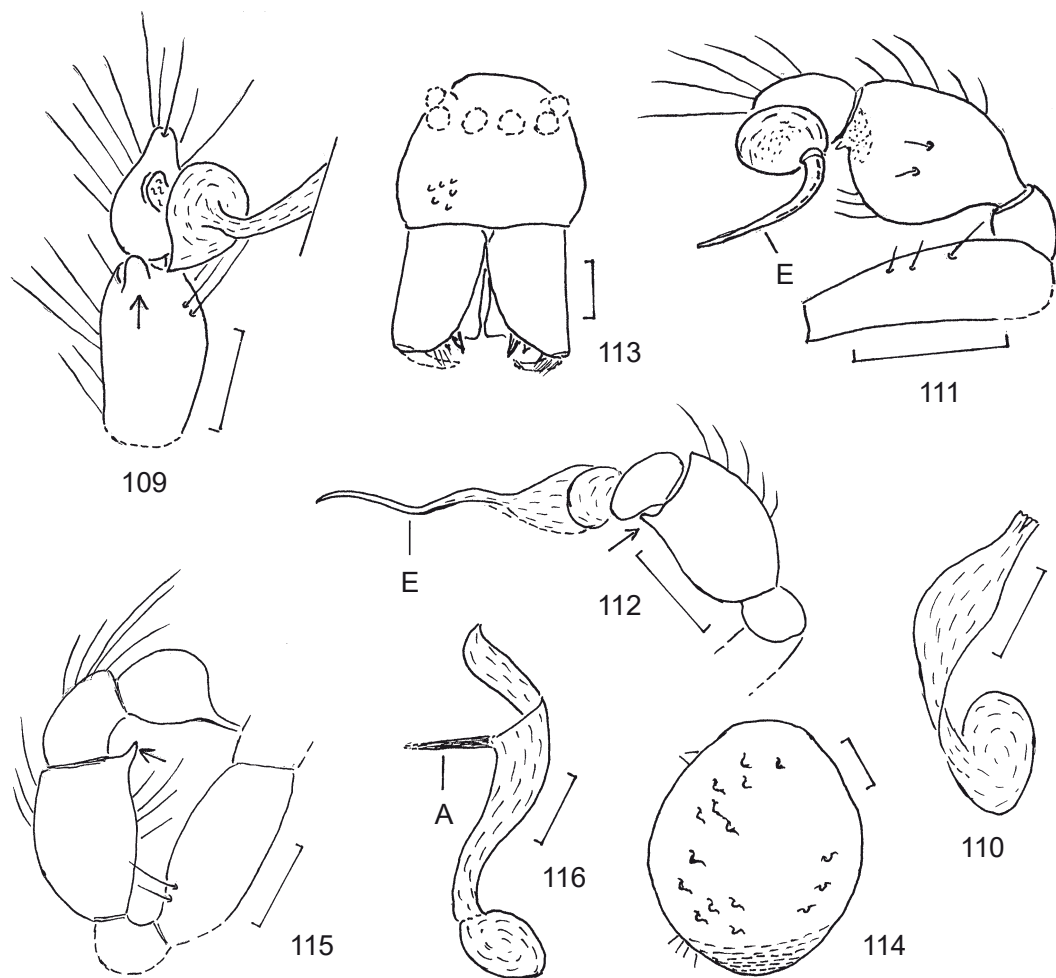
Figs. 99-100: *Propterpsilodermes longisetae* **n. gen. n. sp.** (PSILODERCIDAE), ♂ in Burmite; 99) retrodorsal aspect of the prosoma which is decomposed and partly hidden, e. g. the eyes. Not all hairs are drawn; 100) prodorsal aspect of the left pedipalpus which is partly deformed and hidden by a bubble. The arrow points to the apically bifurcated cymbium, the tip of the embolus is hidden. – Scale bars 0.5 and 0.2.

Fig. 101) ?*Scytodes hani* WUNDERLICH 2012 (SCYTODIDAE), juv. in Jordanian amber, lateral aspect of the prosoma. – Scale bar 0.2.



Figs. 102-104: *Praeterpaculla armatura* n. gen. n. sp. (TETRABLEMMIDAE), ♂ in Burmite; 102) dorsal aspect of the deformed left pedipalpus. The arrow points to the apically bilobed cymbium; 103) left pedipalpus (parts – especially femur and embolus – are distinctly deformed), ventral aspect of the femur and retrodorsal aspect of the remaining articles. Only few hairs are drawn. The arrow points to the artificially strongly narrowed bulbus; 104) right pedipalpus: Ventral aspect of the femur, dorsal aspect of tibia, cymbium, bulbus and embolus which is partly hidden. – A = apophysis of the embolus (E), T = tibia. Scale bars 0.2.

Figs. 105-107: *Praeterpaculla biacuta* n. gen. n. sp. (TETRABLEMMIDAE), ♂ in Burmite; 105) retrodorsal aspect of the right pedipalpus. The long arrow points to the artificial depression of the dorsal part of the bulbus (it is absent on the left bulbus). Note the existence of two tibial trichobothria (short arrows). Only few hairs are drawn; 106) proventral aspect of the right pedipalpal tibia. The arrow points to the proapical outgrowth; 107) apical aspect of the left bulbus and its sclerites. The arrow points to the embolus. – Scale bars 0.2.

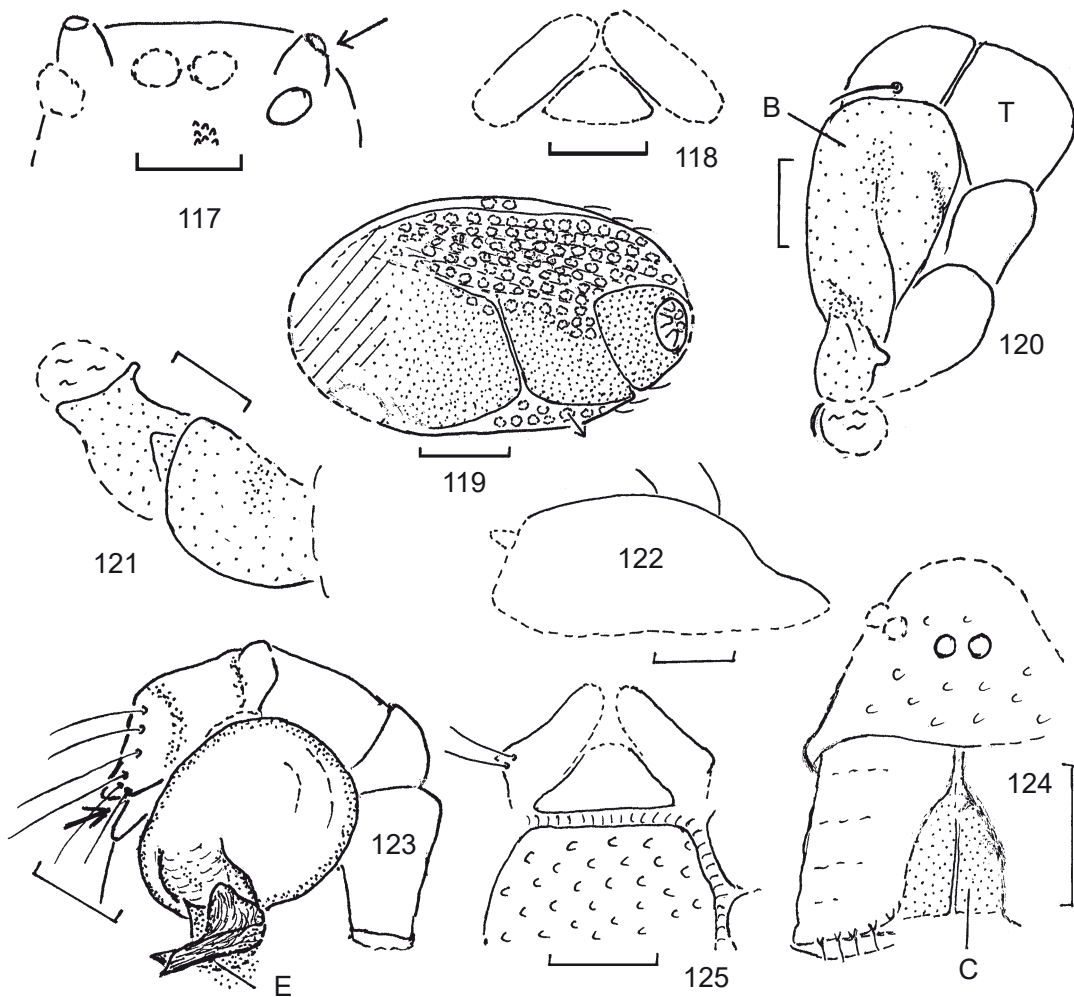


Figs. 108-110: *Praeterpaculla dissolata* n. gen. n. sp. (TETRABLEMMIDAE), ♂ in Burmite; 108) ventral aspect of the mouth parts (parts are hidden); 109) ventral aspect of the left pedipalpus. The distal part of the embolus is hidden. The arrow points to the ventral-apical tibial apophysis. Only few hairs are drawn; 110) ventral aspect of the strongly deformed right bulb and embolus. C = cheliceral carina, G = gnathocoxa, L = labium. Scale bars 0.2.

Figs. 111-112: *Praeterpaculla equester* n. gen. n. sp. (TETRABLEMMIDAE), ♂ in Burmite; 111) retrolateral aspect of the left pedipalpus. The embolus of this pedipalpus is not deformed; see the next drawing; 112) prolateral aspect of the right pedipalpus. The arrow points to the ventral-apical tibial apophysis. The embolus is strongly deformed, see fig. 100. Only few hairs are drawn. – E = embolus. Scale bars 0.2.

Figs. 113-116: *Praeterpaculla tuberosa* n. gen. n. sp. (TETRABLEMMIDAE), ♂ in Burmite; 113) anterior aspect of the prosoma. Some eyes are cut off; 114) dorsal-anterior aspect of the opisthosoma. Note the low humps which mainly are drawn on the left half; 115) retrolateral aspect of the right pedipalpus. The arrow points to the ventral-apical tibial apophysis. Only few hairs are drawn; 116) anterior aspect of the deformed left bulb and embolus. – A = apophysis of the embolus. Scale bars 0.2.



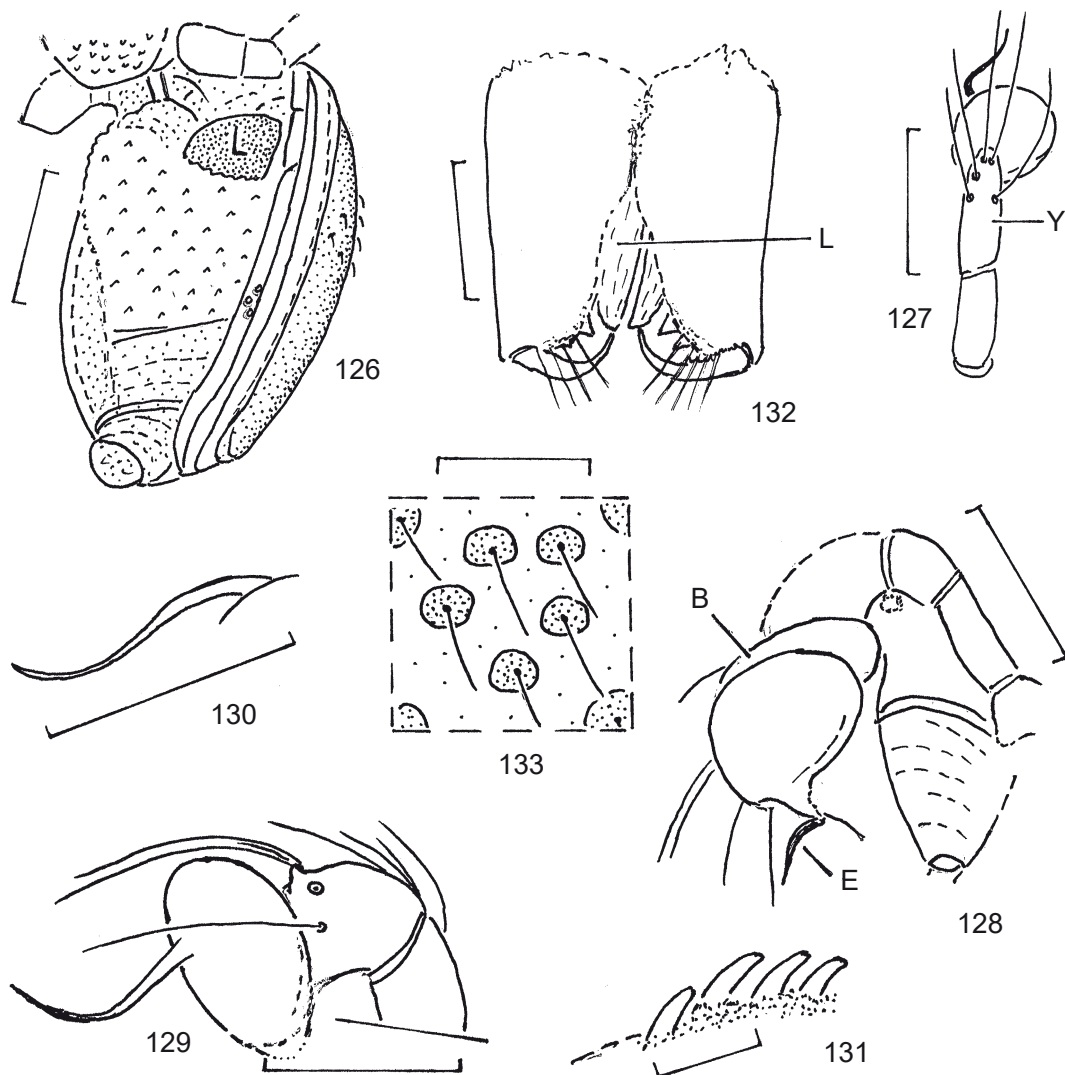


Figs. 117-121: *Bicornoculus levis* n. gen. n. sp. (TETRABLEMMIDAE), ♂ in Burmite; 117) dorsal aspect (slightly from the right side) of the eyes. The arrow points to the staked right anterior eye. Only few of the tiny wrinkles are drawn. The lense of the left posterior eye is deformed; 118) labium and gnathocoxae (parts are hidden); 119) left-ventral aspect of the opisthosoma. The arrow points to an enlarged tiny hair-bearing plate. Hairs of other plates are not drawn; 120) retrolateral and slightly apical aspect of the left pedipalpus; 121) retrolateral aspect of the bulb of the right pedipalpus. – B = bulbus, T = tibia. Scale bars 0.2 in figs. 118-119, 0.1 in the remaining figs.

Fig. 122) ?*Bicornoculus* sp. (TETRABLEMMIDAE), ♂ F2693/BU/CJW in Burmite, outline of the prosoma, lateral aspect. Parts are hidden. Scal bar 0.1.

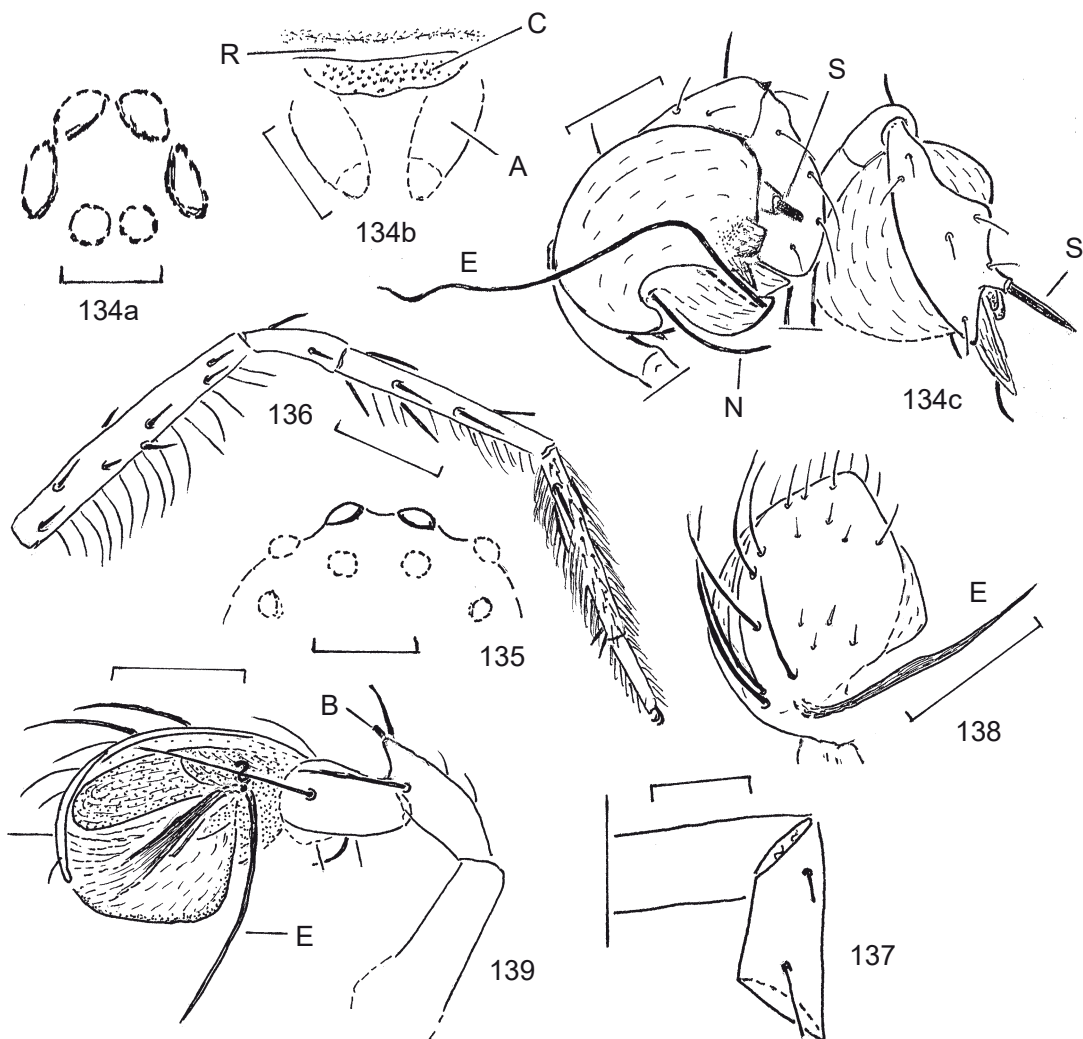
Fig. 123) ?Gen. sp. (TETRABLEMMIDAE), ♂, coll. HUANG 0909, retroventral aspect of the left pedipalpus. The arrow points to the apically divided cymbium. Only few hairs are drawn. – E = embolus. Scale bar 0.1.

Figs. 124-130: ?*Eogamasomorpha clara* n. sp. (TETRABLEMMIDAE), ♂ in Burmite; 124) anterior aspect of the prosoma. Parts of the left side are hidden. Note the large cheliceral lamella;



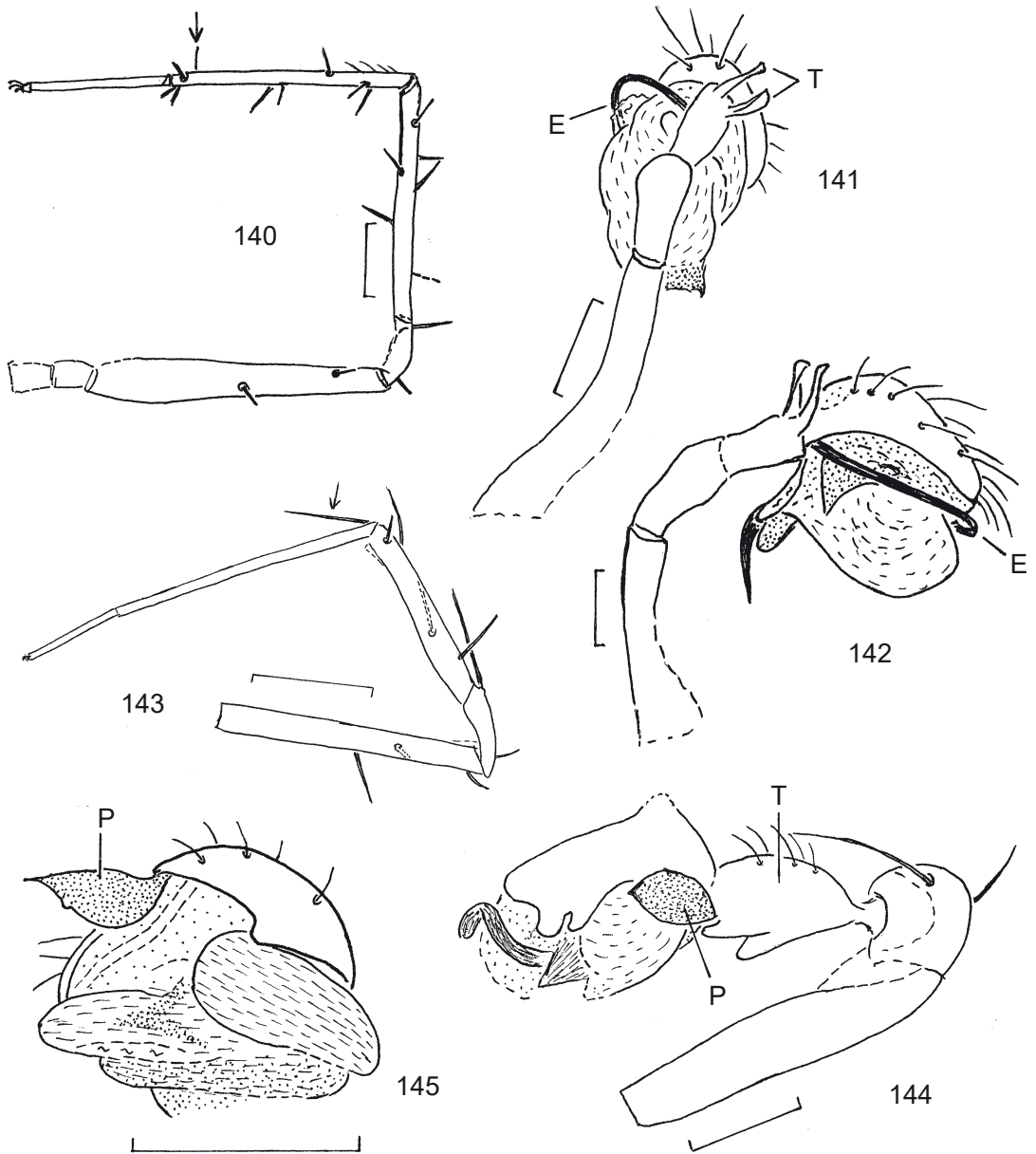
125) ventral aspect (slightly from the left side) of the mouth parts and the anterior part of the sternum which is prominent and deeply declined at its margin (apparently a family character); 126) ventral-lateral aspect of the opisthosoma and posterior part of the prosoma. Note the large dorsal and ventral scuta, the ring around the spinnerets, the long narrow lateral scuta (only three of their tiny plates are drawn) and the lung cover; 127) dorsal aspect of the right pedipalpus; 128) retrolateral and slightly ventral aspect of the left pedipalpus; 129) prolateral aspect of the right pedipalpus; 131) dorsal aspect of the right embolus. – B = bubble basally on the bulb, C = cheliceral lamella, E = embolus, L = lung cover, Y = cymbium. Scale bars 0.2 in fig. 126, 0.1 in the remaining figs.

Figs. 131-133: *Uniscutosoma aberrans* n. gen. n. sp. (TETRABLEMMIDAE), ♂ in Burmite; 131) lateral and slightly anterior aspect of the prosomal margin (it is partly hidden) showing four „horns“ in a transverse row; 132) anterior aspect of the loose and slightly deformed chelicerae which are placed anteriorly above the spiders prosoma; 133) some dorsal plates of the opisthosoma. – L = cheliceral lamella. Scale bars 0.2 in fig. 132, 0.1 in the remaining figs.



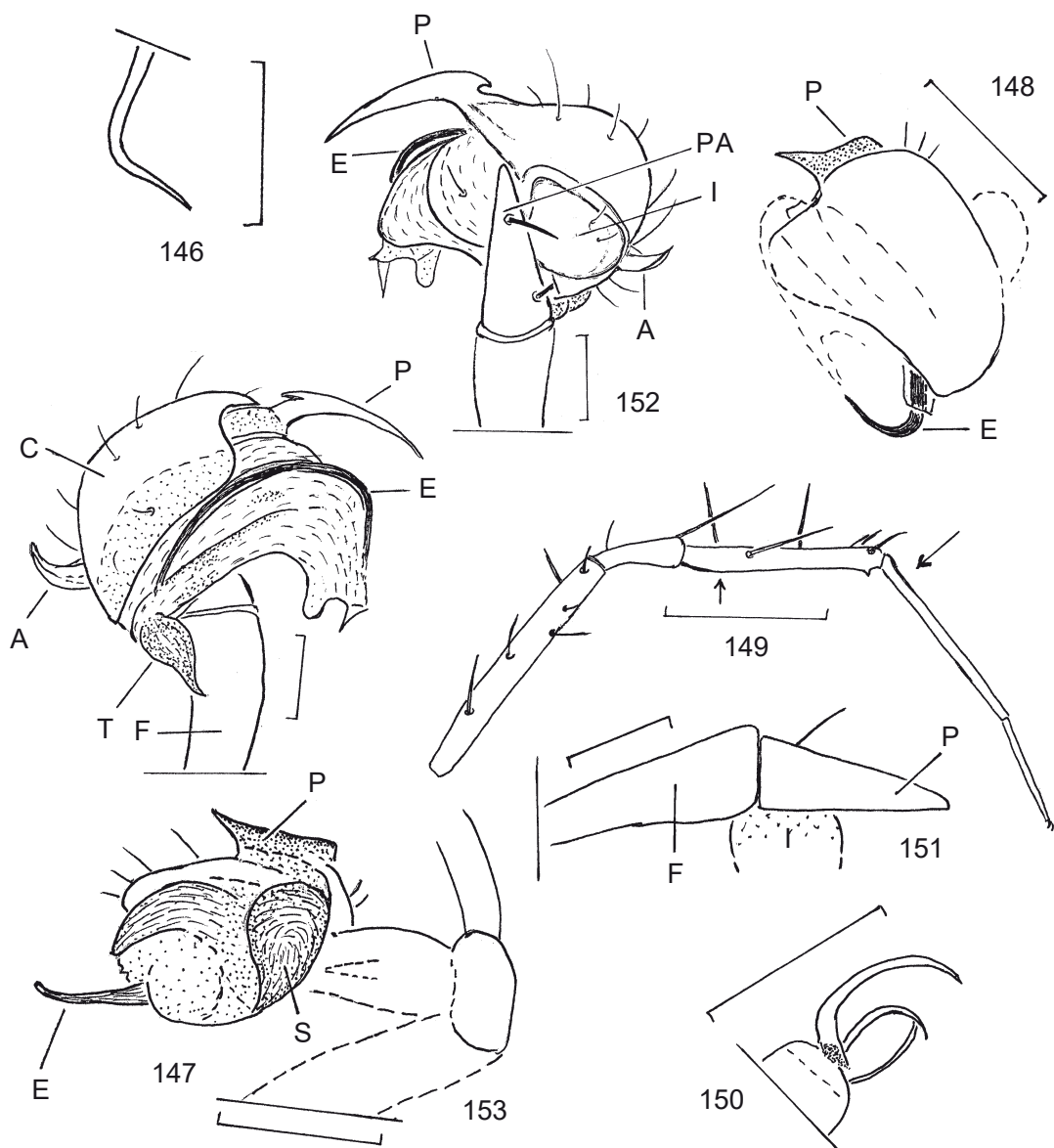
Figs. 134a-c): *Palaeoleoneta calcar* WUNDERLICH 2012 (LEPTONETIDAE: PALAEOLEPTONETINAE), ♂ holotype in Burmite; a) dorsal aspect of the eyes (reconstruction); b) questionable cribellum and widely spaced anterior spinnerets; c) retrolateral aspect of the right pedipalpus and dorsal aspect of the left pedipalpus (drawn from the ventral side of the spider). Both pedipalpi are deformed, only the right embolus is well observable but apparently not in its natural position. Only few hairs are drawn. – A = anterior spinneret, C = cribellum, E = embolus, N = needle-shaped apophysis, R = roll, S = large cymbial spur. Scale bar 0.2.

Figs. 135-139: *Autotomiana hirsutipes* n. gen. n. sp. (PRAETERLEPTONETIDAE), ♂ in Burmite; (135) dorsal aspect of the eyes which are partly covered with an emulsion, attempt of a reconstruction; (136) prolateral aspect of the left leg III. Note the long femoral hairs which look like trichobothria in an almost ventral position, an unusual position of trichobothria. Not all hairs are drawn; (137) part of the right leg IV with probable autotomy beyond the patella; (138) dorsal aspect of the left pedipalpus; (139) retrolateral aspect of the left pedipalpus which is slightly deformed. The area around the question mark is not well observable. Only few hairs are drawn. – B = blunt spine on the patellar outgrowth E = embolus, Y = cymbium. Scale bars 1.0 in fig. 136, 0.5 on the remaining figs.



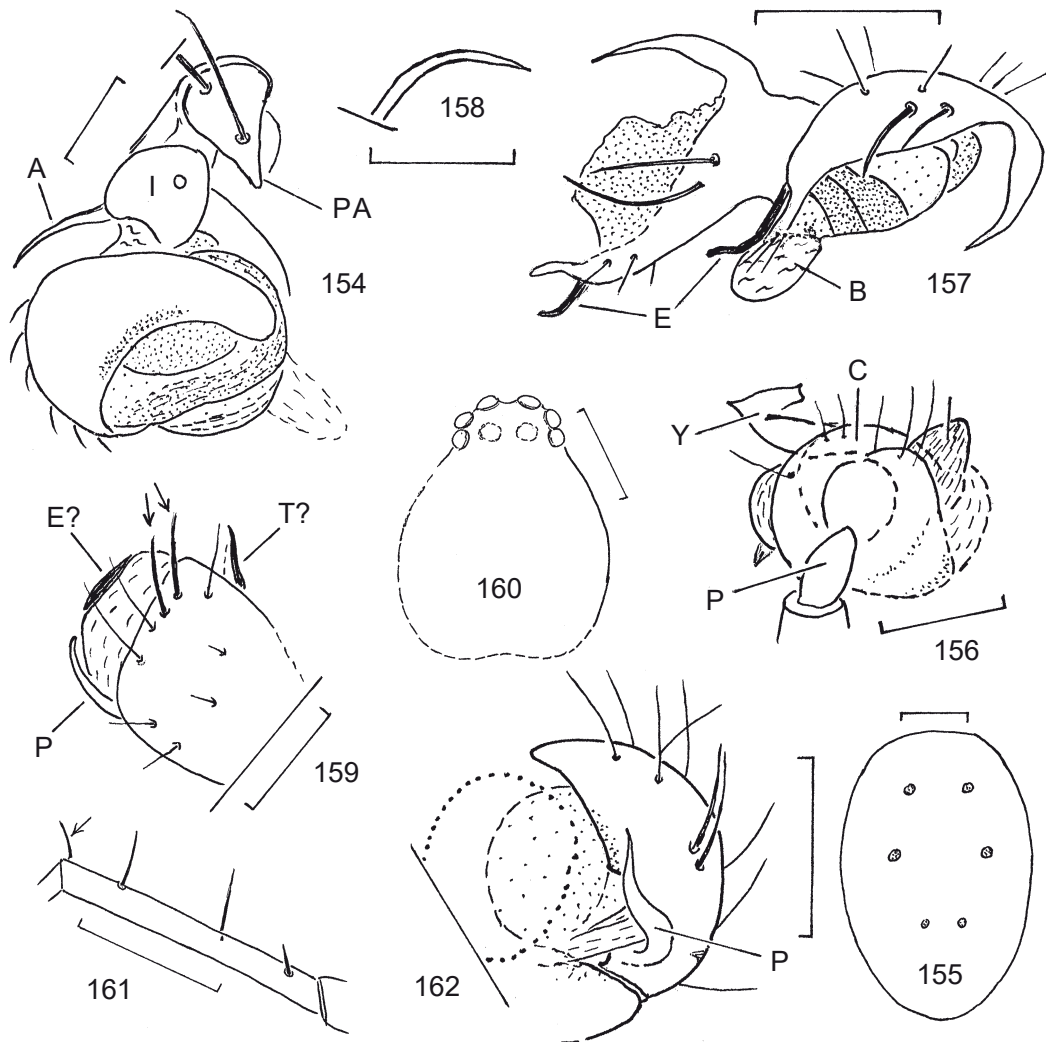
Figs. 140-142: *Biapophyses beate* n. gen. n. sp. (PRAETERLEPTONETIDAE), ♂ in Burmite; 140) prolateral aspect of the right leg I. Note the distal position of the metatarsal trichobothrium (arrow). A tibial bristle which exists on the left tibia (dotted) is added. Only few of the indistinct hairs are drawn; 141) dorsal-basal aspect of the right pedipalpus; 142) prodorsal aspect of the left pedipalpus. The basal half of the femur is deformed. Only few hairs are drawn.- E = embolus, T = tibial apophyses. Scale bars 0.2 in fig. 140, 0.1 in figs. 141-142.

Figs. 143-145: *Crassitibia longispina* n. gen. n. sp. (PRAETERLEPTONETIDAE), ♂ in Burmite; 143) retrolateral aspect of the left leg I. Note the very long proapical bristle on the tibia (arrow). Hairs are not drawn; 144) retrolateral aspect of the left pedipalpus; 145) retrobasal aspect of the left pedipalpus. - P = paracymbium, T = tibia. Scale bars 0.5 in fig. 143, 0.2 in the remaining figs.



Figs. 146-148: *Crassitibia tenuimanus* n. gen. n. sp. (PRAETERLEPTONETIDAE), ♂ in Burmite; 146) prolateral aspect of the right tarsus I claw; 147) retrolateral aspect of the left pedipalpus; 148) apical aspect of the right pedipalpus. Parts are hidden. – E = embolus, P = paracymbium, S = subtegulum. Scale bars 0.02 in fig. 146, 0.2 in figs. 147-148.

Figs. 149-154: *Curvitibia curima* n. gen. n. sp. (PRAETERLEPTONETIDAE), ♂ in Burmite; 149) prolateral aspect of the left leg I. The short arrow points to the thickened tibia, the long arrow points to the concave part of the metatarsus; 150) prolateral aspect of the unpaired and the paired proclaw. Only a single (ventral) hair is drawn; 151) retrolateral aspect of articles of the right pedipalpus; 152) dorsal aspect of the left pedipalpus; 153) ventral aspect of the left pedipalpus; 154) anterior-dorsal aspect of the left pedipalpus. – A = prolateral apophysis of the tibia, C = cymbium, E = embolus, F = femur, I = tibia P = patella, PA = patellar apophysis, T = tegular apophysis.



Figs. 155-156: *Groehnianus burmensis* **n. gen. n. sp.** (PRAETERLEPTONETIDAE), ♂ in Burmite; 155) outline of the opisthosoma, to show the dorsal sigillae; 156) dorsal-anterior aspect of the left pedipalpus. – C = cymbium, P = patella, X = flat apophysis of the bulbus, Y = questionable paracymbium. Scale bars 0.2 and 0.1.

Figs. 157) *Hypotheridiosoma falcata* **n. sp.** (PRAETERLEPTONETIDAE), ♂ in Burmite, retrolateral aspect of the left pedipalpus and dorsal aspect of the right pedipalpus (on the left). Only few hairs are drawn. – B = bubble, E = embolus. Scale bar 0.2.

Figs. 158-162: *Hypotheridiosoma paracymbium* WUNDERLICH 2012 (PRAETERLEPTONETIDAE), holotype ♂ in Burmite; 158) prolateral aspect of the unpaired tarsal claws of the left tarsus III; 159) dorsal aspect of cymbium and bulbus. Only few hairs are drawn. The arrows point to two bristle-shaped hairs; 160) dorsal aspect of the prosoma; 161) retrolateral and slightly dorsal aspect of the left tibia I. The arrow points to the proapical bristle; 162) retrolateral aspect of the left pedipalpus. Strongly dotted: Bubble around the bulbus. – E = questionable embolus, P = paracymbium, T = questionable tegular apophysis. Scale bars 0.02 in fig. 158, 0.1 in figs. 159 and 162, 0.2 in figs. 160-161.

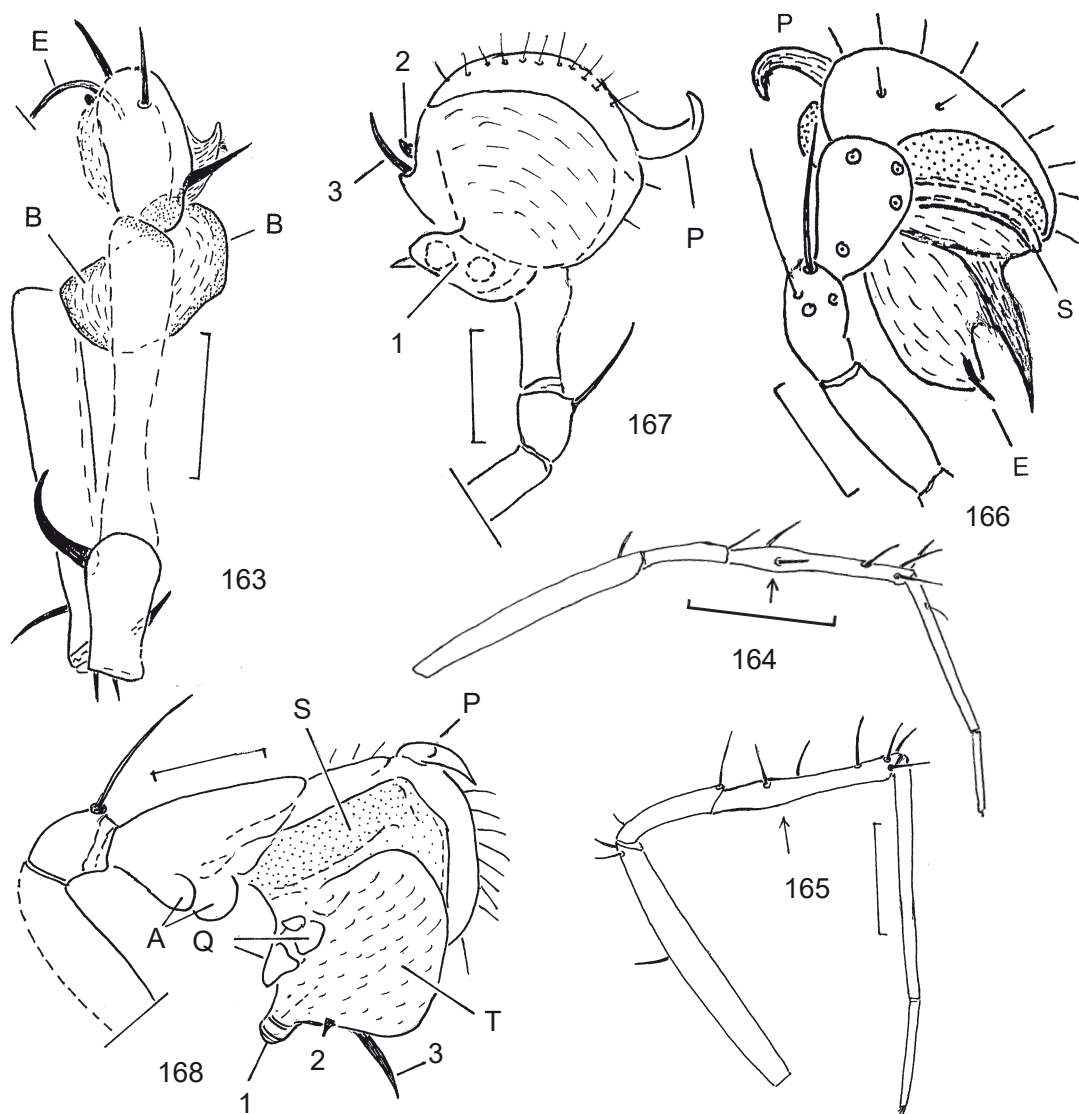
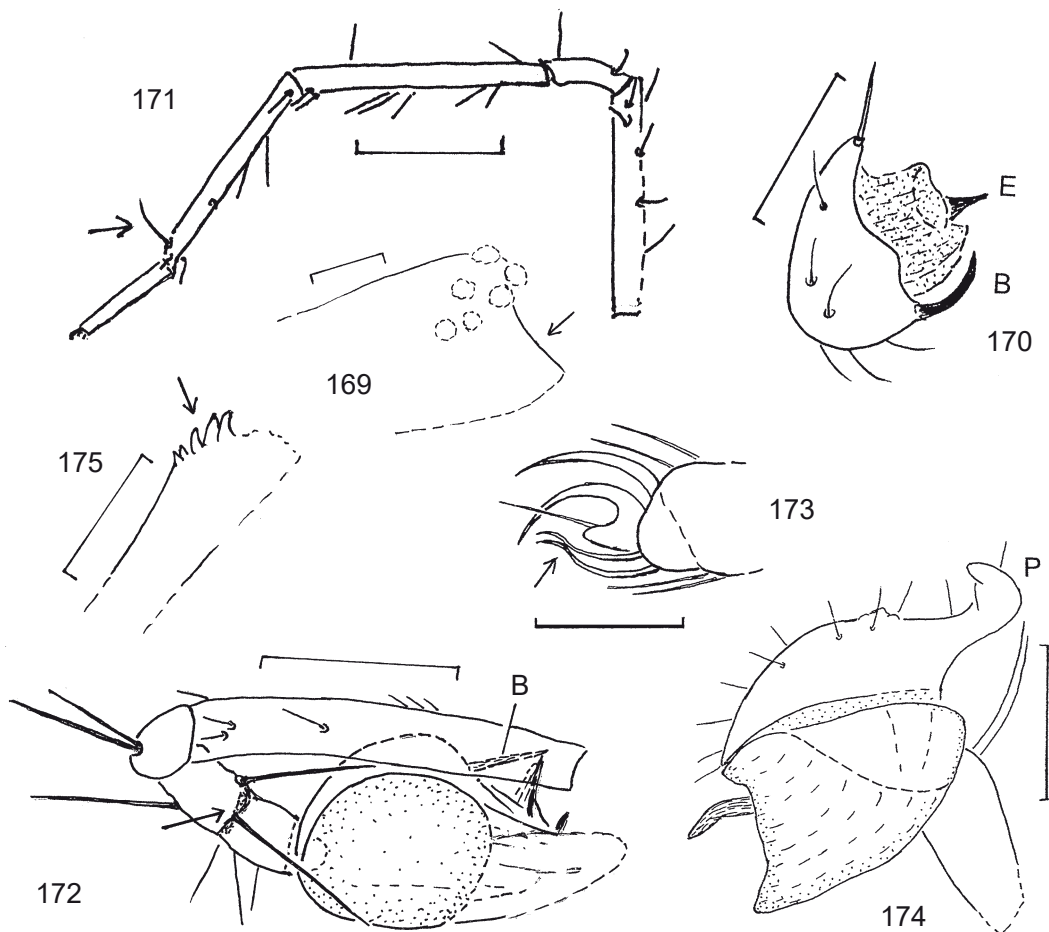


Fig. 163) *Palaeohygropoda myanmarensis* PENNEY 2004 (PRAETERLEPTONETIDAE), holotype ♂ in Burmite, dorsal aspect of the deformed right pedipalpus. Note the very long tibia. – B = bubble, E = embolus. Scale bar 0.5.

Figs. 164-168: *Parvispina tibialis* (WUNDERLICH 2011) (PRAETERLEPTONETIDAE), ♂, holotype in Burmite: Figs. 165-166, F2453/BU/CJW: The remaining figs.; 164) retrolateral aspect of the right leg I. The arrow points to the thickened part of the tibia; 165) prolateral and slightly dorsal aspect of the left leg I. The arrow points to the thickened part of the tibia; 166) prodorsal-basal aspect of the left pedipalpus; 167) retroapical-ventral aspect of the left pedipalpus. The tegular apophysis 1 bears two small bubbles (dotted circles); 168) retrolateral aspect of the right pedipalpus. Parts of the bulbus are hidden by small bubbles which may simulate sclerites. – A = artefacts/ deformations caused by the preservation, 1, 2, 3 = tegular apophyses, E = embolus, P = paracymbium, Q = questionable tegular apophyses (artefacts?), S = subtegulum and “sperm duct” in fig. 166 (see the text), T = tegulum. Scale bars 1.0 in fig. 164, 0.5 in fig. 165, 0.1 in the remaining figs.



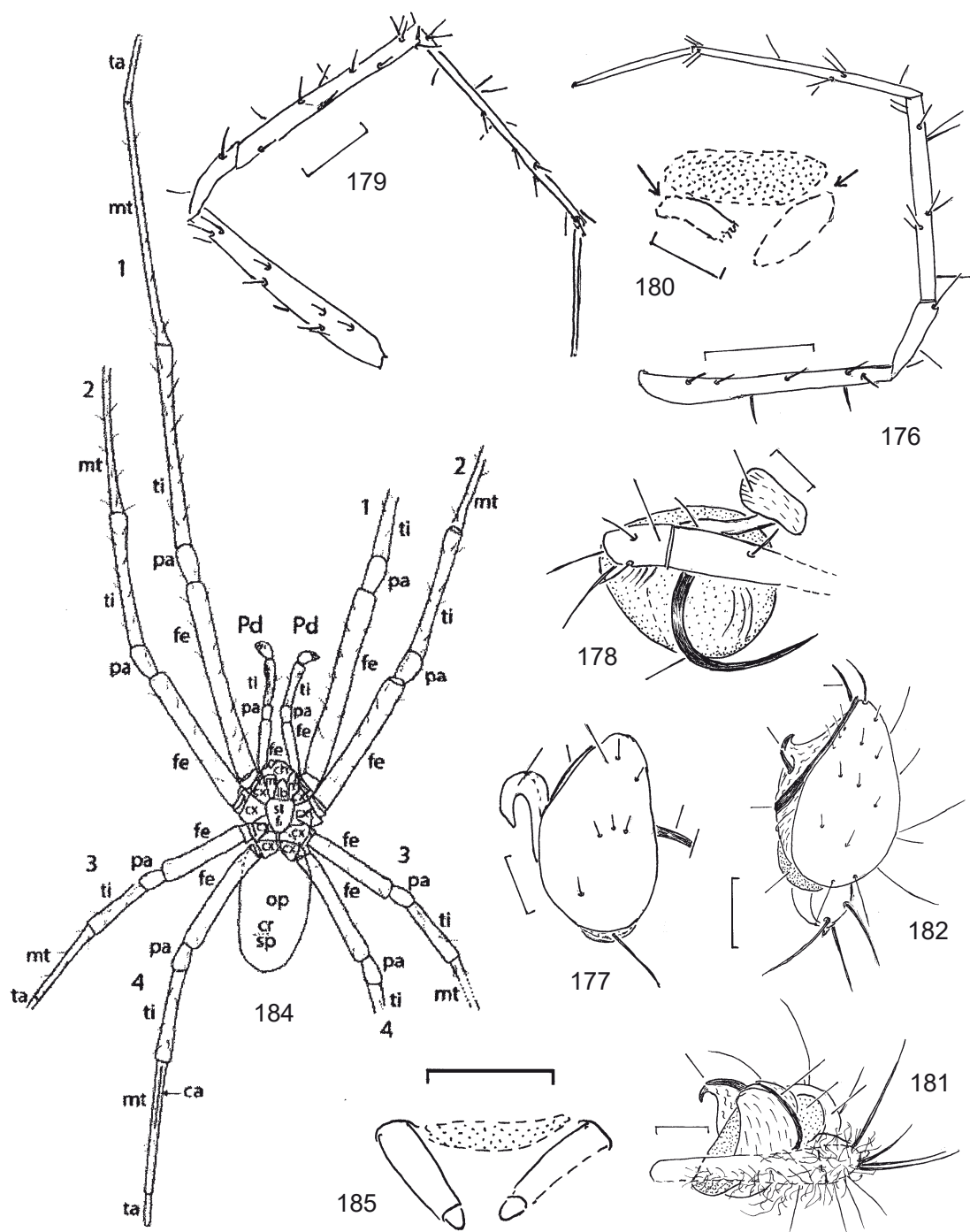


Figs. 169-170: *Praeterleptoneta spinipes* WUNDERLICH 2008 (PRAETERLEPTONETIDAE), ♂ holotype in Burmite; 169) anterior part of the prosoma, lateral aspect. Note the long and protruding clypeus (arrow). The eyes are covered with an emulsion; 170) apical aspect of the right pedipalpus. – E = embolus. Scale bars 0.1.

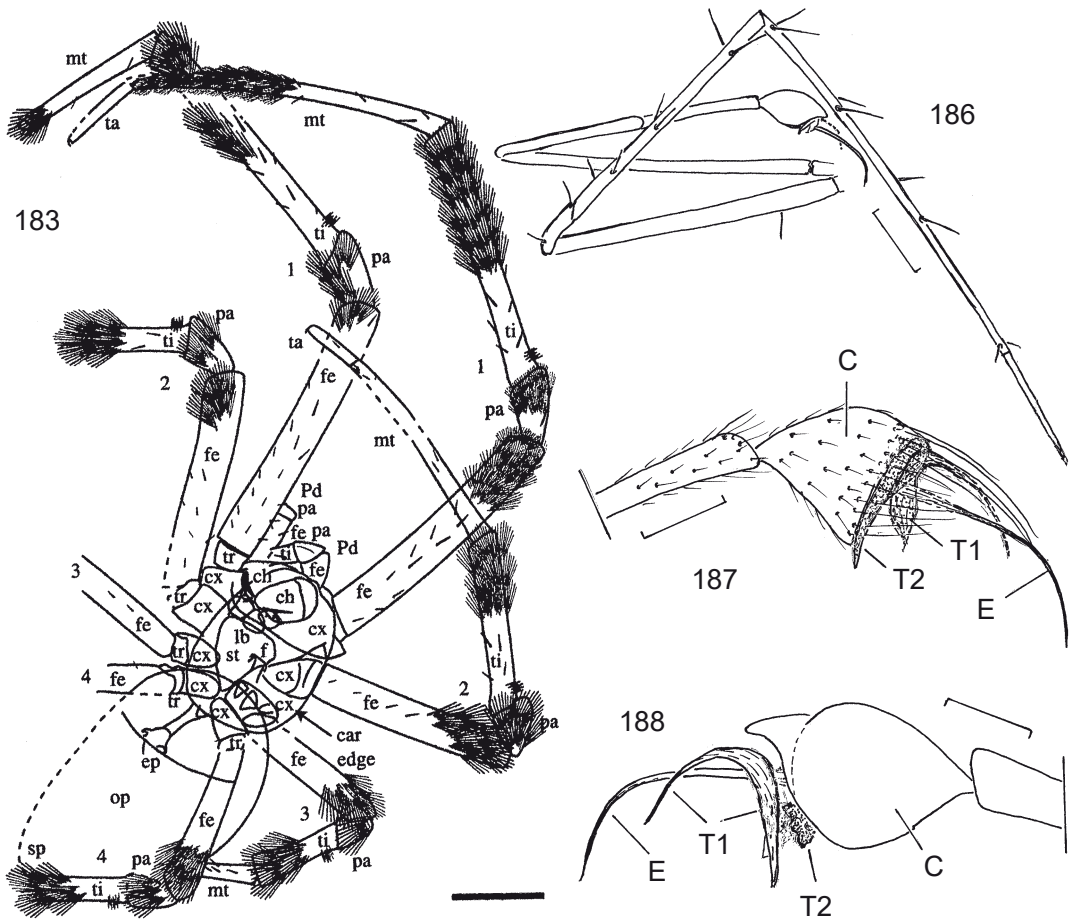
Figs. 171-172: *Spinipalpitibia maior* n. gen. n. sp. (PRAETERLEPTONETIDAE), ♂ in Burmite; 171) prolateral aspect of the right leg I. Note the long metatarsal trichobothrium near the end of the article (arrow). Hairs are not drawn; 172) right pedipalpus: Dorsal aspect of the femur and ventral aspect of the bulbus which apical part is hidden by the clypeus. The arrow points to the ventral tibial rim and the bases of two long ventral tibial bristles. – B = cymbial bristle. Scale bars 0.5 and 0.2.

Figs. 173-174: *Zargareneus hudae* WUNDERLICH 2008 (PRAETERLEPTONETIDAE), ♂ holotype in Jordanian amber; 173) prolateral aspect of the tip of the right tarsus II. The arrow points to the paired „auxiliary hairs“. Note the large unpaired claw; 174) retrodorsal aspect of the left pedipalpus. – P = paracymbium. Scale bars 0.05 and 0.2.

Fig. 175) *Pholcochyrocer pecten* WUNDERLICH 2012 (PHOLCOCHYROCERIDAE), holotype ♂ in Burmite, retrolateral aspect of the right pedipalpal femur. The arrow points to the dorsal-distal comb. – Scale bar 0.2.



Figs. 176-178: *Spinicreber antiquus* n. gen. n. sp. (PHOLCOCHYROCERIDAE), ♂ in Burmite; 176) prolateral aspect of the right leg I; 177) dorsal aspect of the left pedipalpus. Only the basal part of S is observable in this position; 178) right pedipalpus: Dorsal aspect of femur and patella, ventral aspect of the bulbus. – C = cymbium, E = embolus, P = patella, S = slender tegular apophysis, U = u-shaped tegular apophysis. Scale bars 1.0 in fig. 176, 0.2 in figs. 177-178.



Figs. 179-182: *Spinipalpus vetus* n. gen. n. sp. (PHOLCOCHYROCERIDAE), ♂ in Burmite; 179) prolateral aspect of the left leg I; 180) outline of the deformed posterior spinnerets in their unnatural position in front indistinct remains of the cribellum (dotted), ventral aspect. Note the widely spaced bases of the spinnerets (arrows); 181) left pedipalpus: Dorsal aspect of the femur (only some of the covering hyphae are drawn) and ventral aspect of the bulbus. The distal part of the questionable embolus is hidden in this position by the pedipalpal femur; 182) dorsal aspect of the left pedipalpus. Only few hairs are drawn. – C = cymbium, E = embolus, S = questionable subtegulum, T = tegular apophyses. Scale bars 1.0 in fig. 179, 0.2 in the remaining figs.

Figs. 183-184: *Mongolarachne jurassica* (SELDEN et al. 2011) (MONGOLARACHNIDAE) in Jurassic stone of Mongolia; 183) ventral aspect of the female holotype. Note the well developed hair brushes of the legs of this large spider; 184) ventral aspect of the male. Note the long pedipalpal articles and the small pedipalpal tarsi. – Scale bars 1 and 0.5 cm. – Taken from SELDEN et al. (2011, 2013).

Figs. 185-188: *Longissipalpus minor* n. gen. n. sp. (MONGOLARACHNIDAE), ♂ in Burmite; 185) ventral and slightly right aspect of the posterior spinnerets and remains of the cribellum (dotted) which is not well preserved; 186) retrolateral aspect of the left leg I and the left pedipalpus. Hairs are not drawn; 187) retrolateral spect of the right pedipalpus. Only few hairs are drawn; 188) prolateral aspect of the right pedipalpus. Hairs are not drawn. – C = cymbium, E = embolus, T1, T2 = tegular apophyses. Scale bars 0.5 in fig. 186, 0.2 in the remaining figs.

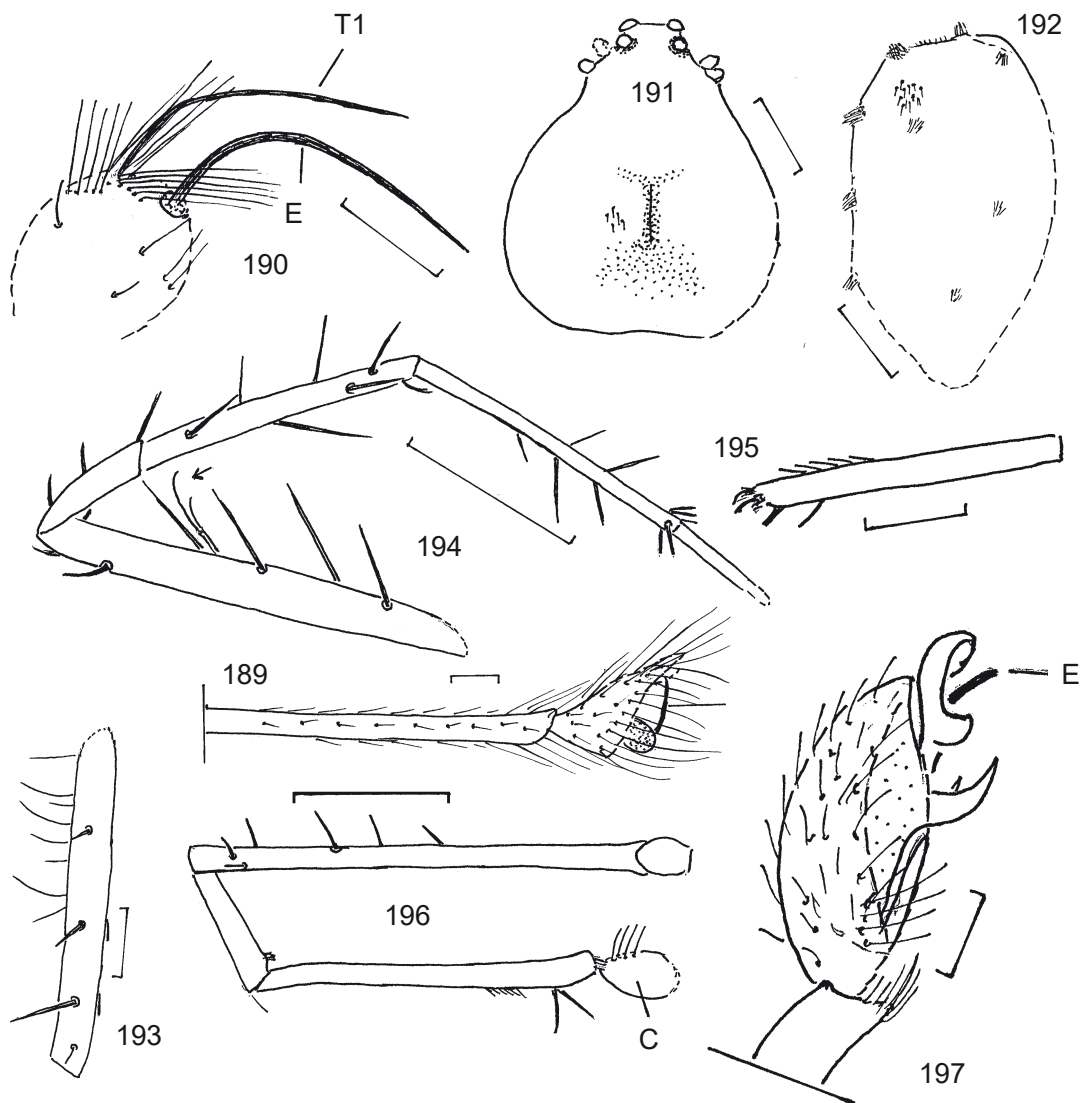


Fig. 189) *Longissipalpus maior* n. gen. n. sp. (MONGOLARACHNIDAE), ♂ in Burmite, retrolateral aspect of the right pedipalpus. – E = embolus. Scale bar 0.2.

Fig. 190) *Longissipalpus magnus* n. gen. n. sp. (MONGOLARACHNIDAE), ♂ in Burmite, retro-lateral aspect of the distal part of the right pedipalpus. Only few hairs are drawn – E = embolus, T1 = tegular apophysis.

Figs. 191-197: *Pedipalparaneus seldeni* n. gen. n. sp. (MONGOLARACHNIDAE), ♂ in Burmite; 191) dorsal aspect of the prosoma; 192) dorsal-left aspect of the opisthosoma which is partly deformed and hidden. Note the hair-bearing humps; 193) prodorsal-distal aspect of the left femur I. Not all of the trichobothrium-like ventral hairs are drawn; 194) retrolateral aspect of the right leg IV. Two of the trichobothrium-like hairs are drawn (arrow); 195) retrolateral aspect of the left tarsus IV; 196) prolateral aspect of the right pedipalpus. Only few hairs are drawn; 197) retrolateral (slightly distal) aspect of the right pedipalpus. – C = cymbium, E = embolus. Scale bars 1.0 in figs. 194 and 196, 0.5 in figs. 191-193, 0.2 in figs. 195 and 197.

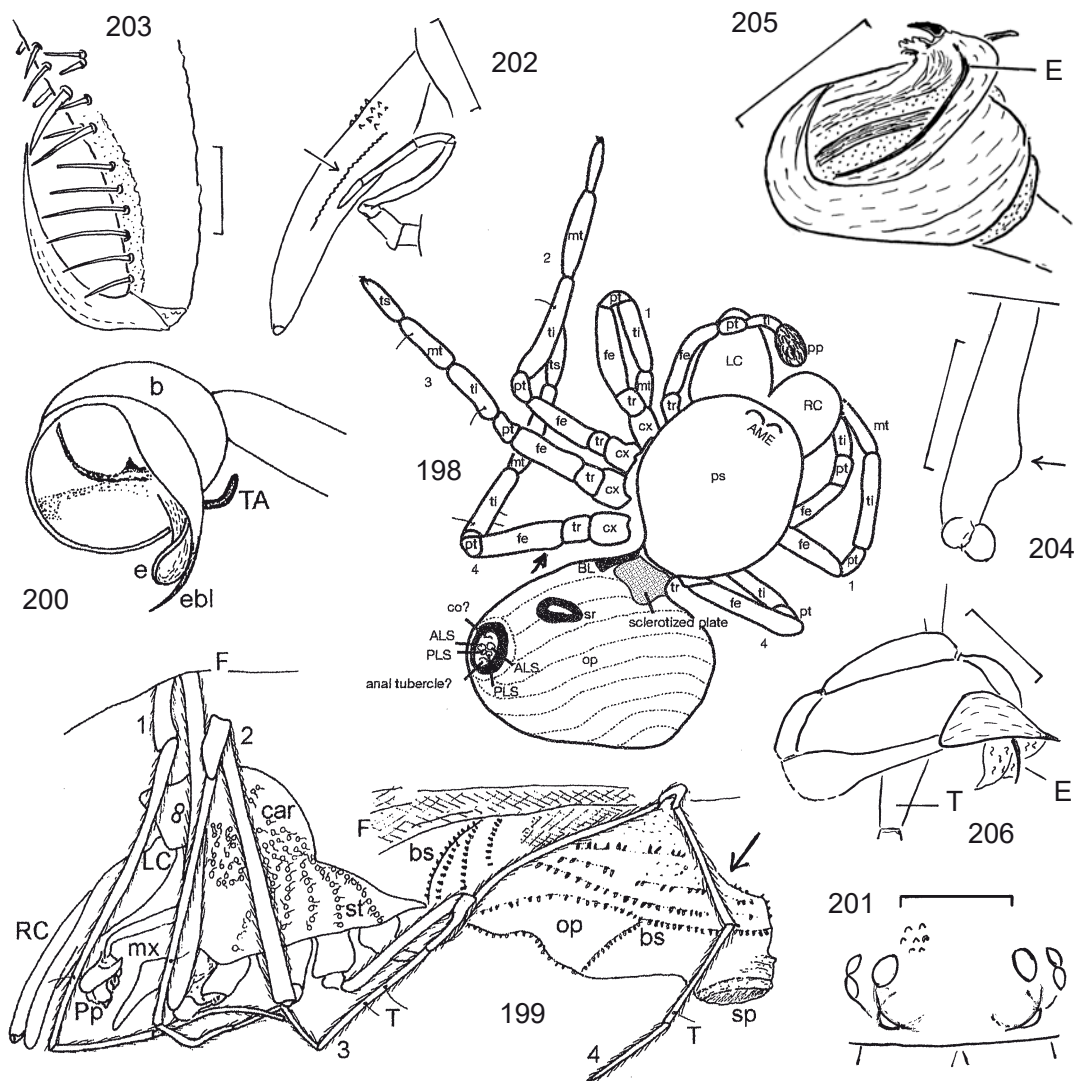


Fig. 198) *Archaemecys arcantiensis* SAUPE & SELDEN 2009 (ARCHAEIDAE), subad. ♂ in amber from France. The arrow points to the questionable hump on the left femur IV. – Scale bar 0.5. Taken from SAUPE & SELDEN (2009).

Figs. 199-206: *Burmesarchaea grimaldii* (PENNEY 2003) (ARCHAEIDAE) in Burmite; 199-200) ♂ holotype; 199) lateral aspect of the spider. Most probably the opisthosoma is distinctly deformed and was originally protruding beyond the spinnerets (arrow) like in other conspecific spiders, see the photos; 200) pedipalpus. – Scale bars 1.0 and 0.1. Taken from PENNEY (2003); 201-203: ♀ F2521/BU/CJW; 201) anterior-dorsal aspect of the eye region. Spines and bristles are not drawn; 202) retrolateral aspect of the left chelicera and the left pedipalpus. The arrow points to the questionable cheliceral stridulatory edge; 203) pro-anterior aspect of the distal part of the left chelicera; 204) probably conspecific ♂ F2519/BU/CJW, retrolateral aspect of the left femur IV, basal half. Note the distinct dorsal hump (arrow); 205) ♂ F2520/BU/CJW, prodistal aspect of the deformed left pedipalpus; 206) ♂ F2534/BU/CJW, retrolateral aspect of the deformed right pedipalpus; E = embolus, T = trochanter. – Scale bars 0.1 in figs. 203, 205, 206, 0.2 in the remaining figs.

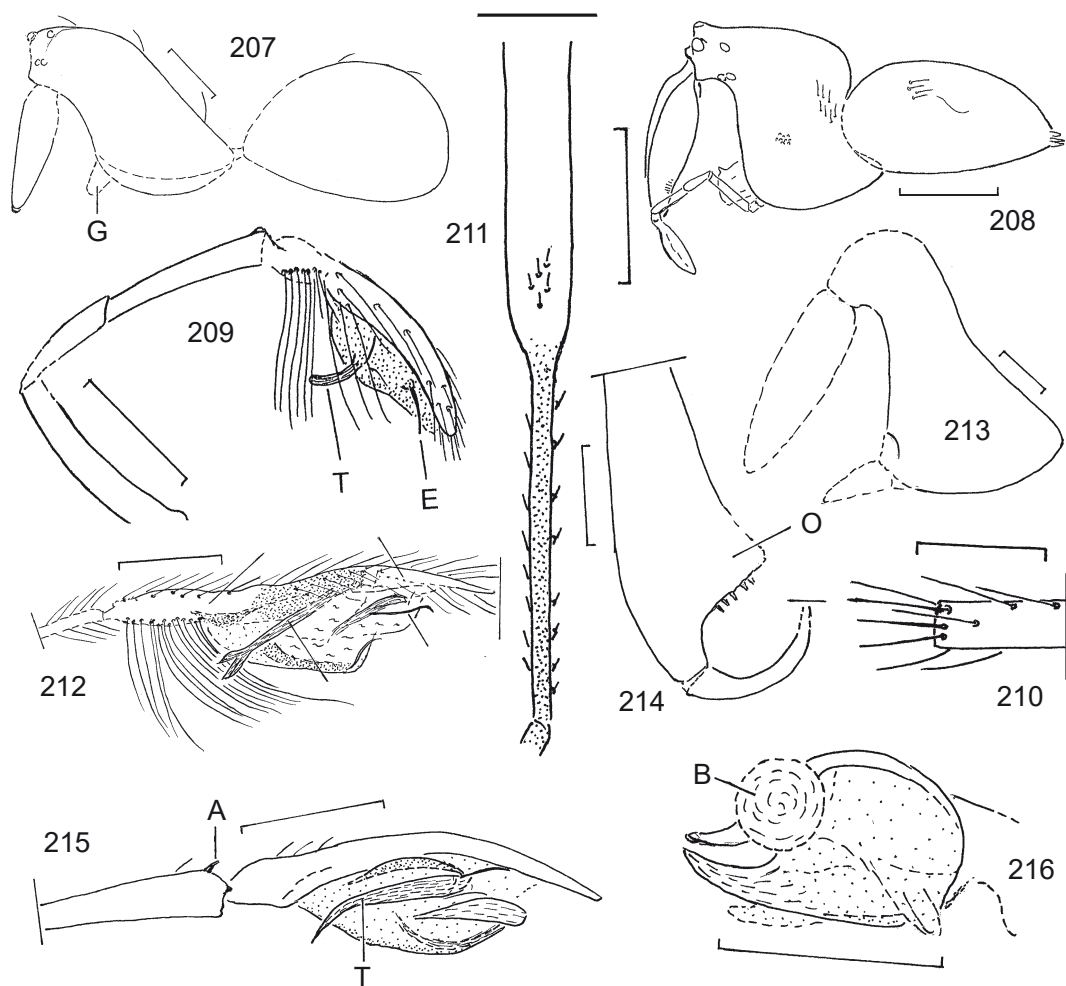


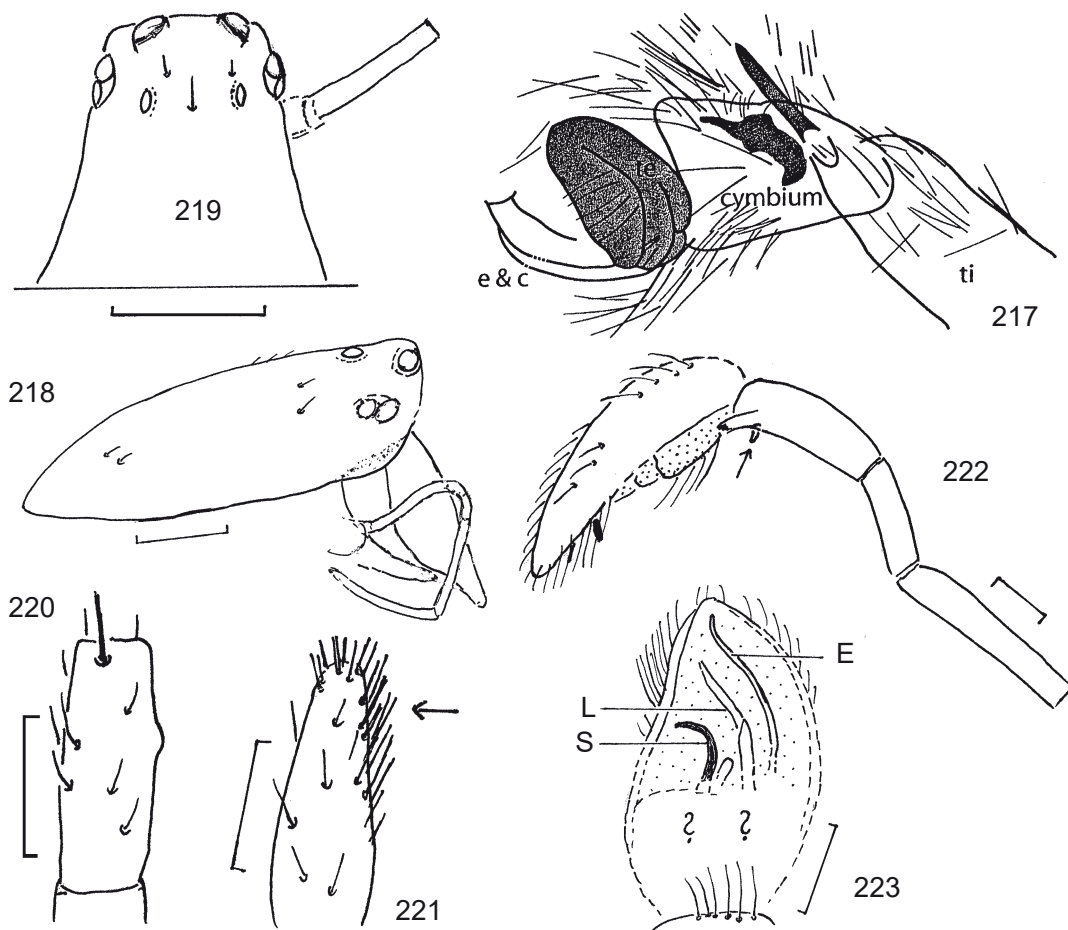
Fig. 207) *Eomysmauchenius septentrionalis* WUNDERLICH 2008 (ARCHAEIDAE), juv. ♀ holotype in Burmite, lateral aspect. – G = gnathocoxa, scale bar 0.2.

Figs. 208-210: *Lacunauchenius speciosus* WUNDERLICH 2008 (ARCHAEIDAE), holotype ♂ in Burmite; 208) lateral aspect of the spider; 209) retroleateral aspect of the right pedipalpus; 210) long ventral-apical hairs on metatarsus IV. Similar hairs exist also on other metatarsi and apparently are not „preening hairs“. – E = embolus, T = tegular apophysis. Scale bars 0.2 in fig. 208 and 0.1.

Figs. 211-212: *Lacunauchenius pilosus* n. sp. (ARCHAEIDAE), ♂ in Burmite; 211) basal part of the right femur which is abruptly shrunk and darkened basally by the natural preservation, retrolateral aspect. Only few of the very short hairs are drawn; 212) retrolateral aspect of the strongly deformed right pedipalpus. Not all hairs are drawn. – C = cymbium, E = questionable embolus, T = retrolateral tegular apophysis. Scale bars 0.5 and 0.2.

Figs. 213-216: *Lacunauchenius longissipes* n. sp. (ARCHAEIDAE), ♂ in Burmite; 213) lateral aspect of the deformed prosoma. The eye region is hidden; 214) anterior aspect of the deformed right chelicera; 215) retrolateral aspect of the strongly deformed right pedipalpus. Only very few of the indistinct hairs are drawn; 216) retrolateral aspect of the strongly deformed left pedipal-





pus. – A = pointed tibial apophysis, B = bubble, O = medial cheliceral outgrowth, T = retrolateral tegular apophysis. Scale bars 0.2.

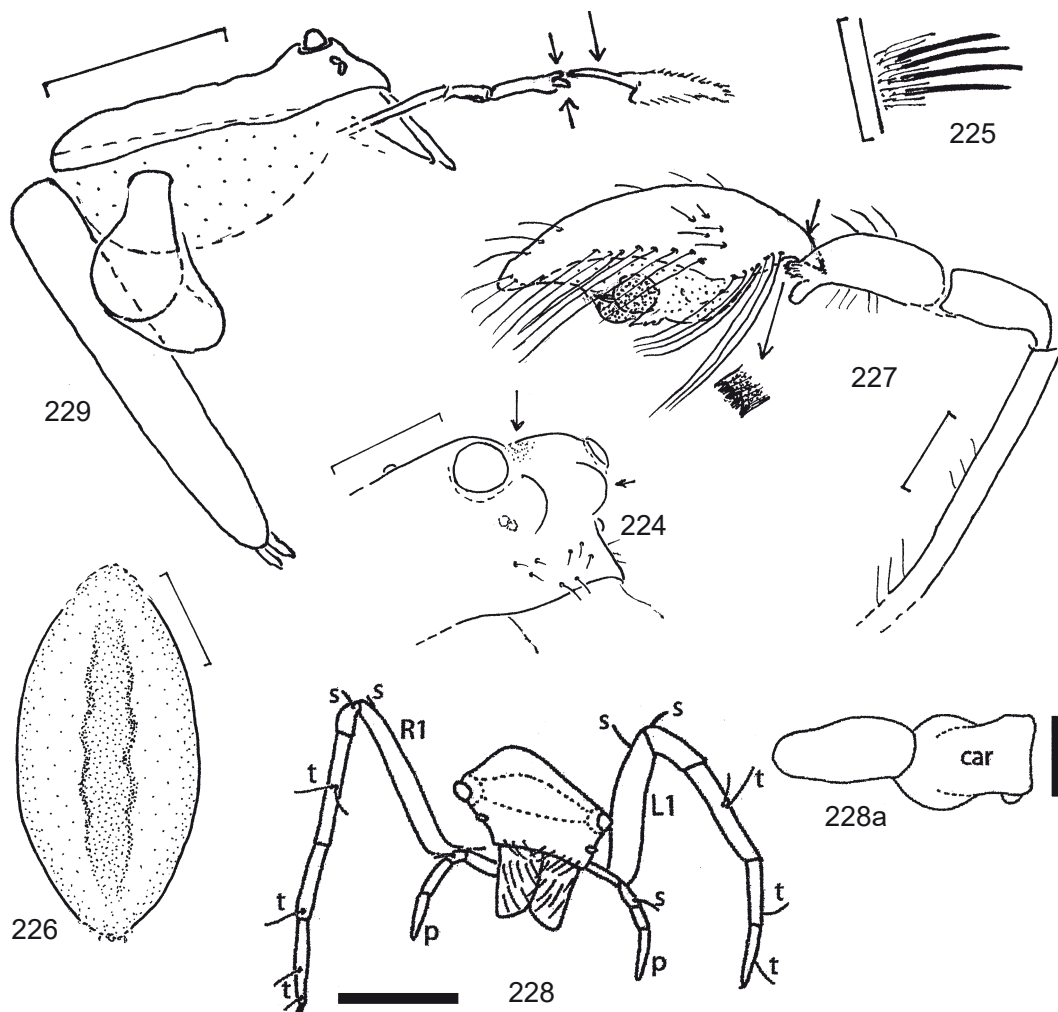
Fig. 217) *Patarchaea muralis* SELDEN et. al. 2008 (ARCHAEIDAE), ♂ „allotype“ in Jurassic stone from China, retroventral aspect of the left pedipalpus. – e & c = embolus and conductor, ti = tibia. Scale bar 1.0. Taken from SELDEN et al. (2008).

Figs. 218-219: *Planarchaea kopp* n. gen. n. sp. (ARCHAEIDAE), ♀ in Burmite; 218) lateral aspect of the prosoma and the right pedipalpus; 219) dorsal aspect of the anterior part of the prosoma and of the right pedipalpal femur. Only few bristles/hairs are drawn. – Scale bar 0.2.

F220-221: ??*Huttoniidae* indet., juv. F2464/NJ/CJW in Cretaceous amber from New Jersey: 220) dorsal aspect of the right patella II which bears an apical bristle; 221) dorsal aspect of the right pedipalpal tarsus. The arrow points to the long hairs. – Scale bars 0.1.

Figs. 222-223: *Archaelagonops scorsum* n. sp. (LAGONOMEGOPIDAE), ♂ in Burmite; 222) retrolateral aspect of the left pedipalpus. The arrow points to the slender ventral tibial apophysis. Only few hairs are drawn; 223) ventral aspect of the right bulbus; basal parts are hidden. – E = questionable embolus, L = long tegular apophysis, S = sickle-shaped tegular apophysis. Scale bars 0.2.

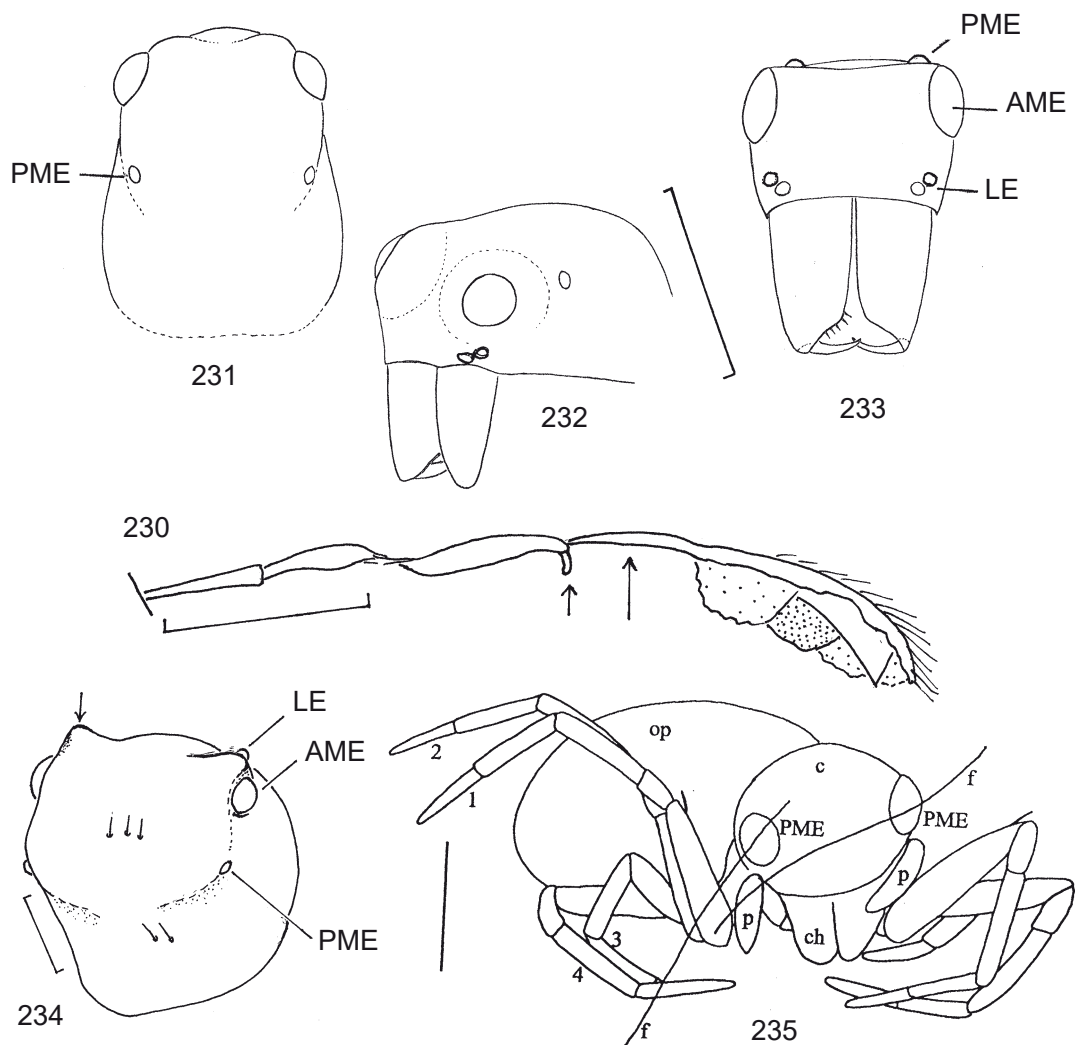




Figs. 224-227: *Archaealagonops propinquus* **n. sp.** (LAGONOMEGOPIDAE), ♂ in Burmite; 224) retrofrontal aspect of the anterior part of the prosoma. The long arrow points to the dorsal depression, the short arrow points to the left hump of the clypeus. Only few hairs are drawn like in the other figs.; 225) retroventral aspect of the preening comb (4 bristles) of the left metatarsus IV; 226) dorsal aspect of the opisthosoma; 227) retrolateral aspect of the left pedipalpus. The short arrow points to the posteriorly elongated cymbium, the long arrow points to the enlarged retroapical tibial apophysis. The femur is artificially depressed by the preservation. – Scale bars 0.1 in fig. 225, 0.2 in fig. 227, 0.5 in figs. 224 and 226.

Fig2. 228-228a: *Burlagonomegops eskovi* PENNEY 2005 (LAGONOMEGOPIDAE), juv. holotype in Burmite, anterior and dorsal aspects. – Scale bars 0.5. Taken from PENNEY (2005b).

Figs. 229-230: *Cymbiolagonops cymbiocalcar* **n. gen. n. sp.** (LAGONOMEGOPIDAE), ♂ in Burmite; 229) lateral aspect of the strongly deformed body and the right pedipalpus. The prosoma is empty ventrally and bears a larger bubble caused by decomposition. I did not recognize the posterior lateral eyes. The short arrows point to the divided retroapical tibial apophysis, the long arrow points to the long basal cymbial apophysis which tip is hidden; 230) prolateral aspect of

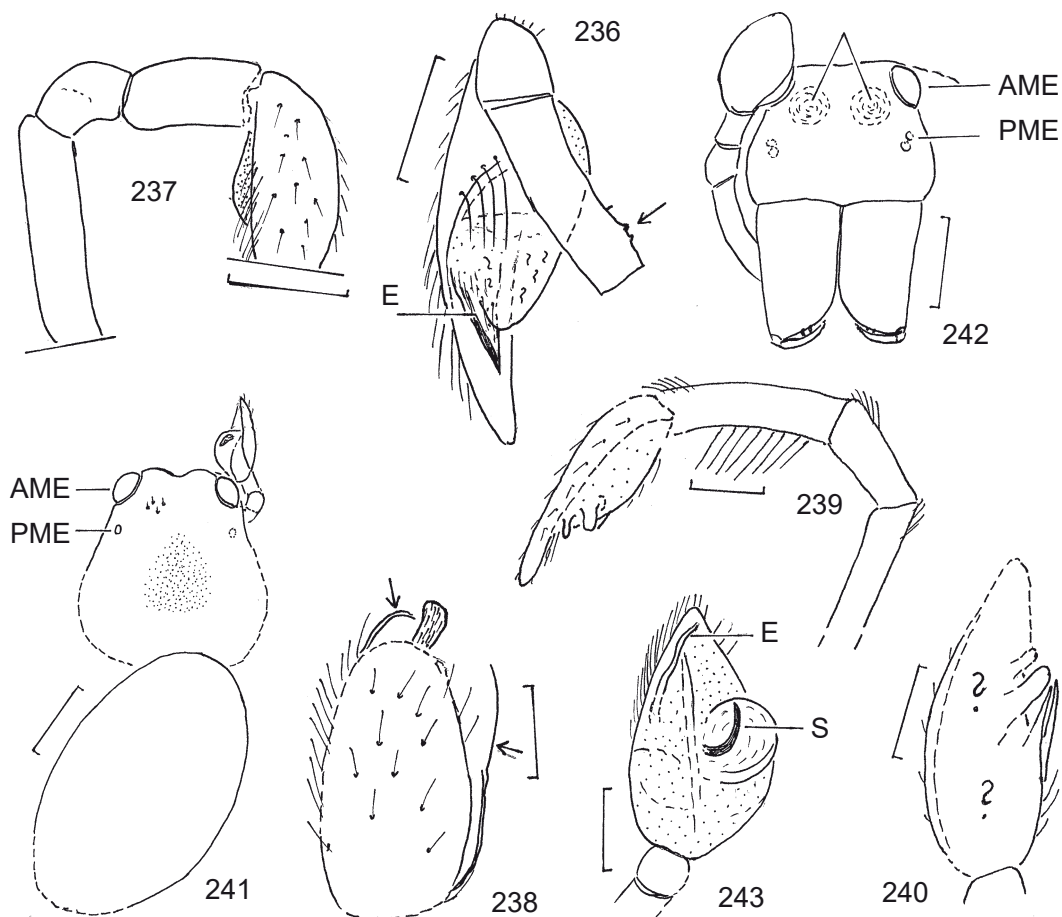


the left pedipalpus which is strongly deformed, the cymbium is loose. The short arrow points to the retroapical tibial apophysis which is undivided, the long arrow points to the long basal cymbial outgrowth. – Scale bars 1.0 and 0.5.

Figs. 231-233: *Lagonomegops sukatchevae* ESKOV & WUNDERLICH 1995 (LAGONOMEGOPIDAE), juv. in Siberian Taimyr amber, dorsal, anterior-lateral and anterior aspects. – AME = anterior median eye, LE = anterior and posterior lateral eyes, PME = posterior median eye. Scale bars 0.5.

Fig. 234) ?*Lagonomegops tuber* n. sp. (LAGONOMEGOPIDAE), juv. holotype, dorsal and slightly right aspect of the prosoma. The arrow points to the left hump. Only few hairs are drawn. – Scale bar 0.2.

Fig. 235) „*Lagonomegops*“ *americanus* PENNEY 2005 (LAGONOMEGOPIDAE), juv. in Upper Cretaceous amber from New Jersey. – Note: The PME are actually the anterior median eyes. Scale bar 0.5. Taken from PENNEY (2005b).

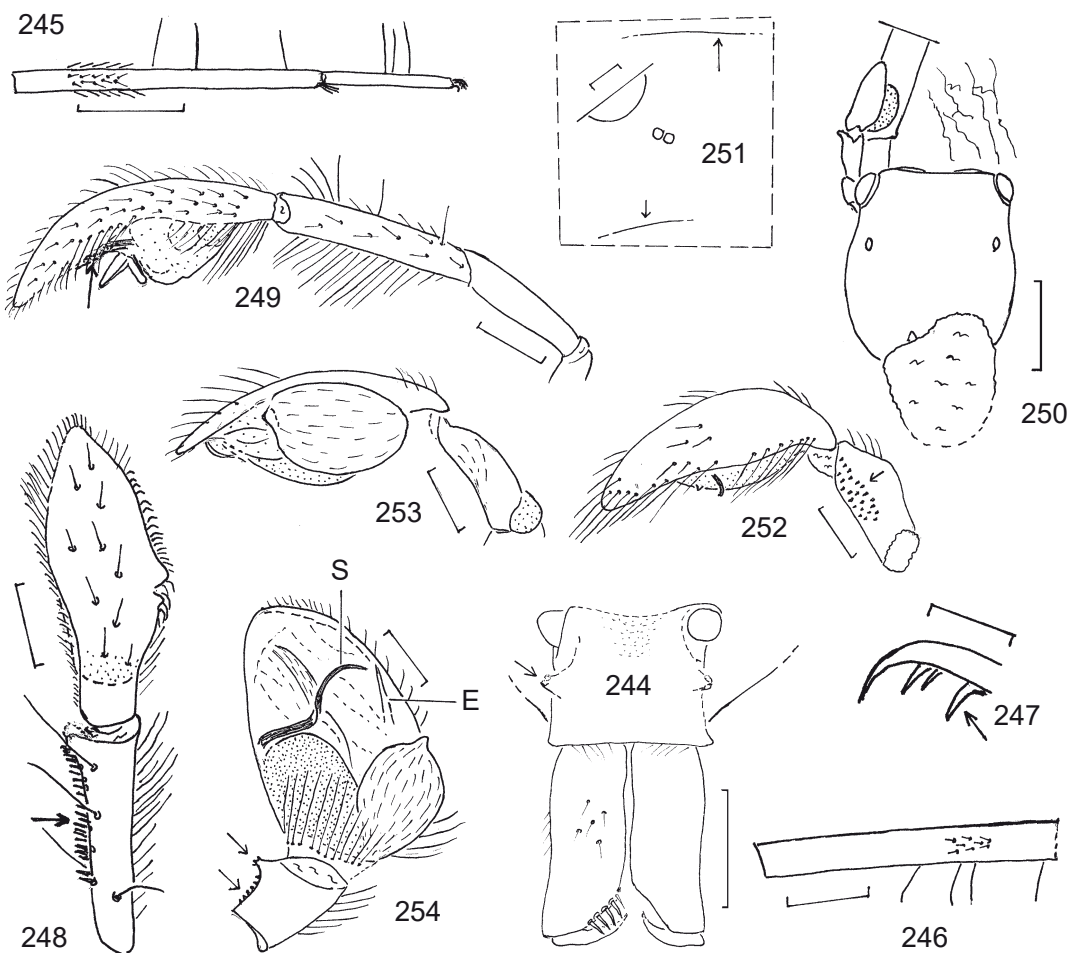


Figs. 236-237: *Lineaburmops beigeli* n. gen. n. sp. (LAGONOMEGOPIDAE), ♂ in Burmite; 236) left pedipalpus: Dorsal aspect of the femur and ventral aspect of the bulbus. Note the prolateral stridulatory teeth of the femur (arrow); 237) retrolateral aspect of the right pedipalpus which cymbium is hidden distally. Only few hairs are drawn. – E = questionable embolus. Scale bars 0.2.

Fig. 238) *Lineaburmops hirsutipes* n. gen. n. sp. (LAGONOMEGOPIDAE), ♂ in Burmite, dorsal aspect of the deformed right cymbium and structures of the bulbus. The arrows point to some long hairs. – Scale bar 0.2.

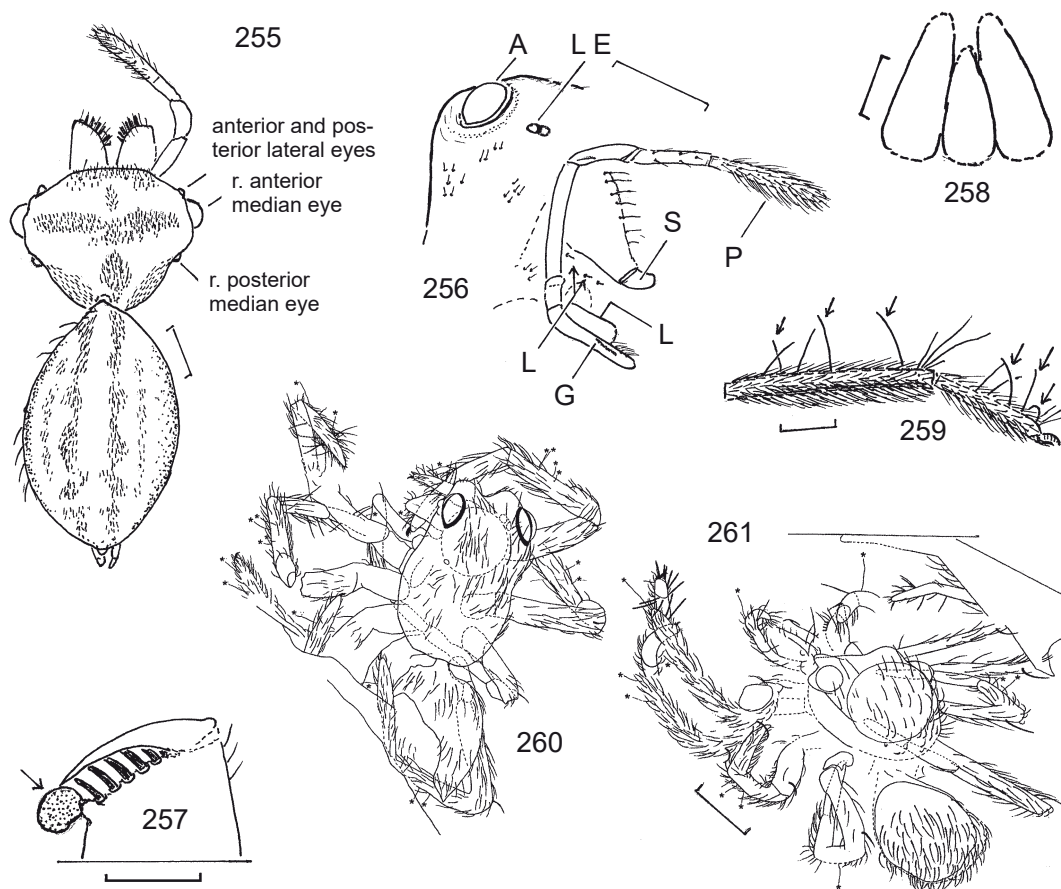
Figs. 239-240: *Myanlagonops gracilipes* WUNDERLICH 2012 (LAGONOMEGOPIDAE), ♂ holotype in Burmite; 239) retrolateral and slightly apical aspect of the left pedipalpus; 240) proventral aspect of the left pedipalpus. The structures of the bulbus are only insufficiently observable, artefacts may exist. – Scale bar 0.2.

Figs. 241-243: *Parviburmops brevipalpus* n. gen. n. sp. (LAGONOMEGOPIDAE), ♂ in Burmite; 241) dorsal aspect of the body and prolateral aspect of the right pedipalpus; 242) anterior aspect of the prosoma and the right pedipalpus. The distal parts of the chelicerae are not well observable, the structures of the bulbus are not drawn; 243) retroventral aspect of the right pedipalpus. – E = questionable embolus, H = humps of the clypeus, S = sickle-shaped tegular apophysis, AME = anterior median eye, LE = anterior and posterior lateral eyes, PME = posterior median eye. Scale bars 0.5 in figs. 241-242, 0.2 in fig. 243.



Figs. 244-249: *Paxillomegops longipes* n. gen. n. sp. (LAGONOMEGOPIDAE), ♂ in Burmite; 244) anterior aspect of the prosoma (slightly from the left side). Note the long and slender „peg teeth“ which are only drawn on the right chelicera, and the deformed „elevated“ right lateral eyes (arrow); 245) prolateral aspect of the left metatarsus and tarsus III. Note the long trichobothria and their position in almost a single row. Only few hairs are drawn; 246) proventral aspect of the right femur III. Note the four long ventral sensory hairs which are similar to trichobothria; 247) prolateral aspect of the unpaired (arrow) and the paired proclaw of the right tarsus III; 248) dorsal aspect of the left pedipalpus. Note the irregular row of short retrolateral bristles on the tibia (arrow) and the four long sensory tibial hairs. Only some hairs are drawn; 249) prolateral aspect of the right pedipalpus. The arrow points to the questionable embolus. – Scale bars 0.5 in figs. 244-246, 0.05 in fig. 247, 0.2 in figs. 248-249.

Figs. 250-254: *?Paxillomegops brevipes* n. gen. n. sp. (LAGONOMEGOPIDAE), ♂ in Burmite; 250) dorsal aspect of the body, the left pedipalpus and the basal part of the left leg I. Note the crumbled and shrunk opisthosoma which probably has been sucked out. Probably the spiders has been a prey of a beetle or a diplurid spider. Few threads are preserved in front of the spider; 251) retrofrontal and slightly ventral aspect of the anterior part of the prosoma. Note the part of the large right anterior median eye and the tiny lateral eyes. The long arrow points to the dorsal prosomal margin, the short arrow points to the clypeal margin; 252) retrolateral aspect of the left pedipalpus. Note the field of peg teeth-like bristles (arrow); 253) Prolateral aspect of the



right pedipalpus. The tibia is injured and deformed. Only few hairs are drawn; 254) ventral and slightly basal aspect of the right pedipalpus. The arrows point to the tibial „peg teeth“. The distal structures are partly hidden by an emulsion, the tibia is shortened perspective. Only few hairs are drawn. – E = questionable embolus, S = sickle-shaped tegular apophysis. Scale bars 1.0 in fig. 250, 0.2 in the remaining figs.

Figs. 255-259: *Picturmegops signatus* n. gen. n. sp. (LAGONOMEGOPIDAE), ♀ in Burmite; 255) dorsal aspect of the body and the right pedipalpus. Drawn are the white hairs of the prosoma and the black hairs between white hairs of the opisthosoma; 256) oblique retroventral-anterior aspect of the anterior part of the prosoma. The arrows point to the area of the foramen. Note the large gap between the labium and the fang. Only few hairs are drawn: 257) posterior aspect of the left chelicera. Not all peg teeth are drawn. The arrow points to a secretion of the large gland mound; 258) labium and gnathocoxae; 259) prolateral aspect of the left metatarsus and tarsus I. The arrows point to the sensory hairs which apparently are trichobothria. – A = anterior median eye, F = right fang, G = right gnathocoxa, L = labium, LE = lateral eyes, P = pedipalpal tarsus. Scale bars 0.5 in fig. 256, 0.2 in the figs. 257-258.

Fig. 260) *Spinomegops aragonensis* FUENTE et al. 2013 (LAGONOMEGOPIDAE), juv. in Cretaceous amber from Spain, dorsal aspect. – Taken from FUENTE et al. (2013).

Fig. 261) *Spinomegops arcanus* FUENTE et al. 2013 (LAGONOMEGOPIDAE), juv. in Cretaceous amber from Spain, dorsal aspect. – Taken from FUENTE et al. (2013).

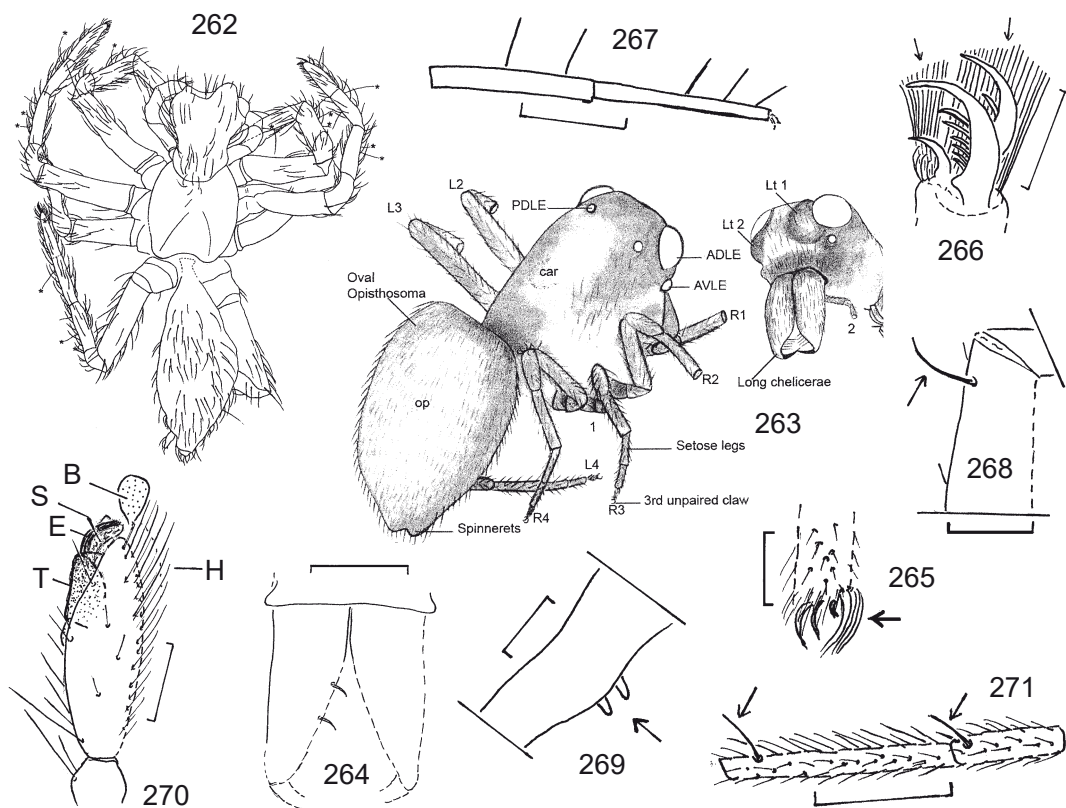


Fig. 262) *Saplaogonomegops unzuei* FUENTE et al. 2013 (LAGONOMEGOPIDAE), juv. in Cretaceous amber from Spain, dorsal aspect. – Taken from FUENTE et al. (2013).

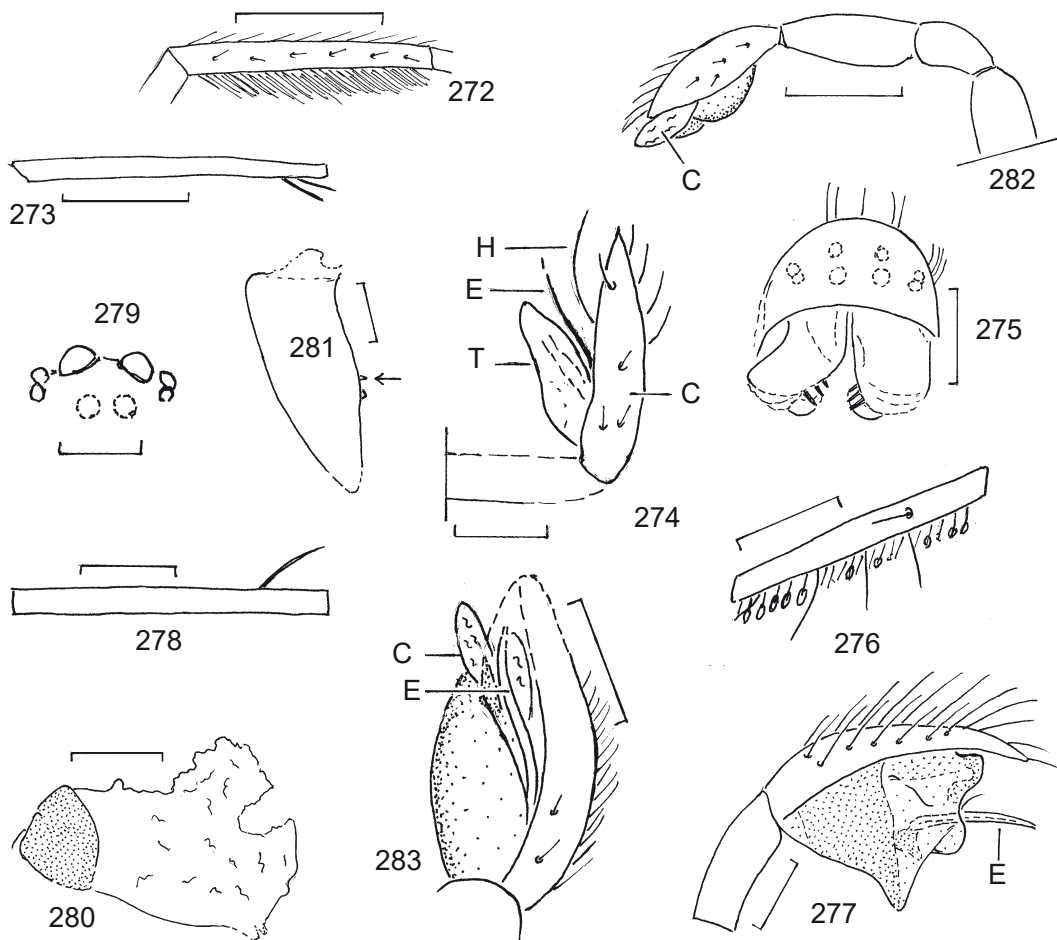
Fig. 263) *Zargagonomegops wunderlich* KADDUMI 2007 (LAGONOMEGOPIDAE), juv. in Cretaceous Jordanian amber; 1) dorsal-lateral aspect of the spider, 2) anterior-lateral aspect of the prosoma. Note: The eyes are not correctly drawn and named. – Taken from KADDUMI (2007).

Fig. 264-266: *Lagonomegopidae* indet. (LAGONOMEGOPIDAE), ♀ F2628/BU/CJW in Burmite; 264) anterior aspect of the chelicerae. „Peg teeth“ and most parts of the fangs are hidden; 265) prolateral aspect of the tip of the right tarsus I. The arrow points to the claw tuft. The teeth of the paired claws are hidden; 266) proapical aspect of the claws of the right tarsus II. Note the divided retrolateral claw tuft hairs (arrows). – Scale bars 0.5 in fig. 264, 0.1 in the figs. 265-266.

Figs. 267-270: *Micropalpimanus ?poinari* WUNDERLICH 2008 (MICROPALPIMANIDAE), ♂ F2511/BU/CJW in Burmite; 267) prolateral aspect of the left tarsus and metatarsus I. Note the long trichobothria. Hairs are not drawn; 268) prodorsal aspect of the distal part of the left femur III. Note the long distal bristle-shaped and bent hair (arrow) which exists on all femora in the same position; 269) dorsal-apical aspect of the right pedipalpal femur which bears two blunt ?stridulatory teeth (arrow) in the basal half; 270) dorsal aspect of the right pedipalpus. Nor all hairs are drawn. – B = bubble, E = embolus, H = dense long retrolateral hairs of the cymbium, S = skinny apophysis, T = tegulum. Scale bars 0.05 in fig. 269, 0.2 in fig. 267, 0.1 in figs. 268 and 270.

Fig. 271) *Micropalpimanus ?poinari* WUNDERLICH 2008 (LAGONOMEGOPIDAE), ♂ F2512 / BU/CJW in Burmite, dorsal aspect of the left patella and tibia III. Note the bristle-shaped hairs (arrows). – Scale bar 0.2.



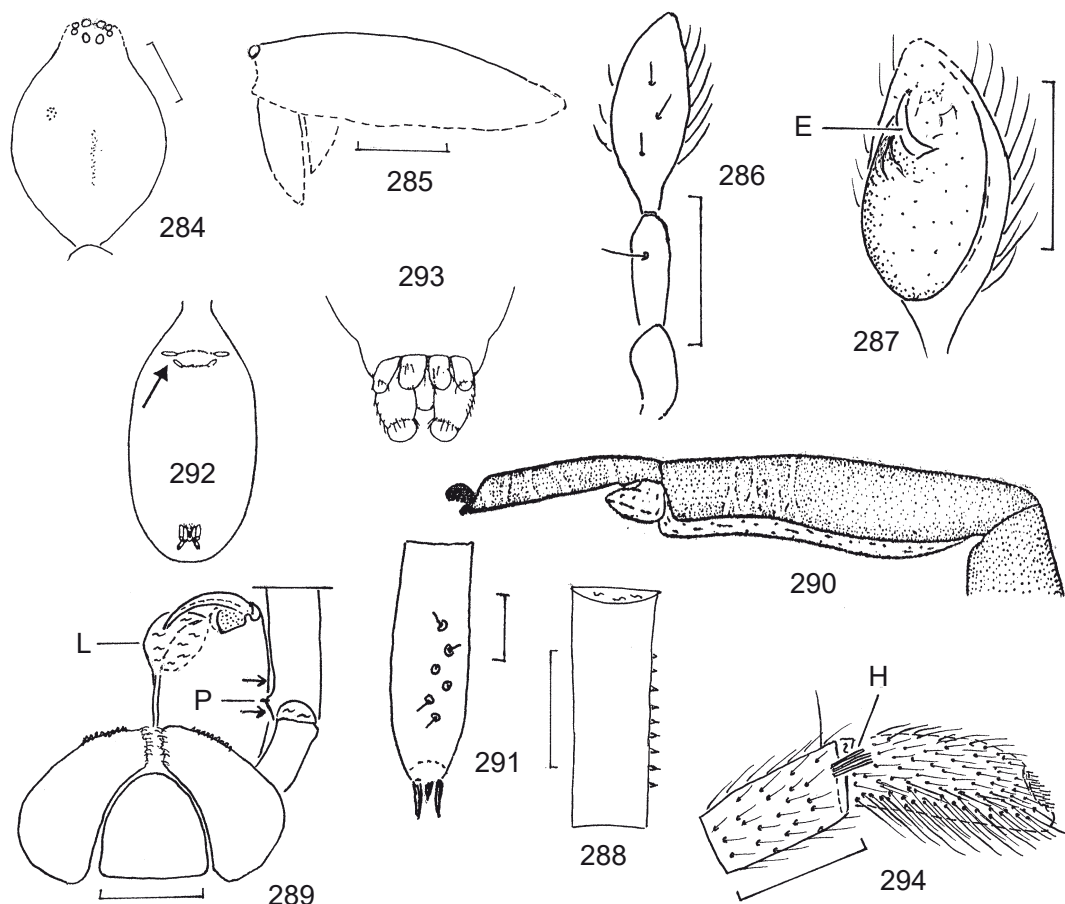


Figs. 272-274: *Micropalpimanus* sp. indet. a (LAGONOMEGOPIDAE), ♂ in Burmite; 272) dorsal aspect of the left metatarsus II. Note the long and dense proventral hairs; 273) prolateral aspect of the left metatarsus IV. Hairs and trichobothria are not drawn; 274) retrolateral aspect of the left pedipalpus. The bulbus may be expanded. Only few hairs are drawn. – C = cymbium, E = questionable embolus, H = hair, T = tegulum. Scale bars 0.1 (fig. 274) and 0.2.

Figs. 275-278: *Micropalpimanus* sp. indet. b (LAGONOMEGOPIDAE), ♂ in Burmite; 275) anterior aspect of the prosoma. The eyes are covered with emulsions, the right chelicera is strongly deformed. Such natural deformation are not rare in Burmite; 276) prodorsal aspect of the right metatarsus I. Several hairs bear apical droplets (artefacts!) which are absent on the left metatarsus I. Hairs – besides three long sensory hairs – are not drawn; 277) Retrolateral aspect of the deformed right pedipalpus; 278) dorsal aspect of the right tibia III. Note the thin prodistal bristle. – E = embolus. Scale bars 0.2 in fig. 275, 0.1 in the figs. 277-278.

Figs. 279-283: *Spatiator putescens* n. sp. (SPATIATORIDAE: SPATIATORINAE), ♂ in Burmite; 279) dorsal aspect of the eyes, reconstruction; 280) left aspect of the injured/decomposed opisthosoma. The anterior-dorsal scutum is dotted; 281) ventral aspect of the right pedipalpal femur. The arrow points to a pointed prolateral stridulatory tooth; 282) prolateral aspect of the right pedipalpus; 283) retroventral aspect of the left pedipalpus which is hidden distally. – C = cymbium, E = questionable embolus. Scale bars 0.5 in fig. 280, 0.1 in fig. 281, 0.2 in the remaining figs.

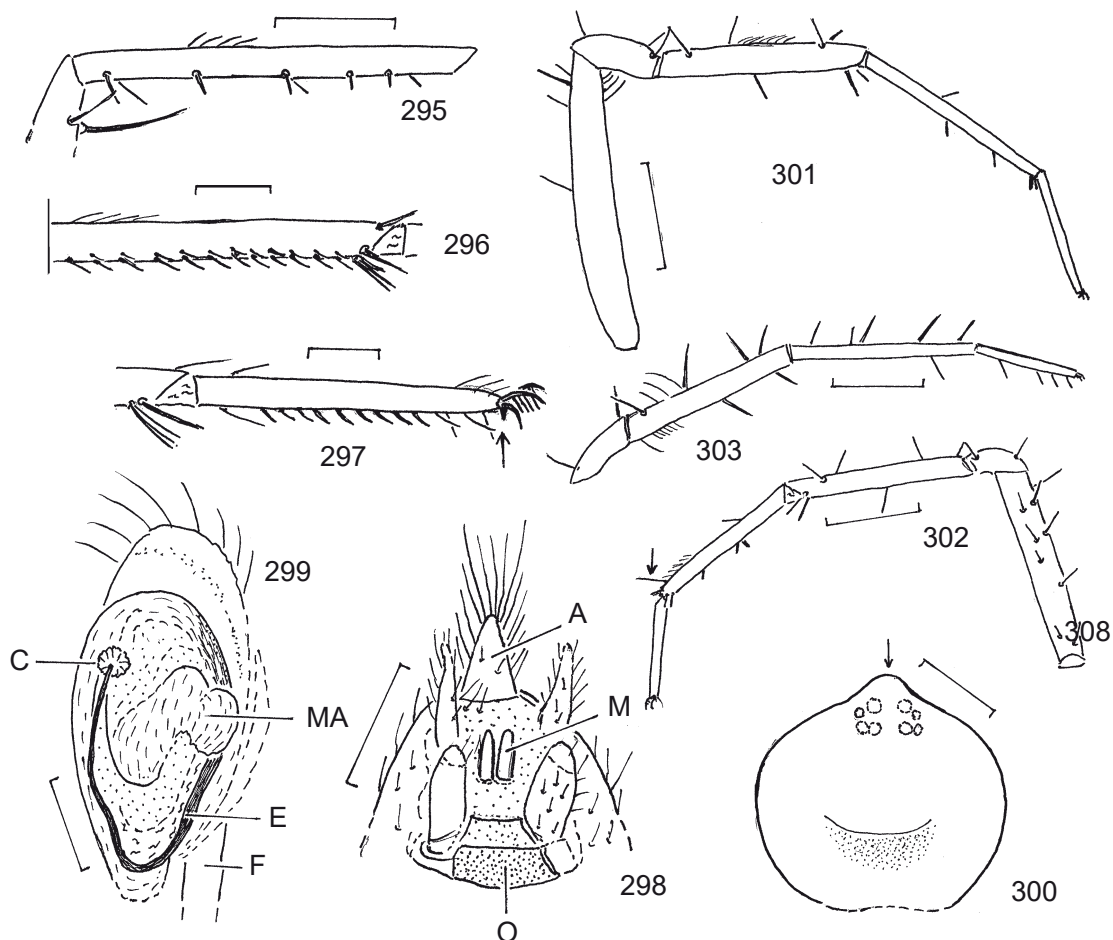




Figs. 284-287: *Vetiator gracilipes* n. gen. n. sp. (SPATIATORIDAE: VETIATORINAE), ♂ in Burmite; 284) dorsal aspect of the prosoma. The fovea is quite indistinct; 285) lateral aspect of the prosoma, outline, parts like most eyes are hidden. The existence of cheliceral stridulatory files is unsure; 286) dorsal aspect of the right pedipalpus; 287) ventral aspect of the left pedipalpus. – E = questionable embolus. Scale bars 0.2.

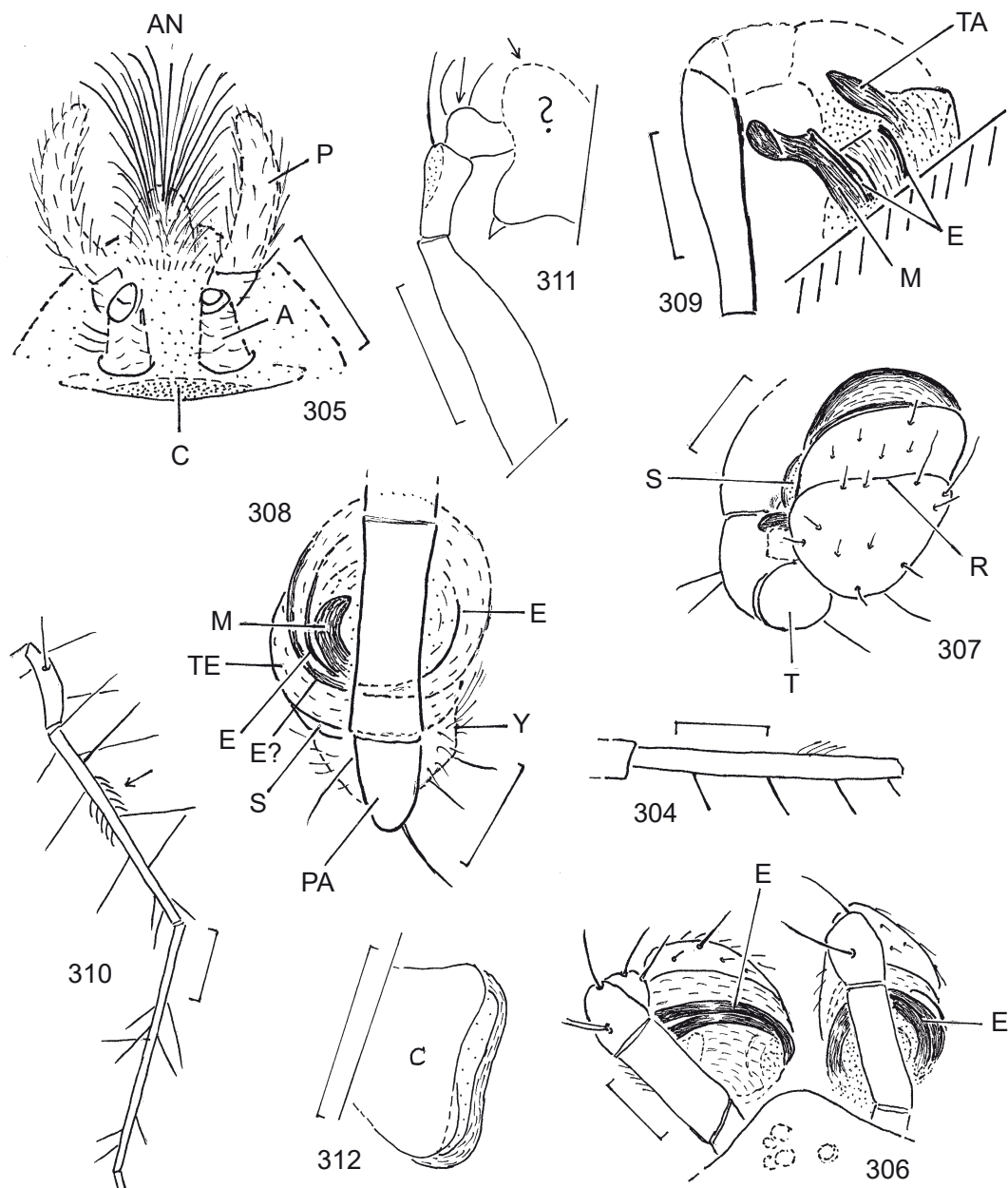
Fig. 288) *Diguetia mojavea* GERTSCH 1958 (PLECTREURIDAE: DIGUETINAE) (extant, USA), ♂, ventral aspect of the right pedipalpal femur. Note the prolateral stridulatory picks. Hairs are not drawn. – Scale bar 0.5.

Figs. 289-294: *Caponiidae indet.* (different extant taxa from the Americas), ♀; 289) ventral aspect of labium, gnathocoxae, left chelicera with its lamella (L), and basal part of the left pedipalpus with its stridulatory pick (P). The arrows point to the area of retrolateral stridulatory files which are not observable in this position; 290) lateral aspect of tarsus and metatarsus I. Taken from CHAMBERLIN (1924). Note the translucent ventral metatarsal keel and the basal tarsal lobe. Hairs and trichobothria are not drawn; 291) dorsal aspect of the left tarsus I. Note the trichobothria in an irregular position. Hairs are not drawn; 292) ventral aspect of the opistosoma showing two pairs of thracheal openings. Taken from JOCQUE & DIPPENAAR-SCHOEMAN (2007); 293) ventral aspect of the spinnerets. Note the transverse anterior row. Taken from JOCQUE & DIPPENAAR-SCHOEMAN (2007); 294) prolateral aspect of the left pedipalpus. Note the apical tibial comb of hairs (H) and the dense long prolateral and proventral tarsal hairs. – Scale bars 0.2 in fig. 291, 0.5 in fig. 289 and 295 or absent.



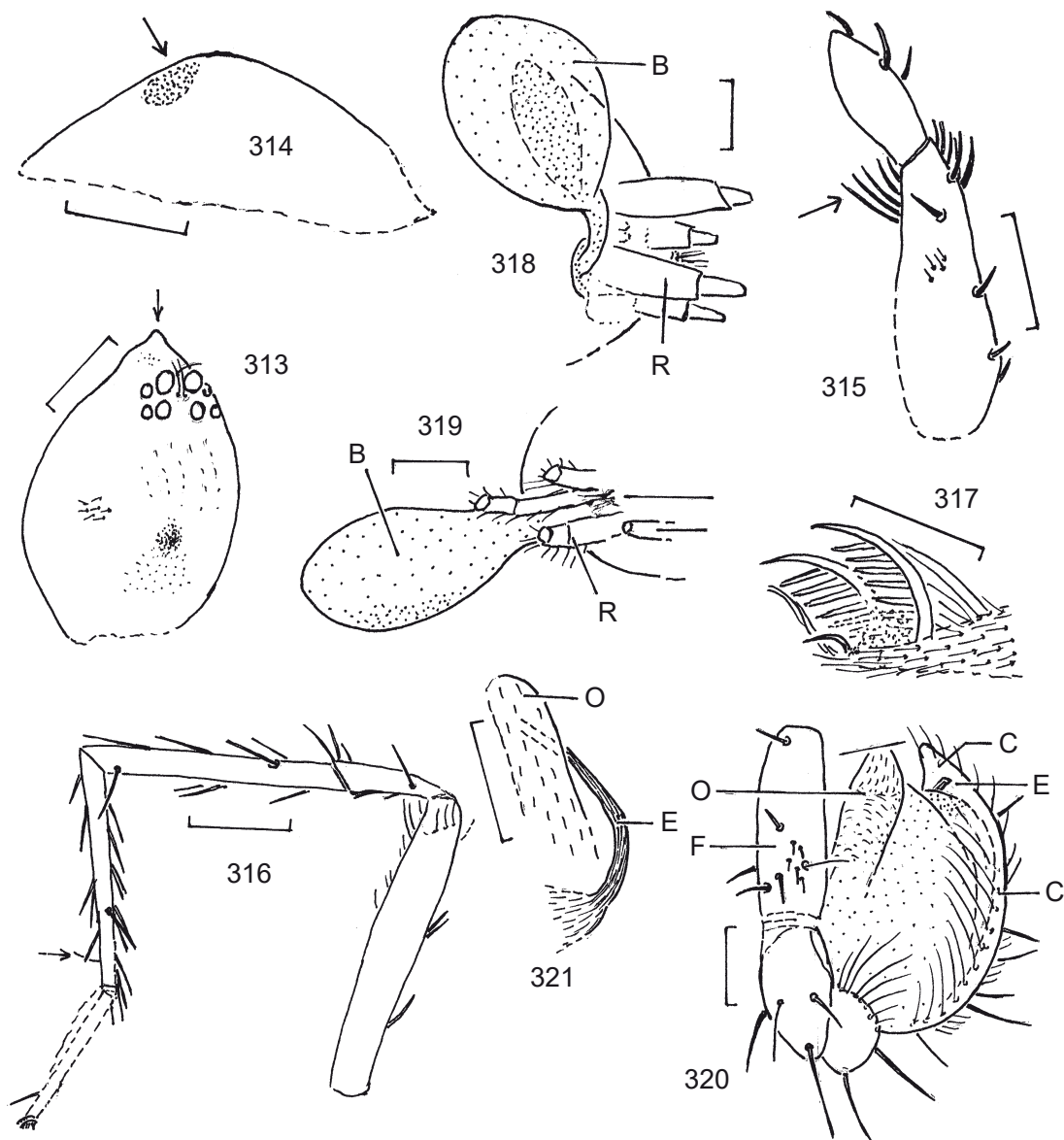
Figs. 295-299: *Zamilia aculeopectens* n. sp. (OECOBIIIDAE), ♂ in Burmite; 295) prolateral and slightly apical aspect of the left metatarsus and apical part of tibia I; 296) prolateral aspect of the distal part of the left metatarsus IV; 297) prolateral aspect of the left tarsus IV and the end of the metatarsus IV. The arrow points to the basal tooth-shaped structure of the long unpaired tarsal claw (onychium); 298) ventral aspect of the deformed left pedipalpus. – A = anal tubercle, C = conductor, E = embolus, F = pedipalpal femur, M = right median spinneret, MA = median apophysis (strongly deformed), O = colulus. Scale bars 0.1 in figs. 296-297, 299, 0.2 in the remaining figs.

Figs. 300-309: ? *Zamilia quattuormammillae* n. sp. (OECOBIIIDAE), ♂ in Burmite; 300) dorsal aspect of the prosoma. The posterior depression may be artificial. Note the nose-shaped ventral margin of the clypeus (arrow). The eye lenses are partly covered with emulsions; 301) retrolateral aspect of the right leg I. Only few hairs are drawn; 302) prolateral aspect of the right leg I, tibia and metatarsus proventral. The arrow points to the metatarsal trichobothrium; 303) retrolateral (slightly dorsal) aspect of the right leg IV beyond the femur. Only few hairs are drawn; 304) retrolateral aspect of the right tarsus IV. The claws and most hairs are not drawn; 305) ventral aspect of the spinnerets, the „pseudocribellum“ and the large and hairy anal tubercle; 306) dorsal aspect of the pedipalpi in front of the clypeus and the eyes which are partly hidden or covered with an emulsion; 307) left pedipalpus, dorsal aspect of the cymbium and retroventral aspect of femur and patella; 308) right pedipalpus, dorsal aspect of patella and femur, ventral aspect of the bulb; 309) retrolateral aspect of the right pedipalpus. The distal parts are hidden by the right

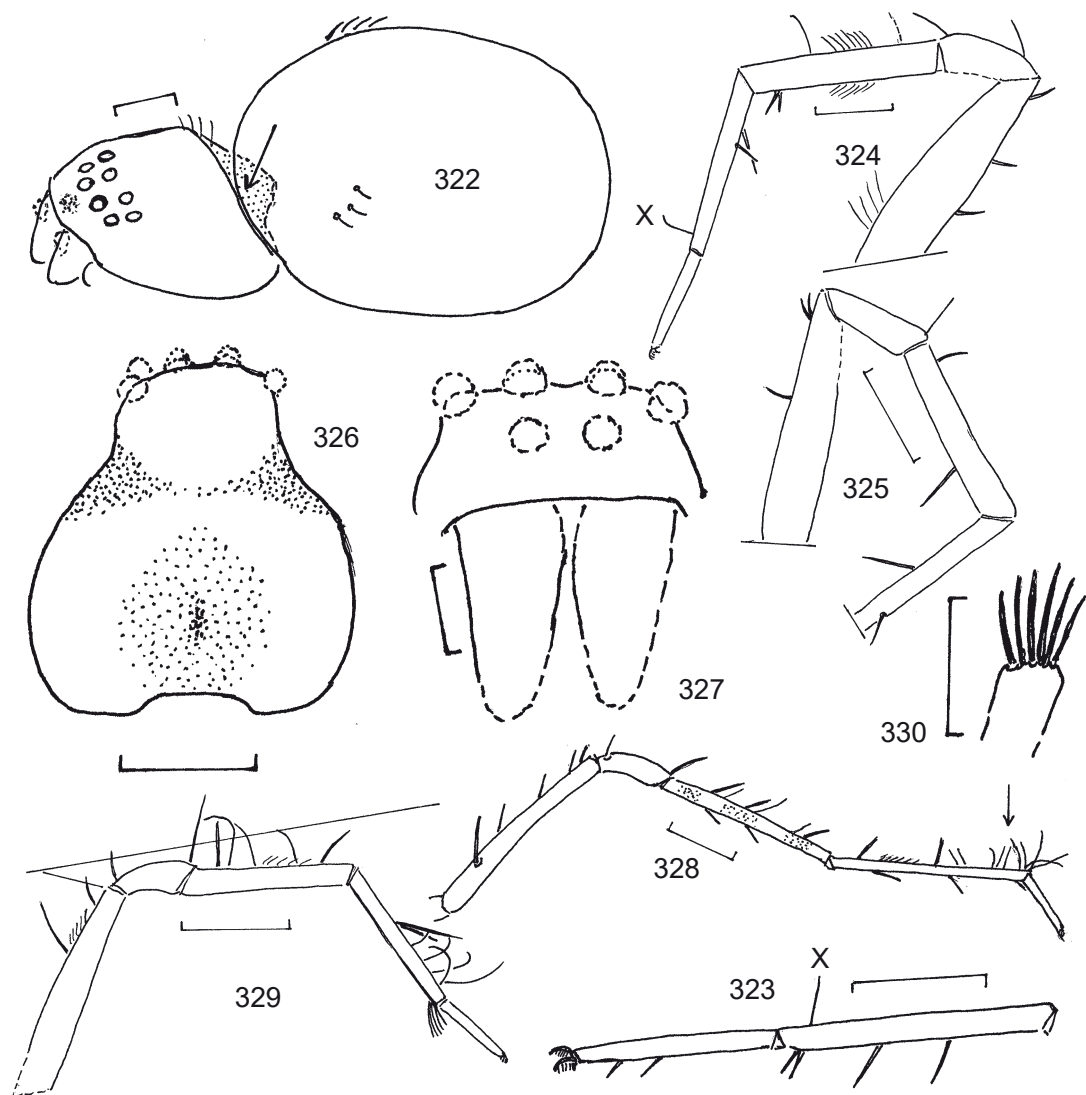


femur I. – A = anterior spinneret, AN = anal tubercle, C = colulus („pseudocribellum“), E = embolus, M = median apophysis, P = posterior spinneret, PA = patella, R = rim, S = subtegulum, T = tibia, TA = tegular apophysis, TE = tegulum, Y = cymbium. Scale bars 0.5 in figs. 301-302, 0.2 in the remaining figs.

Fig. 310-312: ?Oecobiidae indet., ♂ F2737/BU/CJW in Burmite; 310) oblique prodorsal aspect of the left patella, tibia and metatarsus III. Only few hairs (arrow) are drawn; 311) prolateral and slightly dorsal aspect of the left pedipalpus. The long arrow points to the dorsal tibial outgrowth, the short arrow points to the dorsal questionable hump or artefact of the cymbium; 312) dorsal aspect of the left cymbium (C) and part of the deformed bulbus. – Scale bars 0.5.

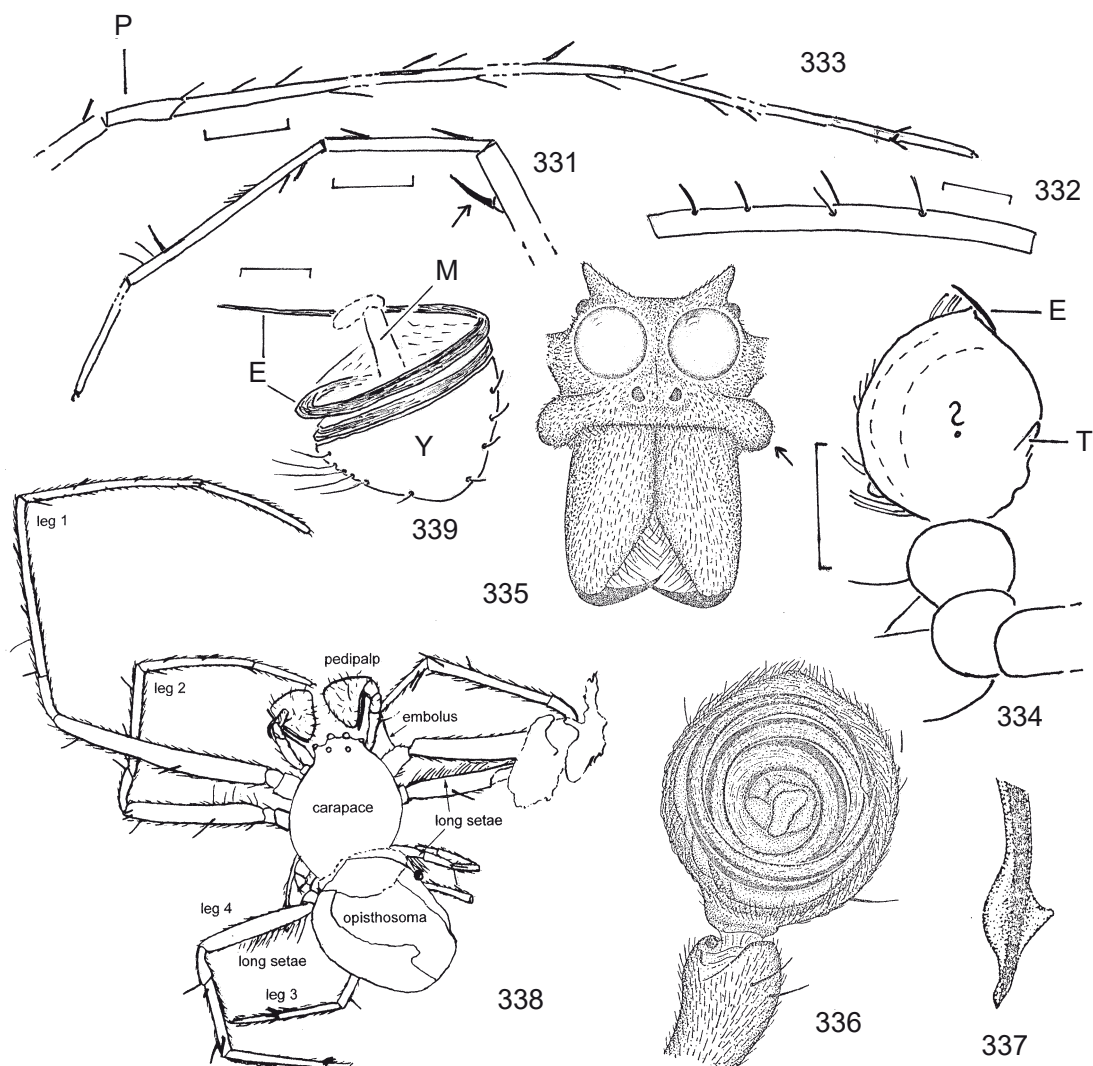


Figs. 313-321: *Retrooecobius chomskyi* n. gen. n. sp. (OECOBIIDAE), ♂ in Burmite; 313) dorsal (slightly left) aspect of the prosoma. Note the clypeal „nose“ (arrow). Mainly the anterior median eyes are covered with an emulsion; 314) right aspect of the prosoma. Note the large fovea (arrow). The eyes are hidden; 315) retrodorsal-apical aspect of the left patella and femur I. The arrow points to the „comb“ of bristle-shaped hairs; 316) retrolateral aspect of the left leg IV. Some bristles may be hidden. The arrow points to the metatarsal trichobothrium; 317) retrolateral aspect of the right tarsal IV claws; 318) ventral aspect of the spinnerets. Only few hairs of the anal tubercle are observable; 319) posterior-dorsal and slightly right aspect of the spinnerets. Only few hairs are drawn. The left anterior spinneret is slightly deformed (depressed); 320) deformed right pedipalpus, ventral aspect of the bulbus and dorsal aspect of femur and patella; 321) ventral aspect of the questionable embolus and conductor. – A = anal tubercle, B = bubble of fluid, C = cymbium, E = questionable embolus, F = femur, P = right posterior spinneret, R = right anterior spinneret. Scale bars 0.5 in figs. 313-316, 0.1 in fig. 317, 0.2 in the remaining figs.



Figs. 322-325: *Retrooecobius convexus* n. gen. n. sp. (OECOBIIDAE), ♂ in Burmite; 322) lateral aspect of the body. The arrow points to the strong artificial posterior depression of the prosoma in which the anterior part of the opisthosoma fits. Clypeus and chelicerae are deformed. Only few hairs are drawn; 323) prodorsal aspect of the right tarsus and metatarsus I; 324) prolateral aspect of the right leg II. The femur is deformed and some bristles may be hidden. Only few hairs are drawn; 325) prolateral aspect of the right leg IV. Some bristles may be hidden or broken off. – X = metatarsal trichobothrium. Scale bars 0.5.

Figs. 326-330: *Burmesiola daviesi* n. sp. (HERSILIIDAE), juv. ♀ in Burmite; 326) dorsal aspect of the prosoma. The eye lenses are covered with emulsions; 327) anterior aspect of the prosoma. The chelicerae are partly hidden; 328) retrolateral aspect of the right leg I. The tibial annulations are relatively distinct. Only few hairs are drawn. Note the numerous distal trichobothria of the metatarsus (arrow); 329) retrolateral aspect of the right leg III. The median part of the metatarsus is hidden by a leg. Note the 5 long trichobothria in the distal half of the metatarsus and the spider's thread above the leg; 330) basal-ventral aspect of the preening comb of the right metatarsus III. – Scale bars 0.2 in figs. 327 and 330, 0.5 in figs. 326 and 329, 1.0 in fig. 327.

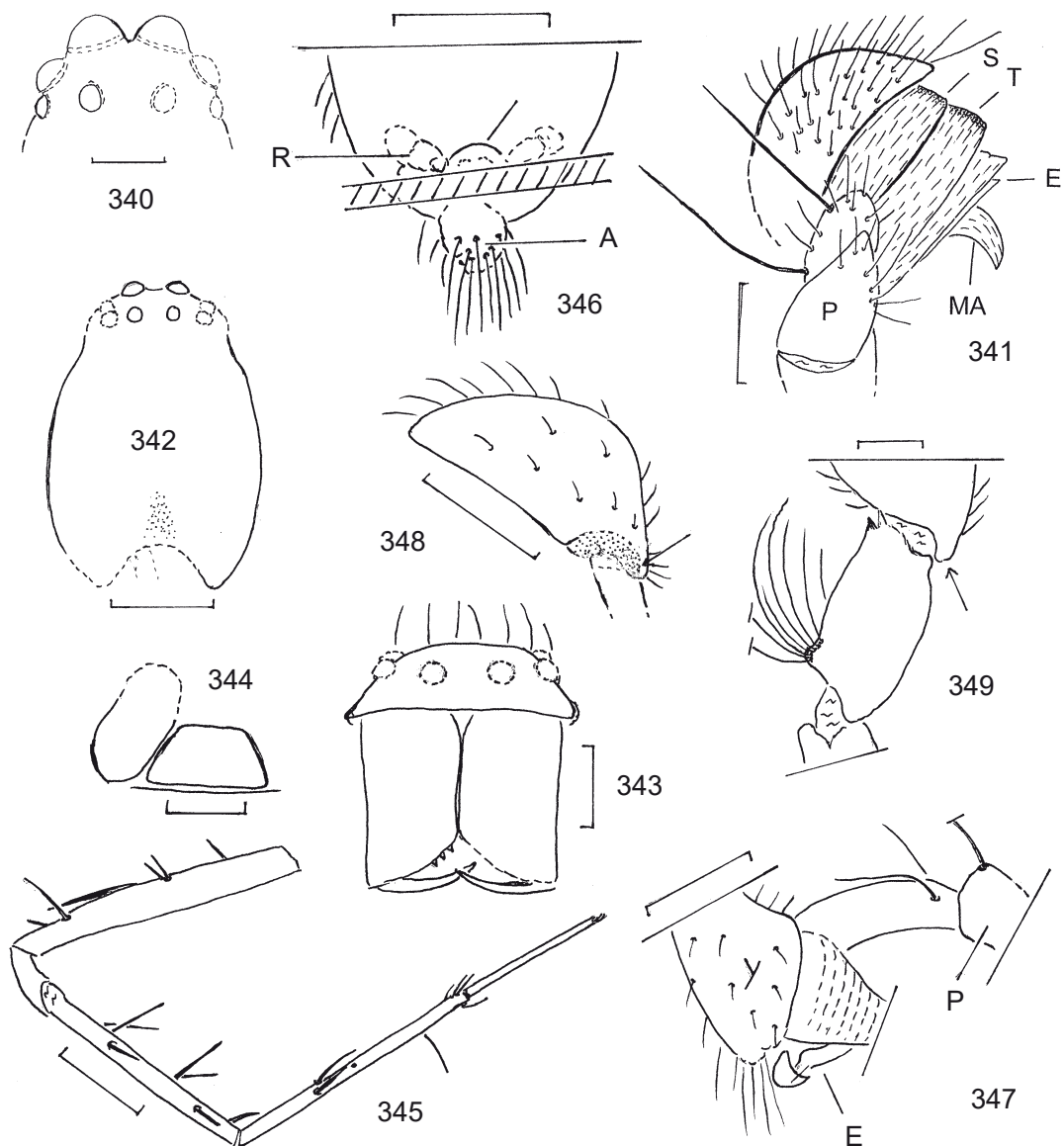


Figs. 331-334: *Spinasilia dissoluta* n. gen. n. sp. (HERSILIIDAE), ♂ in Burmite; 331) prolateral aspect of the right leg I with the tibial „clasping spine“ (arrow). Only two metatarsal trichobothria, few hairs and few bristles are drawn (some bristles are hidden); 332) prolateral aspect of the right femur I. Hairs are not drawn; 333) retrodorsal aspect of the right leg IV. Trichobothria and normal hairs are not drawn; 334) ventral aspect of the right pedipalpus. Central parts of the bulbus are strongly darkened and not well observable. – E = embolus, P = patella, T = tegular apophysis. Scale bars 0.5 in fig. 334, 1.0 in the remaining figs.

Figs. 335-337: *Deinopis diabolica* KRAUS 1956 (DEINOPIDAE), ♂, extant (Central America); 335) anterior aspect of the prosoma. The arrow points to the left anterior lateral eye; 336) ventral aspect of the right pedipalpus. Note the long and coiled embolus; 337) tip of the modified right embolus, the „mating plug“, ventral aspect. – Taken from KRAUS (1956).

Figs. 338-339: *Palaeomicromenneus lebanensis* PENNEY 2003 (SALTICOIDIDAE), ♂ holotype in Cretaceous Lebanese amber; 338) dorsal aspect of the spider (carapace = prosoma); 339) lateral aspect of the left pedipalpus. Note the coiled embolus. – Taken from PENNEY (2003), modified. E = embolus, M = median apophysis, Y = cymbium. Scale bars 1.0 and 0.5.

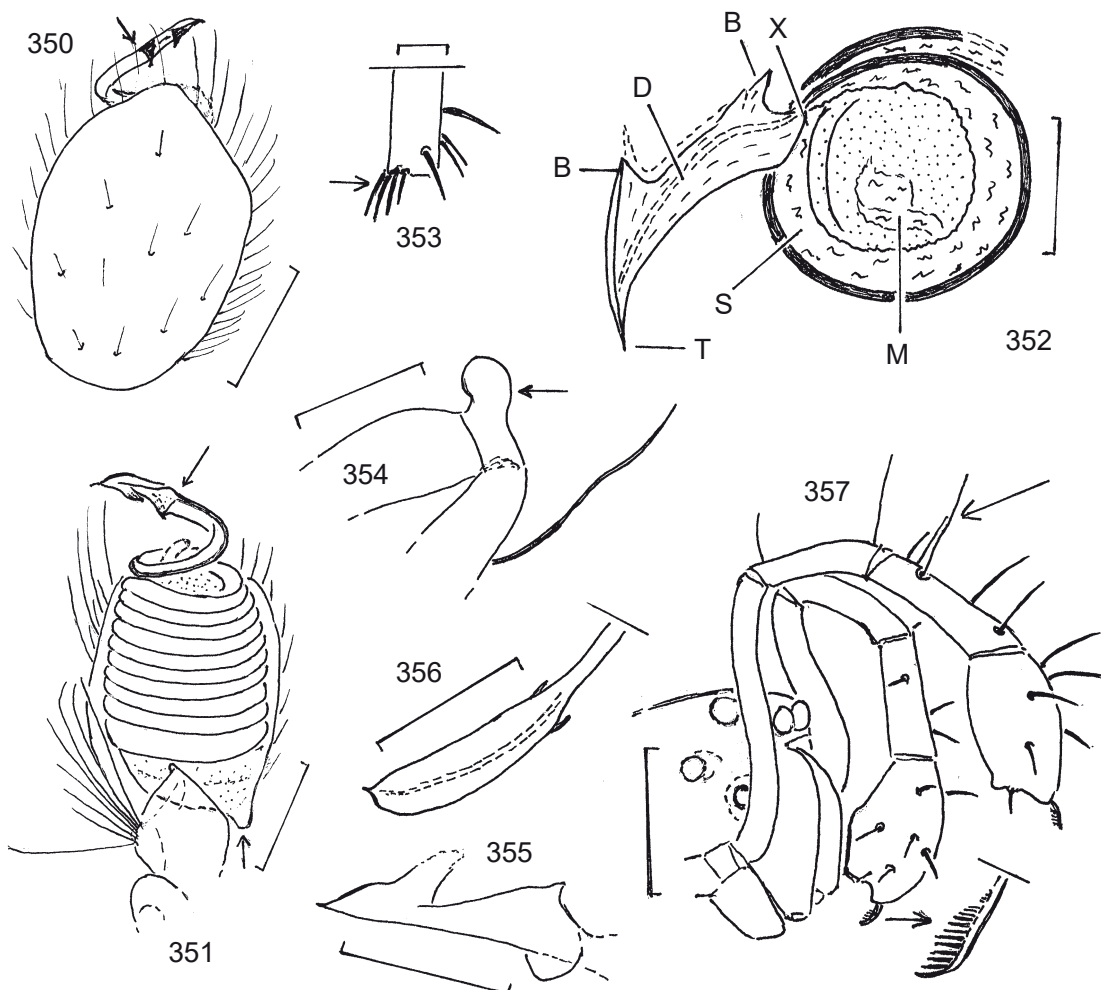




Figs. 340-341: *Salticoididus kaddumiorum* WUNDERLICH 2008 (SALTICOIDIDAE), ♂ holotype in Cretaceous Jordanian amber; 340) dorsal aspect of the eye region; 341) retrodorsal aspect of the right pedipalpus. – E = embolus, MA = median apophysis, P = patella, S = subtegulum, T = tegulum. Scale bars 0.2.

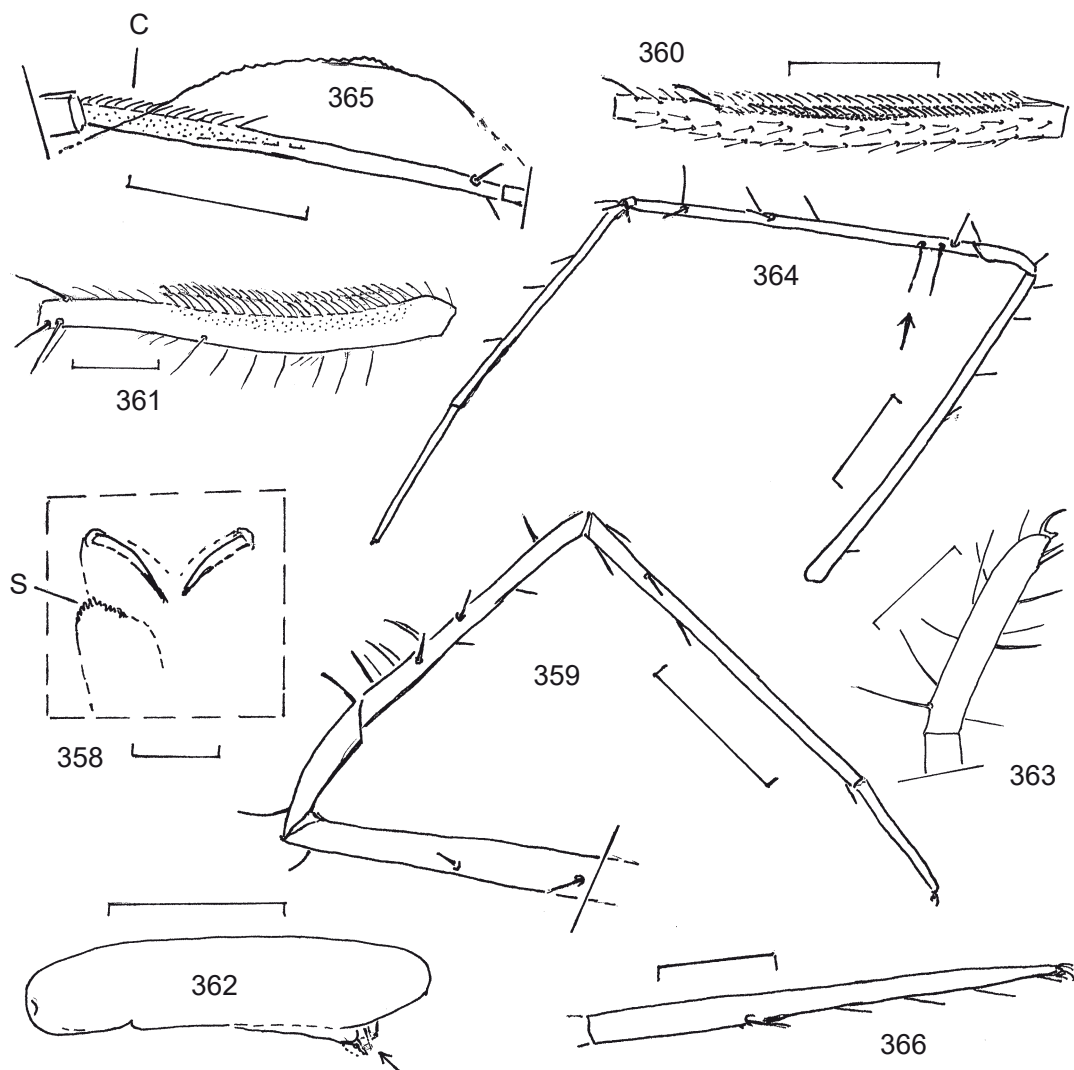
Figs. 342-352: *Burmadiictyna excavata* n. sp. (SALTICOIDIDAE), holotype ♂ (but fig. 346: probably conspecific ♂) in Burmite; 342) dorsal aspect of the prosoma. The posterior incision is most probably caused by the preservation or an injury; 343) anterior aspect of the prosoma. The eyes are partly hidden by bubbles; 344) labium and right gnathocoxa; 345) ca. prolateral aspect of the left leg I; 346) ventral aspect of the distal part of the opisthosoma. Parts are hidden by the left tarsus and metatarsus IV; 347) retrolateral aspect of the left pedipalpus. Parts are hidden, only few hairs are drawn; 348) retrobasal aspect of the left cymbium. Note the retrobasal inclination and outgrowth (arrow); 349) ventral aspect of the tibia and the basal part of the cymbium





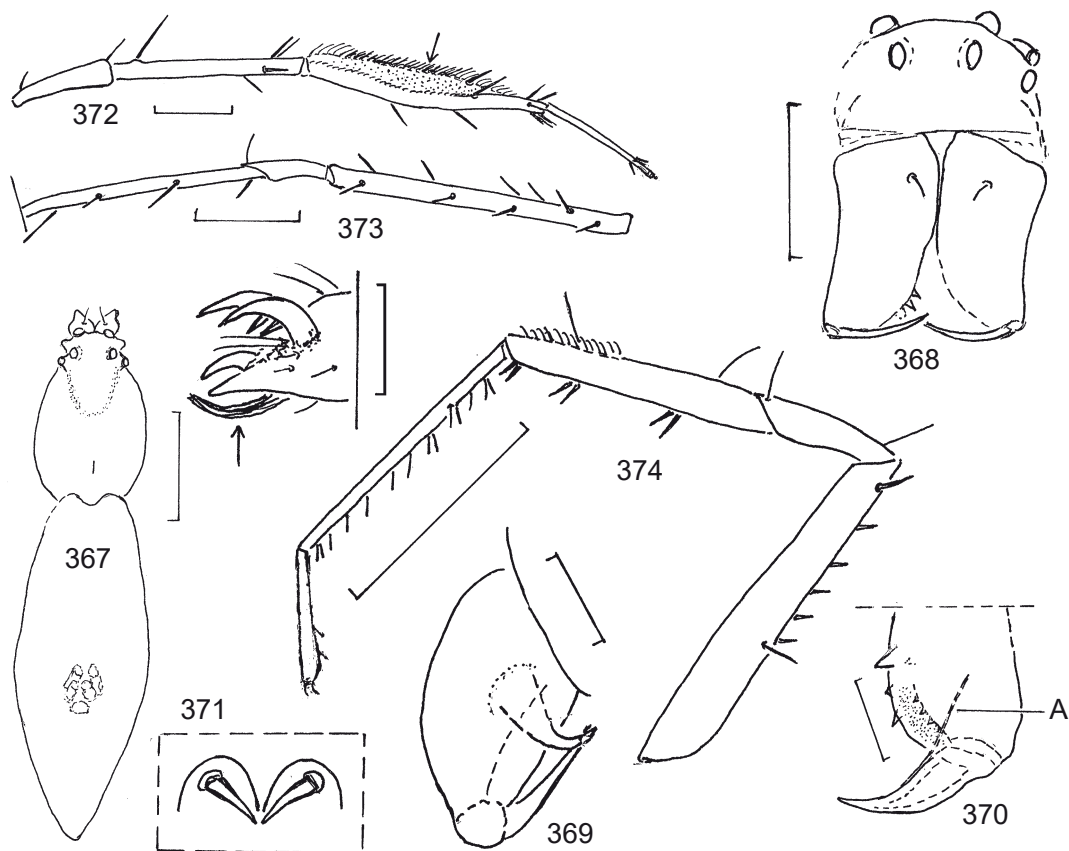
of the right pedipalpus. The arrow points to the probasal outgrowth of the cymbium. Only few hairs are drawn; 350) dorsal aspect of the cymbium and embolus of the right pedipalpus. Note the two barbs of the distal part of the embolus (one is arrowed); 351) ventral aspect of the right pedipalpus. Note the coiled embolus which has apically a complicated structure. The short arrow points to the probasal outgrowth of the cymbium, the long arrow points to the supposed predetermined breaking point of the distal part of the stuck of the embolus which may act as a „mating plug“; 352) apical aspect of the distal part of the right embolus. – A = anal tubercle (deformed), B = barbs, C = edge of the inclination of the questionable cribellum, D = sperm duct, E = embolus, M = artefact on the questionable median apophysis, P = patella with its dorsal elevation, R = deformed right anterior spinneret, S = seam of the embolus, T = tib of the embolus, X = questionable breaking line, Y = cymbium. Scale bars 0.5 in figs. 342 and 345, 0.1 in figs. 349 and 352, 0.2 in the remaining figs.

Figs. 353-356: *Burmadictyna clava* n. sp. (SALTICOIDIDAE), ♂ in Burmite; 353) prolateral aspect of the tip of the left metatarsus III. The arrow points to the comb-like apical bristles; 354) prolateral aspect of parts of the left pedipalpus. Note the large club-shaped dorsal outgrowth of the patella; 355) prolateral aspect of the „mating plug“ of the right embolus; 356) retrolateral aspect of the distal part of the left embolus. Note the two deformed barbs at the basal part. – Scale bars 0.2 in fig. 354, 0.1 in the remaining figs.



Figs. 357-361: *Bicalamistrum mixtum* n. gen. n. sp. (ULOBORIDAE), subad. ♂ in Burmite; 357 and 359 holotype, 358, 360-361 paratype; 357) anterior part of the prosoma and both pedipalpi, lateral aspect. Enlarged (short arrow): Tarsal claw of the right pedipalpus. The long arrow points to the two pedipalpal tibial trichobothria. Hairs are not drawn; 358) ventral aspect of the mouth parts, parts are hidden; 359) prolateral aspect of the left leg I; 360) retrodorsal aspect of the left metatarsus IV. Note the two rows of the calamistrum. Only some hairs are drawn; 361) retrolateral aspect of the left metatarsus IV. Only few hairs are drawn. – S = serrula. Scale bars 1.0 in fig. 359, 0.5 in fig. 357, 0.25 in fig. 360, 0.2 in 358 and 361.

Figs. 362-366: *Burmuloborus antefixus* n. sp. (ULOBORIDAE), ♀ in Burmite; 362) lateral aspect of the opisthosoma. The arrow points to the anterior position of the deformed spinnerets and the anal tubercle; 363) retrolateral aspect of the right pedipalpus. Only bristles and long hairs are drawn; 364) retrolateral aspect of the left leg I. The arrow points to two questionable trichobothria. Probably some bristles are hidden or broken off; 365) retrolateral aspect of the deformed left metatarsus IV with the calamistrum (C). Remains of a probably cribellate thread are preserved above the calamistrum; 366) retroventral aspect of the right tarus IV. Note the thin ventral bristles. – Scale bars 1.0 in figs. 362 and 364, 0.5 in figs. 365, 0.2 in figs. 363 and 366.

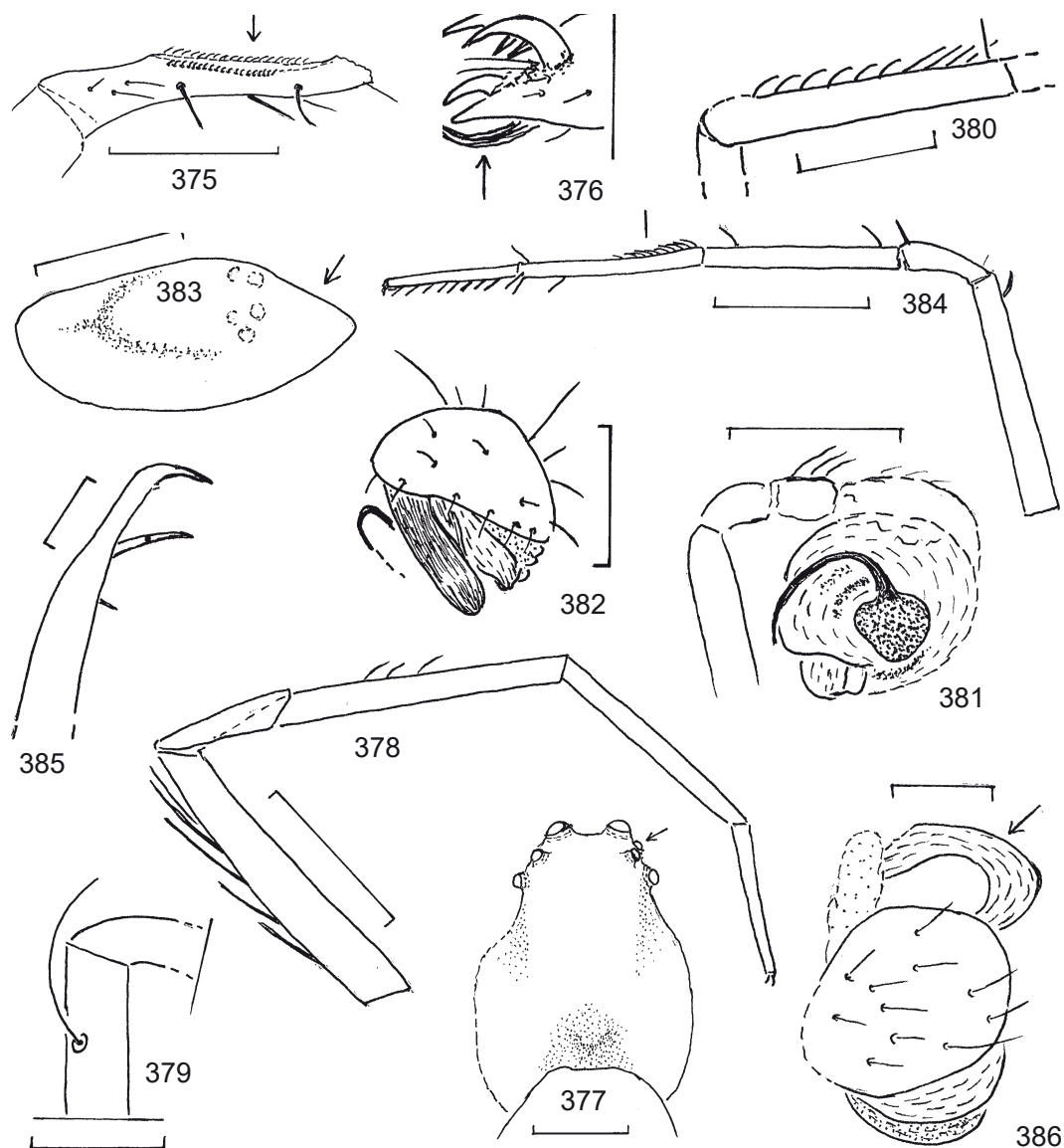


Figs. 367-368: *?Burmuloborus prolongatus* n. sp. (ULOBORIDAE), juv. ♀ in Burmite; 367) dorsal aspect of the body. The VENTRAL and more anterior position of the spinnerets is outlined; 368) anterior aspect of the prosoma. Most right parts of the peltidium are hidden, the chelicerae are slightly deformed. – Scale bars 0.5 and 0.2.

Figs. 369-373: *?Burmuloborus* sp. indet. (ULOBORIDAE), ♀-exuvia F2448/BU/CJW in Burmite; 369) lateral aspect of the fangs and a basal cheliceral article; 370) distal part of the left chelicera. Note the 3 larger teeth of the promargin of the fang furrow and the 4 tiny retromarginal teeth; 371) reconstruction of the fangs, ventral aspect; 372) retrolateral aspect of the left leg IV. Note the tarsal bristles and the long calamistrum on the strongly bent and „furrowed“ metatarsus (arrow); 373) femur, patella and most parts of the tibia of the left leg I, retrolateral aspect. Hairs are not drawn. – A = artefact. Scale bars 1.0 in fig. 373, 0.5 in fig. 372, 0.2 in figs. 369-370; no scale bar in fig. 371.

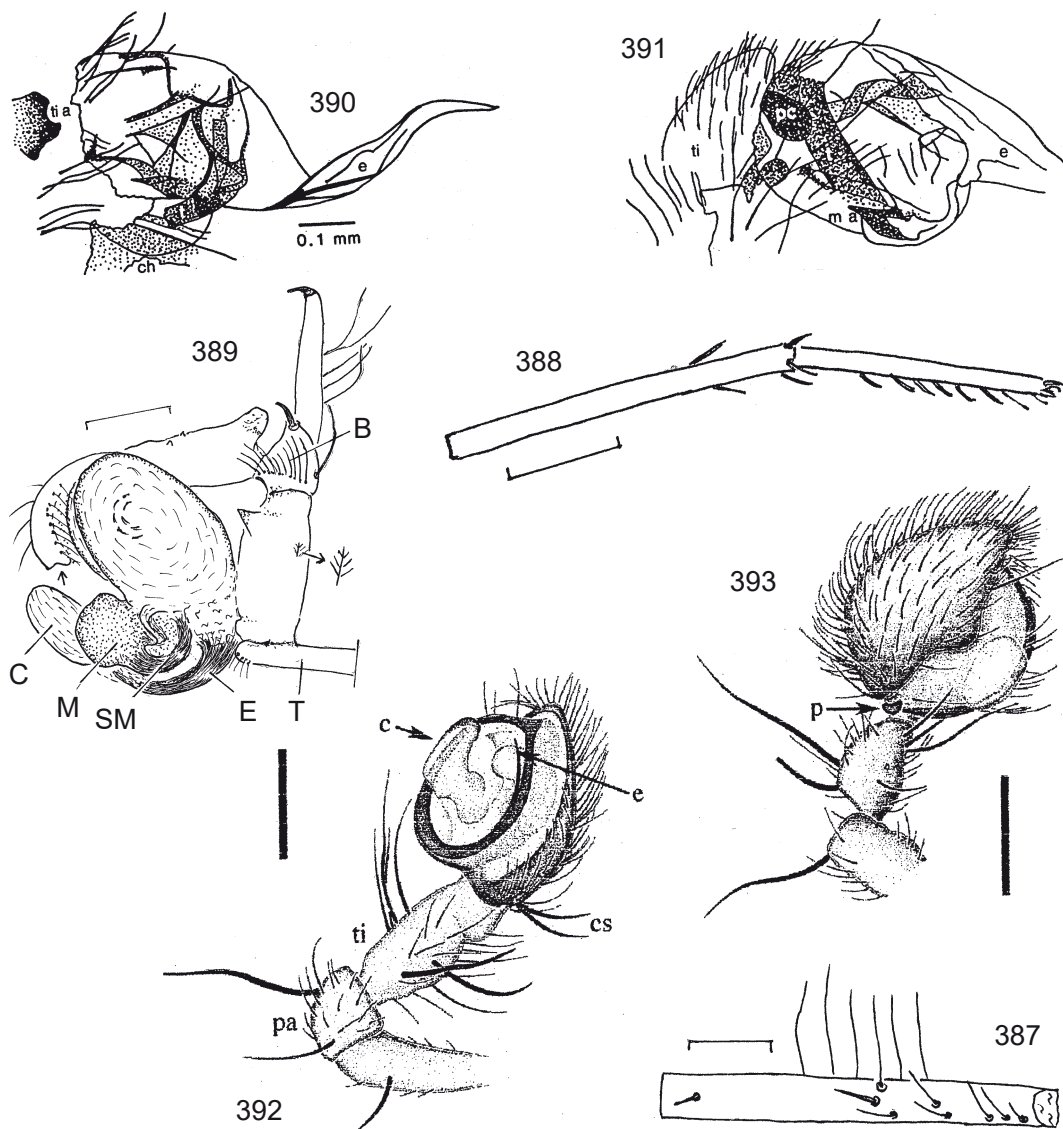
Figs. 374-376: *?Burmuloborus* sp. indet. (ULOBORIDAE), ♀ BU/1/CBS in Burmite; 374) retrolateral aspect of the left leg I. The tarsus is distally slightly deformed; 375) prolateral aspect of the left metatarsus IV (the distal part is cut off). Note the seemingly double rowed calamistrum (arrow). Only few hairs are drawn; 376) retrolateral aspect of the tip of the left tarsus II. Only few hairs and claw teeth are drawn. Note the long „auxiliary“ hairs (arrow) and the long onychium. – Scale bars 0.5 in figs. 374-375, 0.1 in fig. 376.

Figs. 377-382: *Microuloborus birmanicus* n. gen. n. sp. (ULOBORIDAE), ♂ in Burmite; 377) dorsal aspect of the slightly deformed prosoma. The arrow points to the questionable position of the



right anterior lateral eye; the left anterior lateral eye is hidden; 378) retrolateral aspect of the right leg I. Only few hairs are drawn; 379) proventral aspect of the distal part of the left femur IV which bears a long trichobothrium; 380) prodorsal aspect of the left metatarsus IV which bears bent hairs of the calamistrum; 381) retrolateral aspect of the right pedipalpus. Parts of the bulbous are hidden but the embolus is well observable; 382) prodistal aspect of the left pedipalpus. – Scale bars 0.2 in figs. 377-378, 0.1 in the remaining figs.

Figs. 383-386: *Paramiagrammopes longiclypeus* n. sp. (ULOBORIDAE), ♂ in Burmite; 383) scetch of the prosoma which is partly hidden to show the long clypeus (arrow), lateral aspect; 384) prolateral aspect of the left leg IV. Hairs are not drawn; 385) prolateral aspect of the left padipalpal patella; 386) dorsal aspect of the right pedipalpus. Note the large spur of the median apophysis (arrow). – C = calamistrum. Scale bars 0.5 in figs. 383-384, 0.1 in fig. 385 and 0.2 in fig. 386.



Figs. 387-389: *Paragrammopes patellidens* n. sp. (ULOBORIDAE), ♂ in Burmite; 387) retrodorsal aspect of the left femur IV. Note the long trichobothria. Hairs are not drawn; 388) prolateral aspect of the right metatarsus and tarsus I. The calamistrum is not observable in this position. Hairs are not drawn; 389) retrolateral aspect of the left pedipalpus. The short arrow points to the cymbial notch. One of the feathery femoral hairs has been enlarged (the longer arrow). – B = brush of plumose basal hairs on the patella, C = questionable conductor, E = embolus, M = median apophysis, SM = spur of the median apophysis, T = trochanter. Scale bars 0.2.

Figs. 390-391: *Cretaraneus vilaltae* SELDEN 1990 (NEPHILIDAE), ♂ in Cretaceous stone from Spain, pedipalpus. – Taken from SELDEN (1990).

Figs. 392-393: *Mesozygiella dunlopi* PENNEY & ORTUNO 2006 (ZYGIELLIDAE), ♂ in Cretaceous amber from Spain; 392) holotype, proventral aspect of the right pedipalpus; 393) paratype, prolateral aspect of the left pedipalpus. – Scale bars 0.2. Taken from PENNEY & ORTUNO 2006.

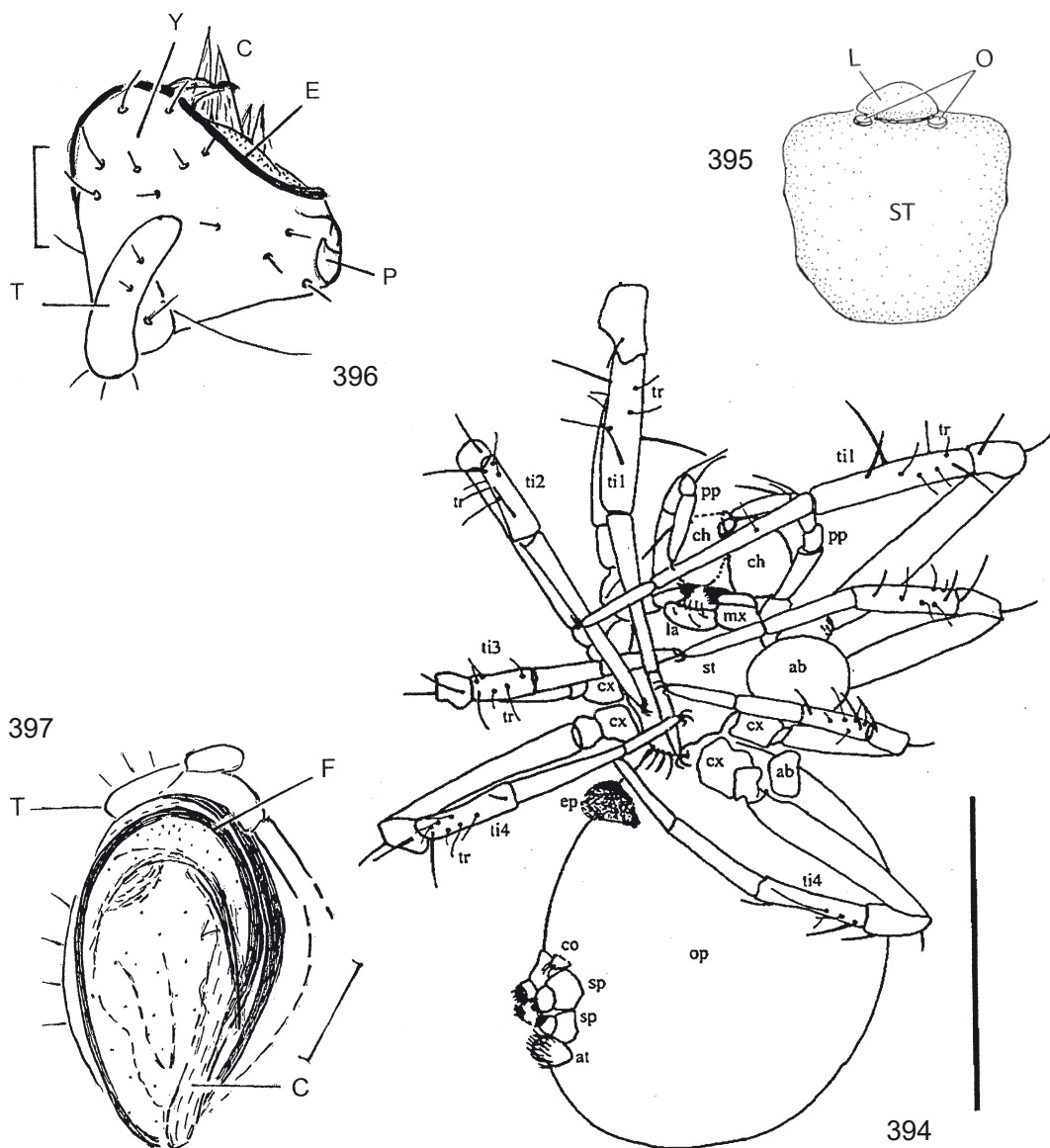
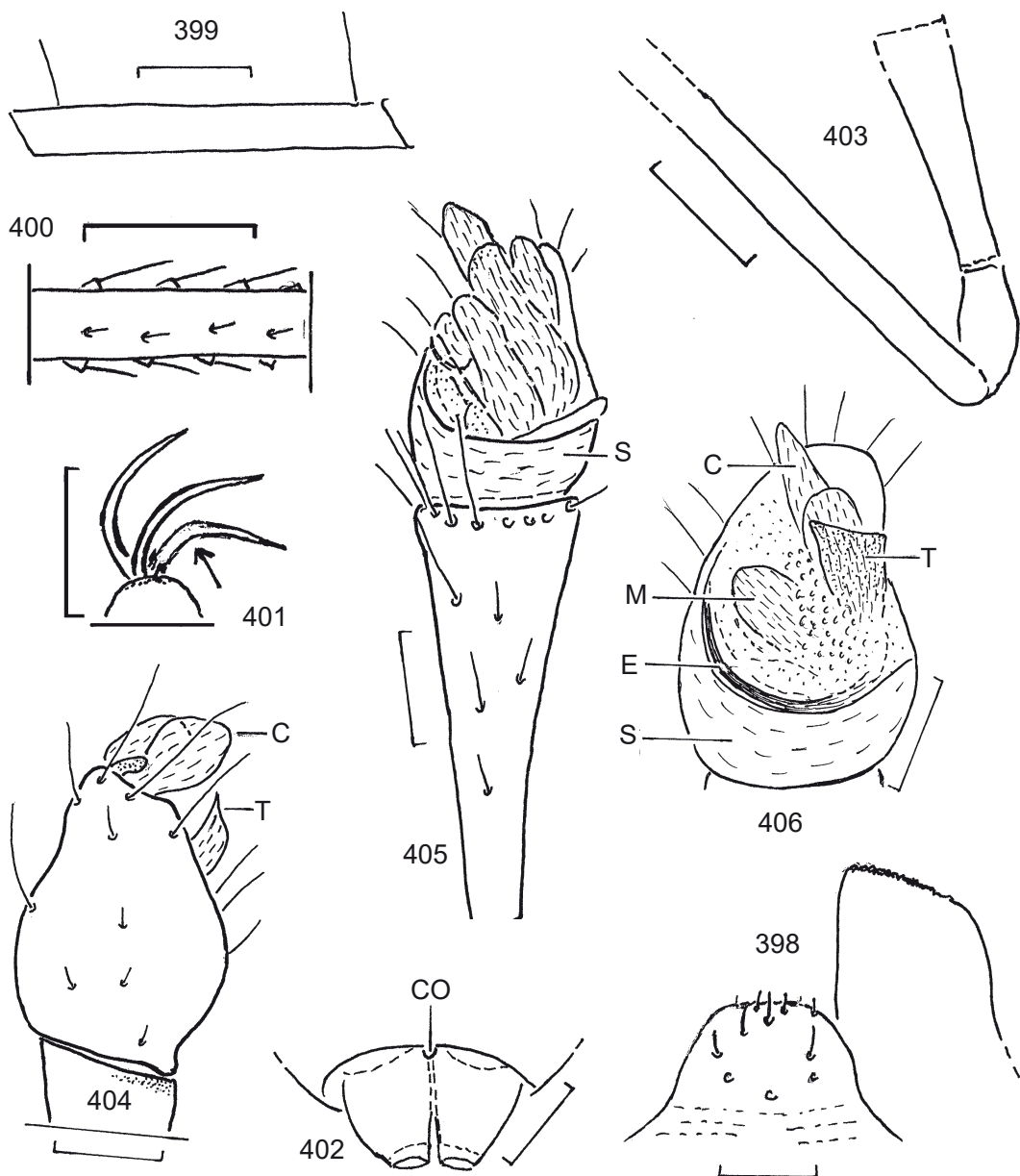


Fig. 394) ?Zygiellidae (under Linyphiidae) indet.: PENNEY & SELDEN 2002, ♀ in Lower Cretaceous Lebanese amber, ventral-lateral aspect of the spider. Note the strongly sclerotized and protruding epigyne (ep). – Scale bar 1.0. Taken from PENNEY & SELDEN (2002).

Figs. 395) THERIDIOSOMATIDAE sp., extant, „sternal-organs“ (O): pits (openings) of the sternal glands near the labium (L) on the sternum (S). These best diagnostic character of the family Theridiosomatidae is usually not or quite difficult to observe in fossil spiders.

Figs. 396-397: Leviunguis bruckschi WUNDERLICH 2012 (THERIDIOSOMATIDAE), ♂ in Burmite; 396) dorsal aspect of the deformed right pedipalpus; 397) ventral aspect of the deformed left pedipalpus. – C= conductor, E = embolus, F = parembolic apophysis, P = questionable paracymbium, T = outgrowth of the tibia, Y = cymbium. Scale bars 0.1.



Figs. 398-406: *Cretotheridion inopinatum* n. gen. n. sp. (THERIDIIDAE), ♂ in Burmite; 398) ventral aspect of the labium and the left gnathocoxa; 399) retrolateral aspect of the left tibia IV. Note the two long and thin dorsal bristles. Hairs and trichobothria are not drawn; 400) retrolateral aspect of a basal area of metatarsus I. Note the basal tubercles of the dorsal and ventral hairs. Not all hairs are drawn; 401) prolateral aspect of the claws of the left tarsus II. Note the long unpaired claw (arrow); 402) ventral aspect of the stout anterior spinnerets and the small colulus (CO); 403) prolateral aspect of femur, patella and tibia of the right pedipalpus; 404) prodorsal-apical aspect of the left pedipalpus. Only few hairs are drawn; 405) ventral aspect of the left pedipalpus; 406) ventral aspect of the left bulbus, slightly different aspect of the previous figure. Some parts are hidden. – C = conductor, E = embolus, M = median apophysis, S = subtegulum, T = theridiid tegular apophysis (?). – Scale bars 0.1.



## NEW AND RARE FOSSIL ARACHNIDA IN CRETACEOUS BURMESE AMBER (AMBLYPYGI, RICINULEI AND UROPYGI: THELEPHONIDA)

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**Abstract:** Selected mesozoic taxa – mainly in Mid Cretaceous Burmite – are treated. (1) Order Ricinulei: A new and monotypic suborder of the arachnid order Ricinulei, Primoricinulei **n. subord.**, is described from Cretaceous Burmite of Myanmar (Birma). It is based on the Primoricinuleidae **n. fam.**, and a nymph of *Primoricinuleus pugio* **n. gen. n. sp.** The second suborder of the Ricinulei includes the remaining fossil and extant Ricinulei, and is designated as Posteriorricinulei **n. subord.** A emended diagnosis of the Ricinulei is given, the close relationship to the extinct order Trigonotarbitida is confirmed. The present specimen is the second ricinuleid from Asia and from the whole Mesozoic. – (2) Order Amblypygi: Two species of the genus *Kronocharon* ENGEL & GRIMALDI 2014 are described: *K. engeli* **n. sp.** and *K. longicalcar* **n. sp.** – (3) Order Uropygi s. l.: Suborder Thelyphonida: *Burmathelyphonia prima* **n. gen. n. sp.** is described as first taxon of this order in Burmite. – Few structures and behaviour of arachnids and insects are compared which evolved in a similar way.

Acknowledgement: I thank JASON DUNLOP for a helpful discussion regarding especially the orders Ricinulei and Uropygi, and PETER JÄGER for the loan of extant arachnids.

**Material:** The fossil arachnids were bought from different dealers and originate from North Myanmar (Burma), the Kachin State, north of Myitkyina. They are kept in the coll. of J. Wunderlich (CJW) in D-69493 Hirschberg, Lab. of Arachnology, and will be given in the future probably to the Senckenberg Museum Frankfurt a. M. Their final deposit will be published.

Archnida is a very diverse class of arthropods today and was also diverse in the Mesozoic, especially the orders Acari and the Araneae. The number of arachnid orders (see below) is a matter of opinion: Today we know 10 to 12 orders (Acari and Uropygi may be splitted), extinct (latest extinct during the Permian) are furthermore 3 or 4 orders (Uraraneida may be a suborder of the Araneae or not). See DUNLOP & PENNEY (2012). In this paper I describe new taxa of the orders Amblypygi, Ricinulei and Uropygi s. l.: Thelyphonida which are preserved in Mid Cretaceous (about 100 million years old) amber from North Myanmar (Burma). Mainly the presence of the orders Ricinulei and Uropygi – but also of the orders Amblypygi and Solifugae – document the tropical character of the Burmese amber forest.

### **The arachnid orders in Burmese amber: Diversity and frequency**

From this kind of amber I know all extant orders except the Palpigradi (as well as of most extant suborders). See the photos 176-188.

ACARI s. l. are very frequent and very diverse.

Suborders ACARIFORMES and PARASITIFORMES.

AMBLYPYGI (fig. a, photos 183-186) are very rare; see below.

Suborders EUAMBLYPYGI and PALAEOAMBLYPYGI.

ARANEAE s. l. (fig. e) are frequent and very diverse; see the paper in this vol.

„Suborders“ URARANEIDA and ARANEAE: Mesothelae and Opisthothelae.

OPILIONES (fig. f) are rare.

Suborders: CYPHOPHTHALMI, DIPNOI, EUPNOI and LANIATORES.

PSEUDOSCORPIONES are fairly rare.

Suborders: EPIOCHEIRATA and IOCHEIRATA.

RICINULEI (photos 177-182) are rare compared with Araneae.

Suborders PRIMORRHICINULE and POSTERRICINULEI n. suborder, see below.

SCORPIONES (see the photos below) are rare but not too rare.

Probably three suborders, see DUNLOP & PENNEY (2012: 25).

SOLIFUGAE (fig. d, photo 188) are extremely rare. The first taxon is presently studied by an author in Germany. No differing suborders.

UROPYGI s. l. (figs. b, c, photos) are rare, especially the Thelyphonida.

Suborders: (a) SCHIZOMIDA (photo 176): The first taxa are presently studied by authors in the USA; and (b) THELYPHONIDA (photo 187): See below.

### **Selected basical typical/diagnostic characters of the class Arachnida:**

With notes on the sperm transfer

- Four pair of legs behind the chelicerae and the pedipalps;
- two (main) body parts: The prosoma and opisthosoma which usually is segmented;
- a flagellum or a „tail“ exist in several orders (photo 187);
- eyes: A pair of median eyes and basically 5 (usually less) pairs of lateral eyes;
- disposition of a changing function of the first or second walking leg to a mainly tactile function of a „feeler“ (see below);
- existence of specialized sensory hairs: trichobothria (lost in the Solifugae),
- basically extraintestinal digestion in connection with a prosomal sucking pump;
- basically digging behaviour and subterranean dwelling at least during broodcare;
- broodcare behaviour: Frequently a praenymph lives up to the first moulting on the body of the mother in a subterranean „brood chamber“ or in an egg sac (in the Araneae); female egg-carrying exists in several taxa of Araneae and Acari;
- sperm transfer, mating behaviour: Basically with the help of spermatophores which are deposited on a substratum; so by the Amblypygi, the Scorpiones, probably the Palpigradi, most Acari (see below) and most Uropygi: Schizomida and most Thelyphonida (see below).

#### Notes on the enormous behavioural and anatomical diversity of sperm transfer in arachnids:

- ~ A penis or penislike structures exist in the Opiliones (\*) and in several groups of Acari;
- ~ Also a direct sperm transfer – but from the male to the female genital opening – exists in several Solifugae and in several Acari;
- ~ an „indirect“ sperm transfer by a SPECIALIZED extremity exists (a) in the Araneae: by their pedipalps and (b) in the Ricinulei: by their third pair of walking legs;
- ~ an indirect sperm transfer (of spermatophors) occurs in certain Thelyphonida with the help of their pedipalps (which are not specialized for this function) or with the help of the male chelicerae: in several Solifugae and in the Acari: Gamasida.

No mating – but parthenogenesis – exists (e. g.) not rarely in the Acari, in some Opiliones, in very few Araneae and probably in some Palpigradi.

TO SUM IT UP: The greatest diversity exists in the Acari; only a single behaviour exists in the Araneae, in the Opiliones and in the Ricinulei. (A steady behaviour exists also in Scorpiones, Schizomida and probably Palpigradi which all simply deposit Spermatophores, see above).

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(\*) A penis of the Opiliones has been reported already in the Palaeozoic, 400 million years ago, see DUNLOP (2003).

Remarks on ARACHNIDS AND INSECTS – Arthropods which are antagonists in some respect; differing in several characters but similar in others

The eight-legged arachnids (\*) are the most diverse class of arthropods besides the insects which are the most diverse class of animals on Earth, extant and fossil, consisting of millions of species.

Why are insects more „successful“ and diverse than arachnids? What are the „advantages“ of insect's characters? (\*\*). Mainly the important „innovations“ of wings and antennae apparently cause the huge „success“ of the insects. Remarkably numerous arachnids evolved certain features – of structures and behaviour – which are comparable in some respect to those of insects but they evolved these in quite different ways. These two characters possess a similar or even THE SAME FUNCTION in both classes but they are not identical and not of the same significance in arachnids like in insects. Here I will discuss only the following characters:

(1) WINGS and LOCOMOTION. The wings of most insects allow a quick locomotion: escape from enemies, flight and attack as well as a dispersal over a short distance (searching for a sexual partner) or a long distance (looking for a different area e. g. to populate a remote island). – Some of (the always wingless) arachnids evolved one of three ways to approach the same or similar functions; two ways are passive locomotion through the air:

- A *jumping behaviour* evolved e. g. in numerous extant spiders (Araneae) (\*\*\*).
- An *aeronautic behaviour* (ballooning) – floating on their own threads – bridging either a short distance from one plant to another or a large distance – e. g. from one island to another – evolved in most members of spiders.
- A *phoretic behaviour* evolved in the orders Acari and Pseudoscorpiones; it is already reported from the Mesozoicum.

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(\*) Only immature Acari and Ricinulei and certain adult Acari possess less than 4 pairs of legs.

(\*\*) The huge diversity of insects is also the result of an enormous specialization on various kinds of food – in connection with the evolution of numerous kinds of mouth parts – in contrast to arachnids which are not feeding on plants (extremely few species feed on pollen or nectar) or dead animals but are raptorial and digest in a very special kind outside their body (extraintestinal); they cannot swallow particles but are only able to take up liquid food. This characteristic excludes the feeding on plant material like leaves. – Dwarfism may cause a huge diversity in certain groups of both classes of arthropods, e. g. in the tiny members of certain arachnids like the Oonopidae and the Linyphiidae: Erigoninae as well as in tiny members of certain insects like Coleoptera, Diptera and Hymenoptera.

(\*\*\*) Apparently a jumping behaviour evolved only late in spiders: Within the mesozoic spiders I know jumping members only of two genera of a single subfamily: the Orchestiniinae of the Oonopidae. In the Eocene this behaviour is documented by the existence of (e. g.) genera of the Jumping Spiders (Salticidae) in Baltic amber, see WUNDERLICH (2004). – (A jumping behaviour also evolved in numerous – winged or not winged – insects).

(2) „FEELERS“, WALKING LEGS and BEHAVIOUR in spiders. The antennae of the insects allow orientation, the localisation of prey, enemies, potential sexual partners, etc. – Antennae are completely absent in the class Arachnida (\*) but members of or within almost all arachnid orders use their modified – lengthened and multi-(pseudo) articulated – anterior or second pair of legs which is raised antennae-like or they use their pedipalps (\*\*) as „feelers“. One pair of legs may be used without any problems for different functions, contrarily to its original walking function. Apparently generally in most arachnid orders four pairs of legs are not necessarily needed for locomotion, and three pairs of legs – as in insects – are „enough“ for a well functioning locomotion. Examples are ...

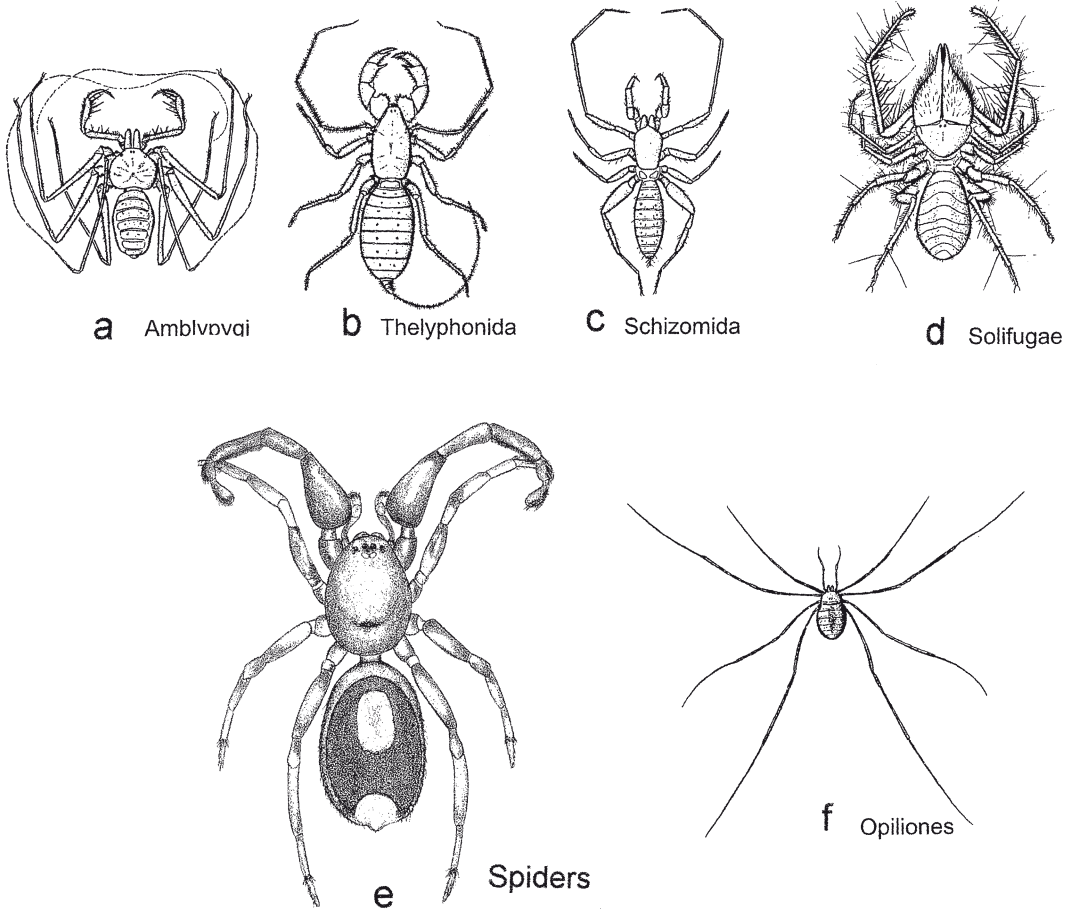
- members of the order Amblypygi (fig. a, photos 183-186),
  - of the order Palpigradi and
  - of the order Uropygi (the suborders Thelyphonida and Schizomida as well, figs. b, c, photos 176, 187):
- All these arachnids usually raise their long antennae-like ANTERIOR pair of legs which possesses a multi-(pseudo)segmented and flexible tarsus.
- Solifugae (fig. d, photo 188) is a special case: Members of this order use and raise their thin and not enlarged ANTERIOR leg and additionally their enlarged – lengthened and fairly thickened – pedipalp as „feelers“.
  - Certain Acari and certain Araneae (fig. e) (\*\*\*) use their first leg – it may be distinctly enlarged (thickened and/or lengthened) in these taxa.
  - Members of the order Ricinulei (photos 177-182) raise their SECOND leg as „feeler“ but in this order it is only fairly lengthened and
  - in numerous Opiliones (the long-legged members, fig. f) also the lengthened SECOND leg – which has a long, flexible and multi(pseudo)segmented tarsus – is used in the same way.

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(\*) The frequently high number of long trichobothria on pedipalpi and legs (absent in the Solifugae) may be a weak compensation of the absence of antennae in most arachnids.

(\*\*) Scorpions and Pseudoscorpions do not use walking legs like feelers but they may raise their huge and sensory pedipalps during locomotion. (Numerous spiders use their pedipalps to detect water, potential sexual partners etc.).

(\*\*\*) Most expressed in spiders is this behaviour in members of the family Palpimanidae (fig. e) which raise their huge first pair of legs like „feelers“. Such behaviour may be most useful in such nocturnal animals. – Long-legged members of certain Pholcidae raise their quite long and multi(pseudo)articulated anterior legs like „feelers“. A quite long (and thin) leg I is known in most nocturnal members of the family Archaeidae; a very long leg I existed also in members of the Cretaceous family Pholcochyroceridae (this volume). – Ant-mimicking members of numerous spider families raise and move their anterior pair of legs, imitating the antennae and the behaviour of ants („antennae illusion“). – During their courtship behaviour male spiders of certain taxa of the families Lycosidae and Salticidae raise and move their first pair of legs which are normally used as walking legs.



Figs. a-f: Dorsal aspect of selecten arachnids:

a) Amblypygi, b) Uropygi: Thelyphonida, c) Uropygi: Schizomida, d) Solifugae, e) Araneae: Palpimanidae, f) Opiliones.

Fig. e) is taken from JOCQUE & DIPPENAAR-SCHOEMAN (2007), the remaining figs. are taken from DUNLOP & PENNEY (2012), with many thanks!

# DESCRIPTIONS of the new taxa

## 1. Order RICINULEI

Ricinulei („Hooded Tickspiders“, in German „Kapuzenspinnen“) are unique among the arachnid orders in that the first one to be discovered was a fossil. Only two years ago the first fossil member of the order Ricinulei preserved in amber has been described, see WUNDERLICH (2012: 233-244). The presently described specimen is also preserved in about 100 million years old Cretaceous amber from Myanmar/Birma (Bur-mite), but is quite different. The diagnostic characters of this taxon are so different from all other known extant and fossil Ricinulei that a new suborder has to be created. I regard its characters as a mixture of plesiomorphic and derived ones. The present small, completely and well preserved specimen – although being only a nymph – allows conclusions on the relationships of the order Ricinulei as well as on higher taxa within this order, and requires an emended diagnosis of the Ricinulei. The conclusions by DUNLOP – and previously already by KARSCH (1892) – about the strong relationships of the relict order Ricinulei and the extinct Palaeozoic order Trigonotarbida are confirmed by characters of the present fossil, e. g., by the large sternum, see fig. 2.

### **Emended diagnosis of the order Ricinulei** (see also below):

- prosoma bearing an anterior movable hood (cucullus) (fig. 1), see also WUNDERLICH (2012: 242, fig. 1 and 243, fig. 3) which covers and hides the chelicerae,
- loss of the median eyes – existence of only two pairs of eyes (in a lateral position) (fig. 1, photo), see WUNDERLICH (2012: 243, fig. 3) (lenses strongly reduced or even absent in extant taxa),
- elongated leg II, see WUNDERLICH (2012: 242, fig. 1), similar to Amblypygi and certain Opiliones,
- male copulatory organ on leg III, see WUNDERLICH (2012: 242, fig. 1). (The existence of such an organ cannot be excluded from the – usually juvenile and not well preserved – members of the extinct order Trigonotarbida; see SELDEN (1992)),
- six-legged larvae (nymphs are eight-legged).

Further character (see also below): Position of the pedipalpus in front of the body and leg I (figs. 2, 8) like in the Trigonotarbida (modified in the Posteriorricinulei).

**Sister order:** The extinct Trigonotarbida in which a narrowed anterior prosomal out-growth exists (figs. 14, 16) but no cucullus (fig. 1); see the next paragraph, the cladogram, and DUNLOP et al. (2009).

### **Synapomorphies of Ricinulei and Trigonotarbida:**

- tergites basically divided into median and lateral plates (figs. 12-14, 16),
- special coupling mechanism between two distinctly separated body parts, the pro-soma and opisthosoma,



- anteriorly prolonged prosoma: narrowed in the Trigonotarbida (figs. 1, 14-16), specified as a wide hood (cucullus, figs. 1, 12) in the Ricinulei,
- very long paired tarsal claws (figs. 4, 6, 10),
- probably an almost laterigrade leg position, see WUNDERLICH (2012: Fig. 1), (male copulatory organ on leg III: See the order Ricinulei).

#### **Selected symplesiomorphies of Ricinulei and Trigonotarbida:**

- two separate body parts – prosoma and opisthosoma – which are strongly flattened and heavily armoured (photo),
- slowly moving animals (unsure in the Trigonotarbida),
- probably basically 8 eyes including triads (fig. 16) (some tiny eye lenses may exist furthermore); the basically existing triads were retained in certain Trigonotarbida, see SHEAR et al. (1987),
- (basically) a well developed sternum which widely separates the leg coxae (figs. 2, 15, photo) similar to the Araneae (in the Ricinulei: Posteriorricinulei a small „Tritosternum“ exists in an anterior position),
- existence of a pointed unpaired tarsal claw, see WUNDERLICH (2012: Fig. 8),
- absence of trichobothria (like in Opiliones),
- a short metasoma („pygidium“) (figs. 1-2),
- pedipalpal article ending in a pincer (nippers) (fig. 11); probably basically large articles,
- terrestrial tropical (rain) forest dwellers which need or prefer dampness (similar to certain primitive Opiliones).

**Diversity and distribution:** See WUNDERLICH (2012: 238-239). No proof of extant Ricinulei in Asia and Australia but the discovery in tropical Asia appears likely to me.

#### **POSTERIORRICINULEI n. suborder**

**Etymology:** From posterior (lat.) = later, younger; pointing to the derived position of this suborder, and ricinulei from the name of the order Ricinulei.

**Taxa included:** The extant superfamilies Ricinoidoidea EWING 1929 (= suborder Neoricinulei SELDEN 1992) which includes only the family Ricinoididae EWING 1929 and the extinct Poliocheroidea SCUDDER 1884 (= suborder Palaeoricinulei SELDEN 1992) including the families Poliocheridae SCUDDER 1884 and Curculiodidae COCKERELL 1916; see WUNDERLICH (2012: 237).

**Diagnosis** (apomorphic characters): Coxae contiguous (reduced sternum) (fig. 13), paired tarsal claws retractable in a large inclination (fig. 9) (less distinct on tarsus II, fig. 10), unpaired tarsal claw blunt, see WUNDERLICH (2012: Fig. 2), position of the pedipalpus below the body and more behind the anterior legs, see WUNDERLICH (2012: Fig. 1).

**Relationships:** See the Primoricinulei n. subgen. and the cladogram.

**Distribution:** Tropical Carboniferous – extant; see WUNDERLICH (2012: 237).

### **PRIMORICINULEI n. suborder**

**Etymology:** From primo (lat.) = the beginning; pointing to the ancient taxon *Primoricinuleus*, and ricinulei from the name of the order Ricinulei.

**Included:** Only the nominal extinct genus *Primoricinuleus* n. gen. (Primoricinuleidae).

**Diagnosis:** Opisthosoma (at least in the nymph) dorsally and ventrally bearing each a single entire scutum (figs. 1-2, photos 177-180) (apomorphies), unpaired tarsal claw most probably absent, tarsi prolonged beyond the claws (figs. 4-5) (apomorphies), pedipalpus (figs. 2, 8, photos): Fixed „finger“ strongly reduced or even absent, movable „finger“ (apothele) dagger-shaped, very long and only fairly bent (apomorphies), sternum (fig. 2, photo) well developed, the leg coxae widely spacing (plesiomorphy).

**Further characters:** Cucullus well developed (figs. 1-2, photos), coxa II largest (fig. 2), leg II longest, tarsal claws not retractable (figs. 4-6), pedipalpus with thick articles (figs. 2, 8, photos).

**Relationships and phylogenetics** (see also below, the paragraph „Ecology, ...“, and the cladogram): DUNLOP (1996, 2009) founded well the sister group relationships of the order Ricinulei and the extinct order Trigonotarbida; see also above. In both orders (e. g.) the pedipalpus ends in a pincer which is modified in the Primoricinulei; in Carboniferous Ricinulei the pedipalpal articles may be thick like in the Primoricinulei, see SHEAR et al. (1987: Fig. 14). In taxa of the Ricinulei except the Primoricinulei – including small nymphs of extant taxa which were studied by me – the opisthosomal scuta are not fused together (figs. 12-13), the position of the leg coxae is close together (fig. 13) (in contrast to the Trigonotarbida, fig. 15), a pincer exists which has a well developed fixed „finger“ (fig. 11) (like in the Cretaceous ?*Poliochera cretacea* WUNDERLICH 2012 (fig. 4 p. 243) which is also preserved in Burmite). I regard the large sternum and the pedipalpal pincer as plesiomorphic characters which also exist in the sister group of the Ricinulei, the Trigonotarbida.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Birma).

## **PRIMORICINULEIDAE n. fam.**

Etymology: See the new suborder.

Type genus (by monotypy): *Primoricinuleus* n. gen.

**Diagnosis, relationships and distribution**: See above, the new suborder.

***Primoricinuleus* n. gen.** (figs. 1-8), photos 177-180

Etymology: See above.

The gender of the name is masculine.

Type species (by monotypy): *Primoricinulei pugio* n. sp.

**Diagnosis, relationships and distribution**: See above, the new suborder.

***Primoricinuleus pugio* n. gen. n. sp.** (figs. 1-8) photos 177-180

Etymology of the species name: From pugio (lat.) = dagger, pointing to the dagger-shaped movable „finger“ of the pedipalpus.

**Material**: Holotype nymph (probably nymph 2) in Burmite and a separated piece of amber, F2635/BU/CJW.

**Preservation and syninclusions**: The arachnid is rather well and completely preserved in a clear yellow piece of amber. The prosoma and several leg articles are fairly deformed, the opisthosoma is distinctly depressed. The leg articles except the basal ones are bent under the body (see the photos) like in spiders which are killed e. g. by alcohol; therefore I conclude that the arachnid died within the fossil resin. Within leg articles dark structures are preserved. – two gas bubbles are preserved between leg articles and the body. Tiny gas bubbles, stellate plant hairs and tiny particles of detritus are also preserved in the two pieces of amber.

**Diagnosis (nymph), relationship and distribution**: See above.

**Description (nymph):**

Measurements (in mm): Body length 1.8; prosoma: Length without cucullus ca. 0.63, width 0.6; opisthosoma: Length 1.2, width 1.0; legs (see also the photos; some articles are shortened perspective): femur I ca. 0.5, femur II ca. 0.65, femur III ca. 0.5, leg IV: Femur 0.5, patella 0.45, tibia 0.43, metatarsus 0.43; length of the movable pedipalpal „finger“ 0.18.

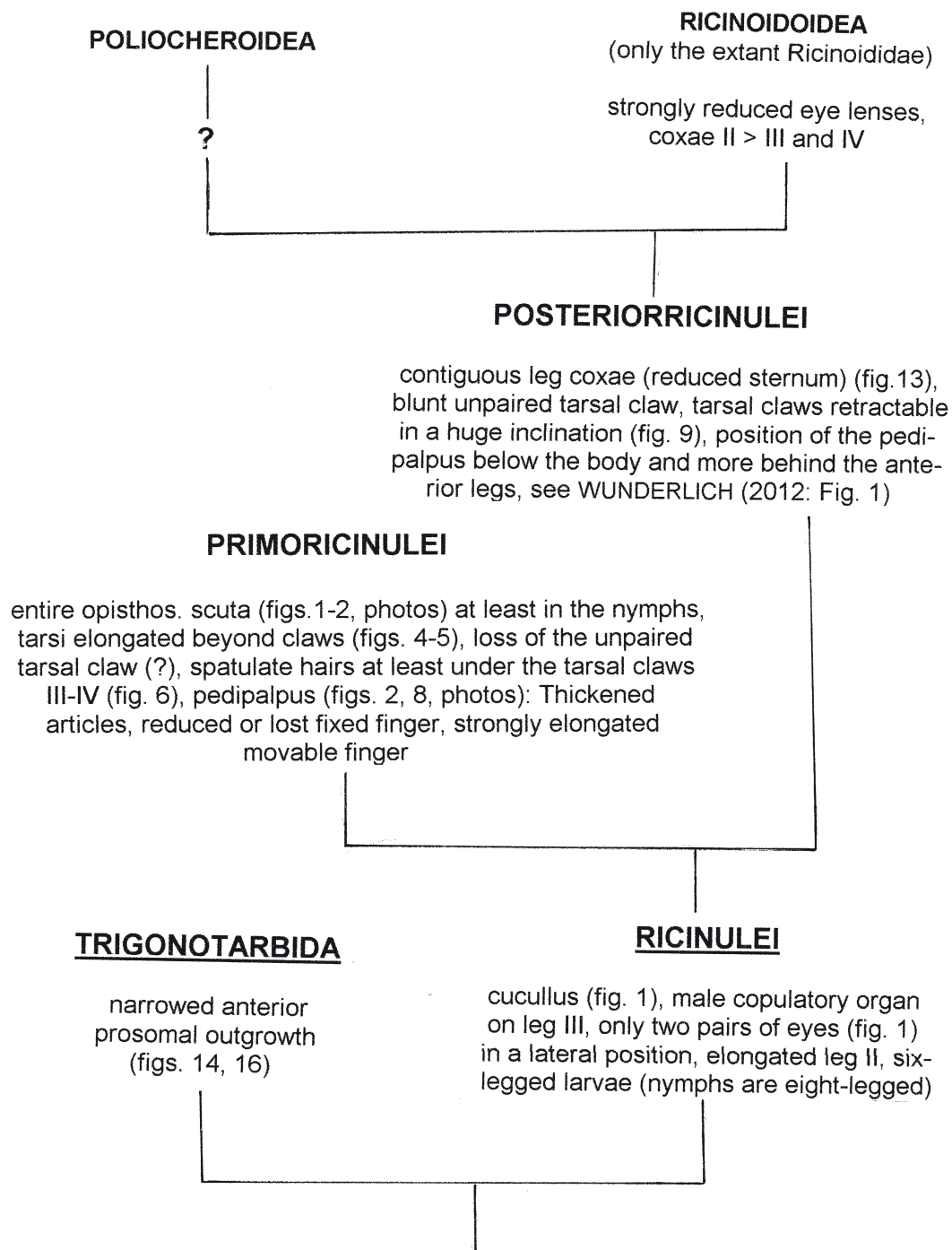
Colour (photos) mainly medium brown, partly yellow brown (some leg articles), the prosoma and some leg articles bear dark structures inside which may have been caused by heating and pressure of the preservation.

Prosoma (figs. 1-2, photos) almost as wide as long, flat, quite finely corniculate, hairs short, two deformed pairs of lateral larger eyes which are close together, cucullus large/wide, dorsally hiding the two-jointed chelicerae, gnathocoxae large and contiguous, sternum large, as wide as long, spacing widely the coxae I-III, pedipalpus (figs. 2, 8) (its sense organs have to be studied with the help of x-rays in the future) with thick articles, its position obliquely anteriorly (not ventrally like in the Posteriorricinulei), femur most voluminous, tibio-tarsus longer than wide, movable „finger“ (apothele) very long, about as long as the tibio-tarsus, only fairly bent, immobile „finger“ strongly reduced or even absent. – Legs (figs. 3-7) (some articles are deformed) fairly long and slender – according to the position of the basal articles – originally directed more sideways, see above („preservation“), order II/IV/I/III, hairs short, bristles and trichobothria absent, coxae IV contiguous, I-III widely spaced, III largest, I smallest. Unpaired tarsal claw apparently absent (or strongly reduced?), paired claws very long, distinctly bent, toothless, originating not at the end of the tarsus (which is fairly flattened) but distinctly more basally, not retractable in a tarsal inclination like in the Posteriorricinulei; at least tarsi III-IV bear flattened hairs (fig. 6). – Opisthosoma (figs. 1-2, photos) (it is dorsally depressed) oval, flattened, hairs fairly short, dorsally and ventrally completely covered with an entire scutum, ventrally bearing three pairs of structures whose function is unknown (x in fig. 2), metasoma retracted, bearing some apical spines. The connection between prosoma and opisthosoma is hidden. – Pedipalpus (figs. 2, 8) (see also above) with thick articles, the patella being largest.

**Ecology, behaviour, functional morphology and evolutionary changes of fossil and extant Ricinulei**

The unusual new taxon: At the moment of their preservation 100 million years ago members of the Ricinulei existed already more than 200 million years. Therefore the find of an unusual extinct branch like the Primoricinulei n. suborder is not a great surprise.

The incomplete preservation: Similar to dead spiders captured in pit falls and preserved in alcohol most of the leg articles – except the basal ones – of Ricinulei specimens are bent below the body, see the photos. This position may be the reason for the absence of distal leg and pedipalpal articles of most Ricinulei which are preserved in stone, and



Possible cladogram of the Ricinulei and the related Trigonotarbida  
Synapomorphies and symplesiomorphies: See above.

therefore are strongly depressed and incomplete. In contrast to such fossils the presently described fossil is enclosed by fossil resin; it is completely preserved including its pedipalpi – see the photos and the figs. 2 and 8 – which are of special taxonomical value. A fossil ricinuleid pedipalpus including its distal articles and pincer has previously been reported only of *?Poliochera cretacea* – see WUNDERLICH (2012: 243, fig. 4) which is also preserved in amber and also in Burmite.

Phylogenetics: How did changes of life stile and environment influence the evolution of morphological structures during long time spans?

Extant Ricinulei are terrestrial dwellers of leaf mould and soil of (rain) forests, many species seem to prefer dampness; most known fossils apparently lived in Carboniferous coal swamps. Probably members of some species are able to advance deeply into the ground – like certain primitive Opiliones – where they are hard to collect and could only rarely be preserved in stone or get in contact with resin. It is remarkable that Ricinulei in Burmite are not extremely rare – I already saw half a dozen specimens. Probably drops of the very fluid fossil resin enclosed animals on the ground. Or did some specimens climb along tree trunks? (See below: Structures of the tarsi).

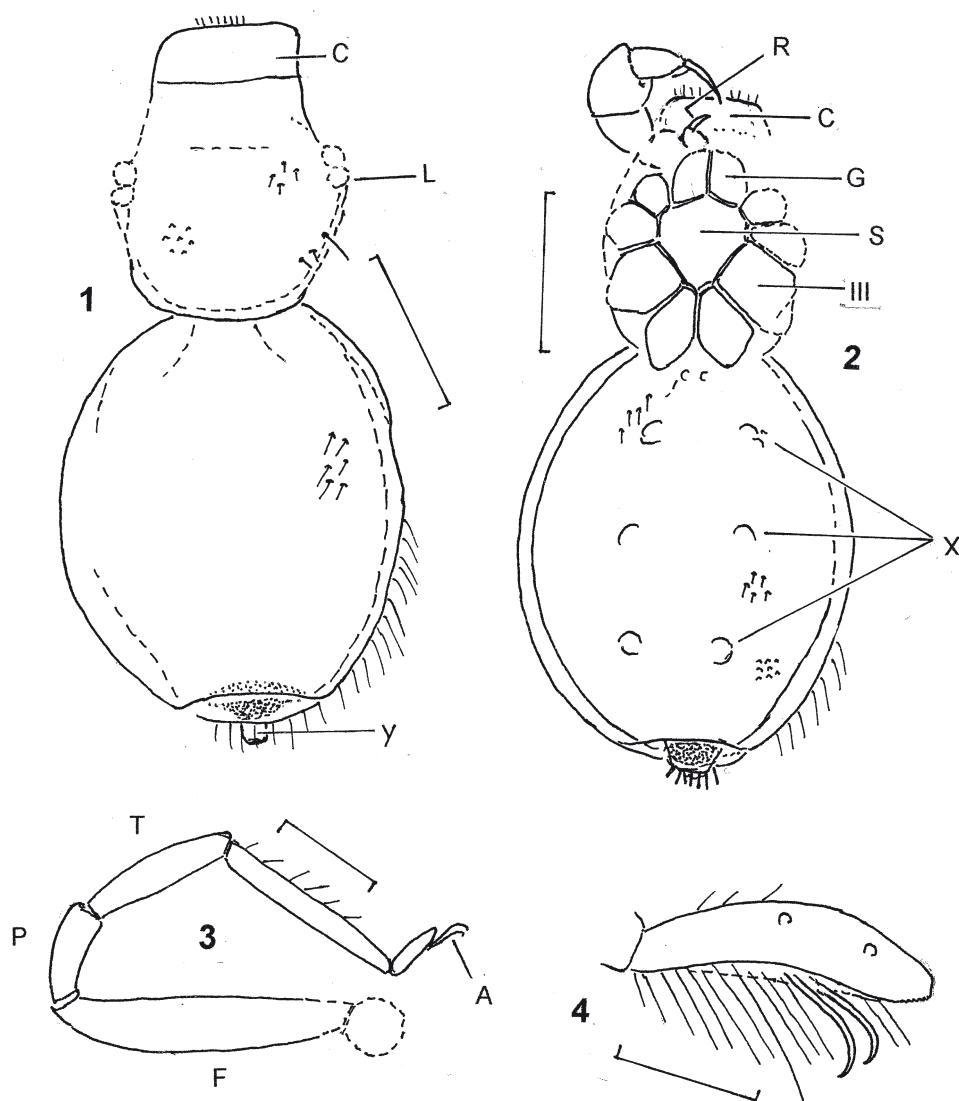
Ricinulei are slowly moving animals which do not use their quite long second legs for locomotion but use these like „feelers“ – see WUNDERLICH (2012: 242, fig. 1) -, similar to members of the orders Amblypygi, Uropygi as well as certain Opiliones and Acari, see above. Like these animals (and also certain Acari) legs and body of the Ricinulei are strongly armoured, so already in nymphs. Their strong sclerotization (this was similar in the extinct order Trigonotarbida) may protect Ricinulei from predatory enemies like Acari, Araneae and Opiliones but may also be useful for their locomotion within soil. Their hood (cucullus) may also possess this function and furthermore protect their mouth parts.

The reduction/absence of the eye lenses of extant Ricinulei may be connected with their subterranean life style. Interestingly the lenses of two pairs of eyes were well developed in fossil Ricinulei, see fig. 1 and the photos. These extinct animals were probably dwellers more on the ground, and the eye lenses were reduced in their descendents which changed their habitat to more soil dwelling for their relict surviving.

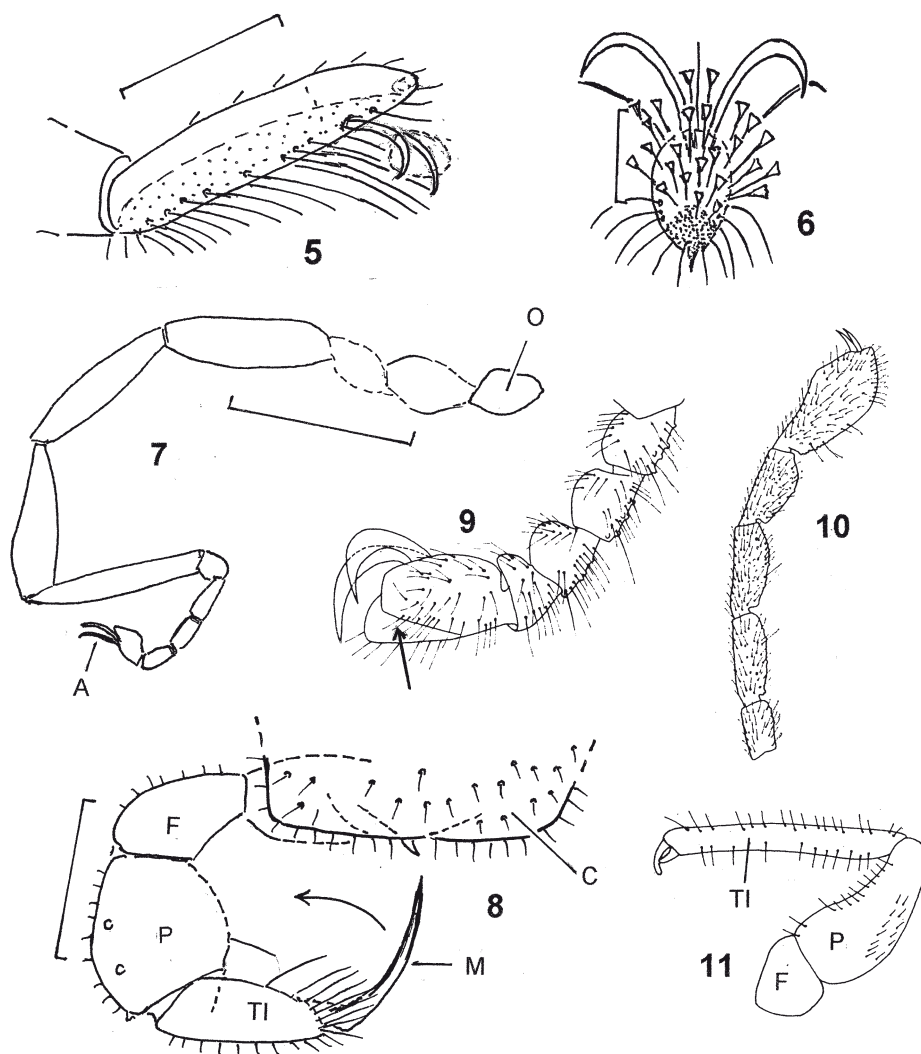
Ricinulei are known to feed on tiny arthropods like Collembola which they clamp between the two distal pedipalpal articles. With the help of the pedipalpal pincers (nippers) (fig. 11) the prey is transported to the mouth parts which are hidden below the hood (cucullus). Such pincers existed in the extinct Trigonotarbida – see DUNLOP et al. (2009) – and in all extinct and extant Ricinulei with the exception of the presently described Cretaceous *Primoricinuleus pugio* in which the pedipalpus is strongly modified: Functioning pincers (fig. 11) – consisting of a smaller fixed „finger“ and a larger movable „finger“ – are absent. The fixed „finger“ is strongly modified or even absent in *Primoricinuleus* in contrast to the movable „finger“ which is strongly developed (elongated), see fig. 8 and the photos. With the help of this large movable article prey could be captured and clasped by folding to the tibiotarsus and femur (arrow in fig. 8). (The transport of the prey to the mouth parts appears unknown, but see below). This means that the ancient „nippers-mechanism“ of capturing has changed to a „clamping-mechanism“ in *Primoricinuleus*. Furthermore the position of the pedipalpus has changed from below the prosoma – see WUNDERLICH (2012: 242, fig. 1) – to an obliquely anterior position, see the photos and fig. 2. Because of this pedipalpal position the prey could be transported directly to the mouth parts, and pincers were superfluous. Apparently this is a derived/apomorphic mechanism of prey capturing and feeding compared to the conditions in the remaining Ricinulei (the Posteriorricinulei) and the Trigonotarbida.

(Contrarily to this feature the large size of the sternum is a plesiomorphic character of the Primoricinulei).

The apical structures of the tarsi – as well as the tarsal claws – have also undergone changing during the ricinuleid evolution: (1) The basically (in the Trigonotarbida) pointed unpaired tarsal claw – see SHEAR et al. 81987: Fig. 48) – turned to a blunt claw in the ricinuleid suborder Posteriorricinulei – see WUNDERLICH (2012: Fig. 2) -, and is lost (at least strongly reduced) in the extinct genus *Primoricinuleus* (the suborder Primoricinulei) in Burmite, see the figs. 4-5, 7, and the cladogram. – (2) The very long paired tarsal claws are apparently retractable into a larger apical inclination of the tarsi in the Posteriorricinulei, see fig. 9. (A smaller inclination apparently exists in the Trigonotarbida, see SHEAR et al. (1987: Figs. 46 and 48). – (3) The apical part of the tarsi is strongly elongated beyond the claws in *Primoricinuleus* (figs. 3-5), flattened ventrally, and bearing – at least on III-IV – spatulate hairs. The function of these modifications is unclear to me. Are these modifications connected with the ability to climb tree trunks?





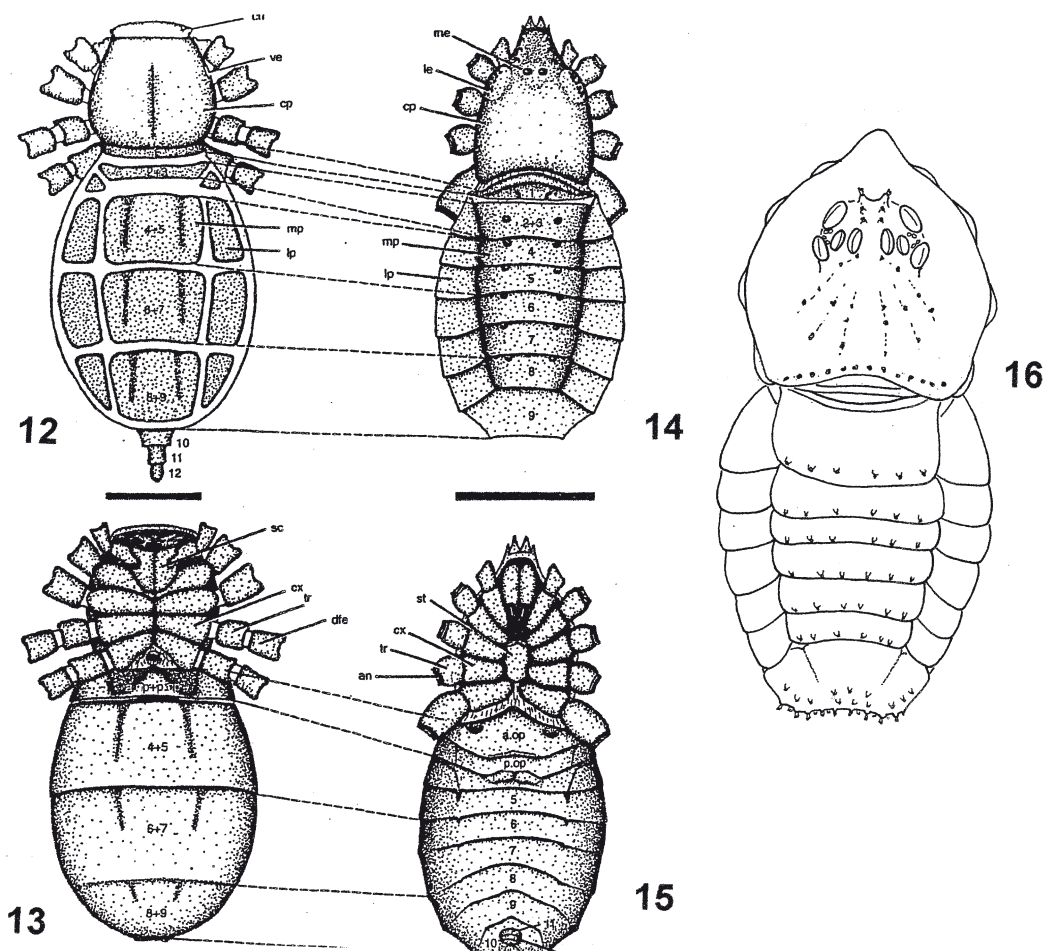


Figs. 1-8: *Primoricinuleus pugio* n. gen. n. sp. (Ricinulei: Primoricinulei: Primoricinuleidae), extinct, in Burmite, nymph; only few hairs are drawn; 1) dorsal aspect of the body; the prosoma is deformed, the opisthosoma is inclined/depressed; 2) ventral aspect of the body and the right pedipalpus; 3) prolateral aspect of the left leg I; 4) prolateral aspect of the distal article of the right tarsus I with its paired claws; 5) prolateral-ventral aspect of the distal article of the left tarsus II with its paired claws; 6) apical aspect of the left tarsus III; note the partly spatulate hairs; 7) prolateral aspect of the right leg IV; 8) dorsal and slightly anterior aspect of the right pedipalpus and the anterior part of the cucullus. The arrow points to the mobility of the „clasp-knife“ long mobile „finger“ (A).

Scale bars (in mm): Figs. 1-2 and 7 0.5, figs. 3 and 8 0.2, figs. 4-6 0.1.

A = paired tarsal claws, C = cucullus, F = femur, G = gnathocoxa, L = lateral eyes, M = movable „finger“ of the pedipalpus (apothele), O = coxa, P = patella, R = right fang, S = sternum, T = tibia, TI = tibiotarsus, Y = pygidium, X = three paired structures of unknown function, III = left coxa III.

Figs. 9-11: *Cryptocellus prope bolivari* GERTSCH 1971 (Ricinulei: Posteriorricinulei), extant, Mexico, ♂; 9) lateral aspect of tarsus IV; the arrow points to the deep apical inclination; 10) lateral aspect of tarsus II; 11) lateral aspect of the pedipalpus. – Taken from BRIGNOLI (1973).



Figs. 12-13: An extant member of the Ricinulei, the suborder Posteriorricinulei: *Pseudocellus* sp., dorsal and ventral aspect of the body. – Taken from DUNLOP (1996).

Figs. 14-16: Extinct members of the order Trigonotarbitida. 14-15: *Plaeaocharinus* sp., dorsal and ventral aspect of the body. – Taken from DUNLOP (1996).

Fig. 16) Dorsal aspect of the reconstructed body of the Devonian *Gilboarachne giersoni*. Note the existence of 8 eyes in contrast to fig. 14. – Taken from SHEAR et al. (1987).

## 2. Order AMBLYPYGI

Members of the order Amblypygi – Whip Spiders, German name Geisselspinnen – resemble members of the related spiders (Araneae) in certain respect but spinnerets, poison glands and male copulatory pedipalpi are absent in the Amblypygi, leg I is much longer, thinner and (pseudo)multiarticulated (antenniform, feeler-like, see fig. a above) (\*) than the other (the „true“ walking) legs, the body is distinctly depressed (similar in certain spiders), and the pedipalpi build a powerful and spiny „capturing basket“ in both sexes (fig. 1, photos) which is a bit similar in some other arachnids like certain Opiliones. The pedipalpal teeth (called „spines“ by some authors) are important taxonomical structures and are well preserved in both specimens described below.

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(\*) These legs are excellently preserved in *Kronocharon engeli* n. sp., see the photo 183.

Oldest fossils and extant SE-Asian genera: „Typical Whip spiders have evolved already in the Carboniferous“, WEYGOLDT (2000: 142), the genera *Charinus* SIMON 1892 and *Stygophrynus* KRAEPELIN 1895 are widely distributed in SE-Asia today.

Ecology: „The majority of whip spiders inhabit tropical rain forests ... the different species hide in hollow trees, in burrows of small mammals at the base of trees, under tree bark, in rock crevices, or under loose stones during the day.“ WEYGOLDT (2000: 129). The three known Amplypygi species lived in the fossil tropical Burmese (rain) forest probably on/under the bark of trees. Both species described below are partly decomposed, and thus were enclosed by the fossil resin as dead animals.

Broodcare behaviour: The female digs a subterranean „brood chamber“, carries the eggs in a sac on the opisthosoma and later on the youngs. Already known from Burmite, see ENGEL & GRIMALDI (2014).

**Kronocharon** ENGEL & GRIMALDI 2014

Type species (by monotypy): *Kronocharon prendinii* ENGEL & GRIMALDI 2014 in Mid Cretaceous Burmite.

**Selected diagnostic characters** (see ENGEL & GRIMALDI (2014: 8-9 and 13-14)): Six eyes: A pair of anterior median eyes and two lateral diads (figs. 1, 3), pulvillus (fig. 6)

well developed, cleaning hairs (fig. 8) existing, tritosternum small, two very large teeth and one short basal pedipalpal tibial tooth existing (figs. 1, 7), small animals.

**Relationships:** See ENGEL & GRIMALDI (2014: 13-14). These authors regard *Kronocharon* as the single member of the extinct clade Unidistitarsata ENGEL & GRIMALDI 2014 of the suborder Euamblypygi and the infraorder Neoamblypygi.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma). *Kronocharon* is the first Cretaceous genus of Whip spiders preserved in amber.

**Key to the species of the genus *Kronocharon*:**

1 Dorsal/prolateral pedipalpal tibial teeth 1 and 2 equal in length, only few pedipalpal femoral teeth existing (fig. 9). Prosoma distinctly wider than long (fig. 9). . . . . *prendinii*

- Pedipalpal tibial tooth 1 longer than 2, pedipalpal femoral teeth more numerous, figs. 1, 7-8. . . . . 2

2(1) Pedipalpal teeth as in figs. 1-2, femur with a large distal tooth (arrow in fig. 1), prosoma distinctly wider than long (photo183). . . . . *engeli*

- Pedipalpal teeth as in figs. 7-8, femur without a large distal tooth. Prosoma (deformed!) as wide as long. . . . . *longicalcaris*

***Kronocharon engeli* n. sp.** (figs. 1-6), photos 183-184

**Derivatio nominis:** The spider is dedicated to M. S. ENGEL who described the first Cretaceous Amblypygi in amber, *Kronocharon pendelinii* ENGEL & GRIMALDI 2014.

**Material:** Holotype, probably adult ♀, in Mid Cretaceous Burmite, F2728/BU/CJW.

**Preservation and syninclusions:** The holotype is partly decomposed, preserved in a flat and partly yellow piece of amber which is full of detritus, its chelicerae, the ventral parts of pro- and opisthosoma, as well as several leg articles are lost, both pedipalpi and some leg articles are loose, most left legs (including the breakable leg I) are complete, the right leg I is broken between patella and tibia (autotomy). – **Syninclusions:** 1 Acari (right behind the holotype), 1 Coleoptera, remains of 2 Diplopoda and decomposed remains of plants like leaves.

**Diagnosis** (♂; ♀ unknown): Pedipalpus as in figs. 1-2.

**Description** (♀):

Measurements (in mm): Body length 6.3; prosoma: Length ca. 3.0, width 3.6; opisthosoma: Length 3.5, width 2.8; leg I: Femur 5.3, patella 0.55, remaining ca. 65 articles ca. 23.0; II: Femur 3.7, patella 0.7, basitibia 2.9, distitibia 1.7; III: Femur 4.1, patella 0.7, basitibia 3.5, distitibia 2.0, basitarsus ca. 0.65, remaining tarsal articles 0.7; IV: Femur 3.6, patella 0.65, basitibia 4.1, distitibia 1.9, basitarsus 0.7, remaining tarsal articles ca. 0.7; diameter of an anterior median eye 0.15; pedipalpal tibia at least 2.0.

Colour: Body and pedipalpi light grey, legs grey to dark brown, indistinctly annulated (IV).

Prosoma (fig. 1, photo) (the ventral part is lost) distinctly wider than long, anteriorly not elongated, cuticula finely corniculate, fovea large, apparently 6 eyes in triads, anterior median eyes fairly large, on a low tubercle, basal cheliceral articles fairly small, slender, fangs long. – Pedipalpi (they are partly decomposed) as in figs. 1-2, tibia longer than femur, femur, tibia and basitarsus bear long teeth, most parts of the tarsus are lost. – Legs (figs. 4-6, photos) long, only partly preserved, an autotomy exists between patella and tibia of the right leg I, leg I very long and slender, the left one is completely preserved and situated on the body of the Whip spider, ca. 65 articles exist beyond the patella. Tibia of the walking legs biarticulate, basitibia much longer than distitibia (see above). Trichobothria (several are broken off) numerous, existing especially in the distal half of the distitibia, at least 17 on IV. Pulvillus well developed. – Opisthosoma (photo) (the ventral part is lost) oval, smooth, hairs absent or rubbed off; 9 tergites are observable.

**Relationships:** See the key.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

***Kronocharon longicalcaris* n. sp.** (figs. 7-8), photos 185-186

Etymology: The species name refers to the very long teeth (they are similar to spines) of the pedipalpal tibia, longus (lat.) = long, and calcar (lat.) = spine.

**Material**: Holotype, probably adult ♀ in Mid Cretaceous Burmite, F2729/BU/CJW.

**Preservation and syninclusions**: The holotype is partly decomposed, preserved in a larger yellow-orange piece of amber; the prosoma (especially anteriorly), the pedipalpi and some leg articles are distinctly deformed, several leg articles are cut off, the right leg II is lost beyond the patella by autotomy, both legs IV are completely preserved. – Syninclusions: 1 Acari, 1 Coleoptera, 3 Diptera: Nematocera, detritus, remains of plants including hairs, as well as probably Bacteria on the body of the holotype.

**Diagnosis** (♂; ♀ unknown): Pedipalpus as in figs. 7-8.

**Description** (♀):

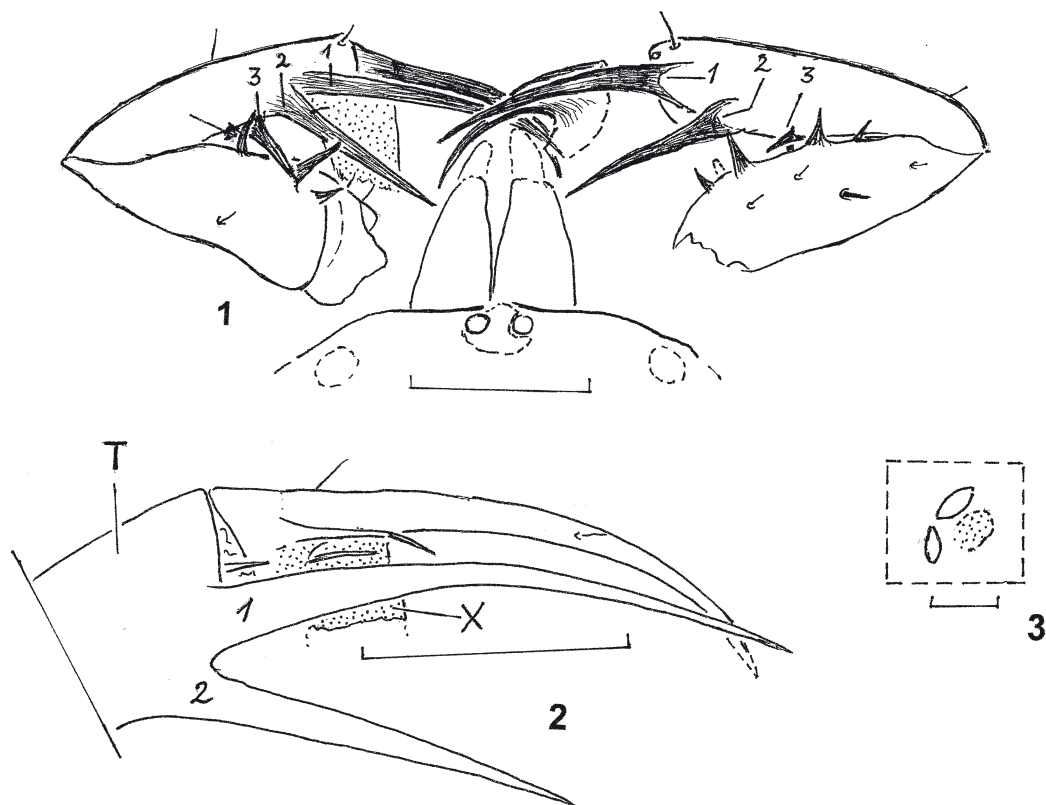
Measurements (in mm): Body length 5.8; prosoma (it is deformed!): Length and width 2.75; opisthosoma: Length 3.0, width 2.3; the incomplete leg I: Femur 5.2, patella 0.5, the basal 17 articles of the tibia occupy 6.2; II: Femur 3.4; III: Femur 3.4, patella 0.5; IV: Femur 4.0, patella 0.65, basitibia 3.6, distitibia 2.1, tarsus 1.5; pedipalpus: Femur 1.9, tibia ca. 2.0.

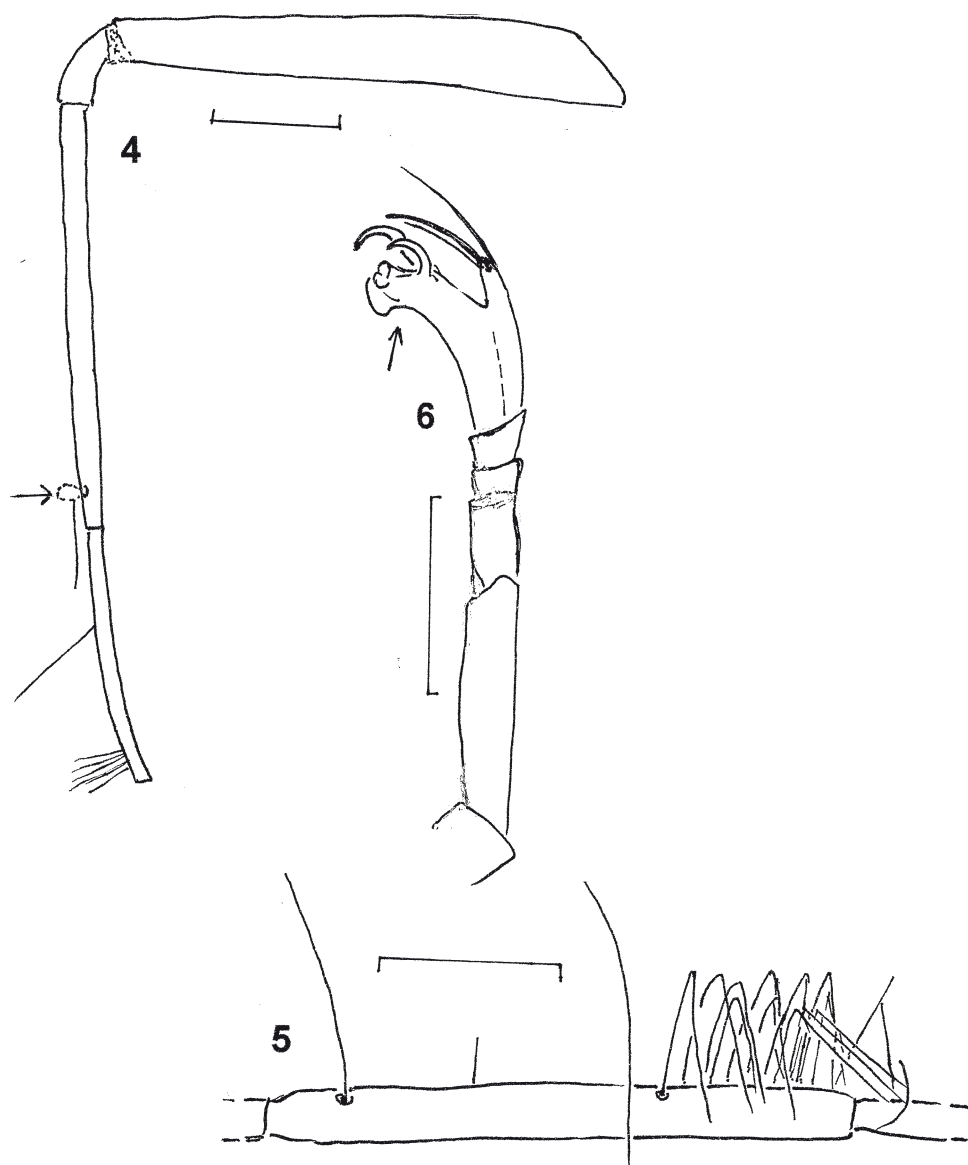
Colour: Body and pedipalpi light grey, legs medium to dark brown, not annulated.

Prosoma (photo) partly decomposed and deformed (e. g. the eyes), preserved as wide as long, almost smooth, fovea large, probably 6 eyes in diads, left diad observable at the prosomal margin, basal cheliceral articles slender; most ventral prosomal parts are decomposed, tritosternum small. – Pedipalpus (figs. 7-8, photo): Femur, tibia and basitarsus with long teeth, the left tibial tooth is almost lacking in contrast to the right tooth 3 which is well developed, cleaning hairs existing (fig. 8). – Legs (photos) only partly preserved (e. g. most parts of I, deformed by decomposition, tibiae biarticulate, trichobothria apparently numerous but most are rubbed off, pulvillus well developed. – Opisthosoma (photo) oval, ventrally decomposed.

**Relationships:** See the key.

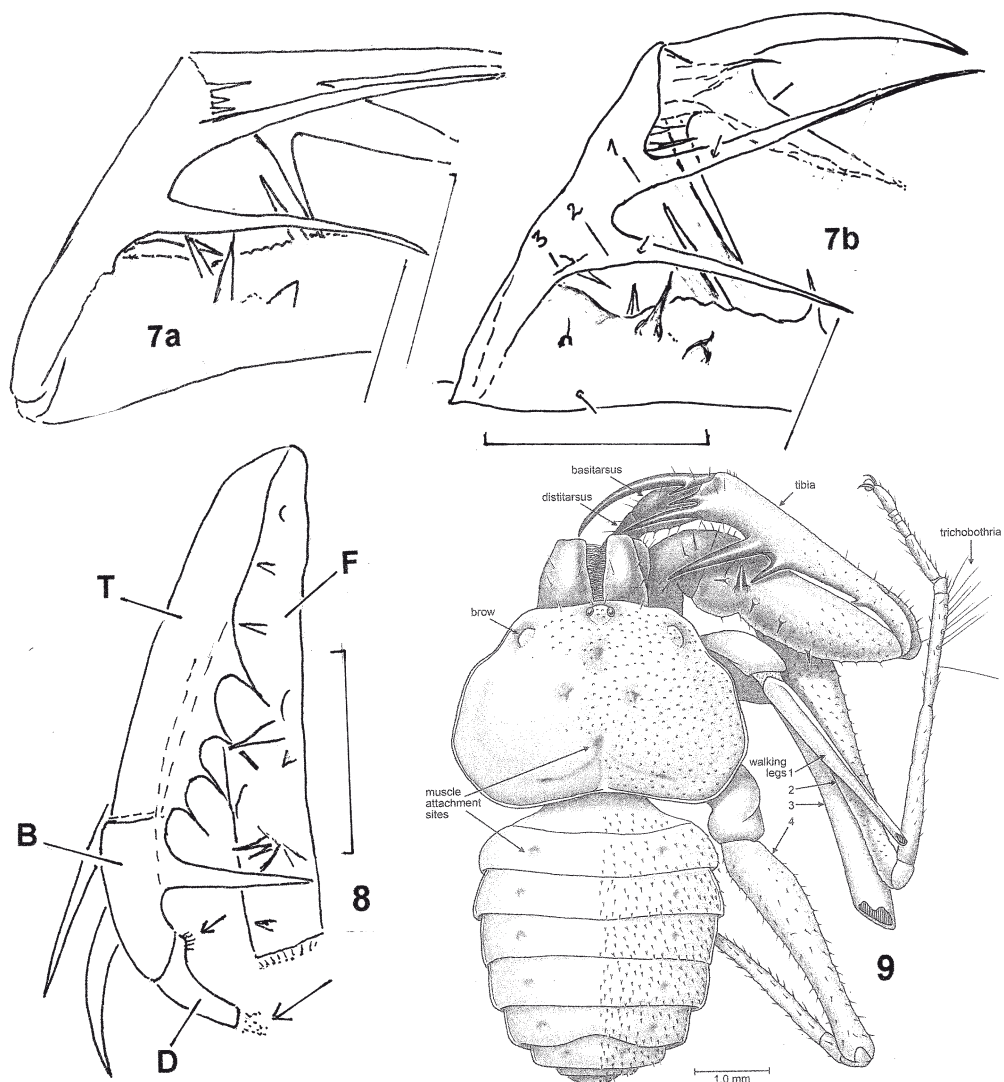
**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).





Figs. 1-6: *Kronocharon engeli* n. sp., ♀; 1) dorsal aspect of the pedipalpi and the anterior part of the prosoma. Both pedipalpal femora are loose, most parts of the tarsi are lost, remains of the left tarsus are dotted; 2) dorsal and slightly anterior aspect of the distal articles of the left pedipalpus. Most parts of the tarsus (x) are lost; 3) left diad of the lateral eyes and an emulsion (dotted); 4) prolateral aspect of the right leg III: Femur, patella and the divided tibia. The arrow points to the questionable position of a trichobothrium of the basitibia which is broken off and hidden at its base. Only few of the partly hidden trichobothria of the distitibia are drawn; 5) Prolateral aspect of the left distitibia IV. Most of the trichobothria are strongly bent in their middle and few are loose; 6) prolateral aspect of the distal articles of the right leg III. The arrow points to the pulvillus. Hairs are not drawn; 1-3 on the pedipalpus point to the tibial teeth.





figs. 7-8: *Kronocharon longicalcaris* n. sp., ♀; 7a-b) prodorsal aspects of the deformed left pedipalpus, slightly different aspects. In contrast to the tooth 3 of the right tibia (which is normally developed) this tooth 3 is only quite weakly developed; 8) deformed left pedipalpus, retrodorsal aspect (femur retroventral). The long arrow points to remains of the pedipalpal claw which is decomposed; the short arrow points to the cleaning hairs of the distitarsus;

fig. 9: *Kronocharon prendinii* ENGEL & GRIMALDI 2014, ♀, dorsal aspect. Taken from ENGEL & GRIMALDI (2014).

Scale bars (figs. 1-8): 0.2 in fig. 3, 0.5 in figs. 2 and 5-6, 1.0 in figs. 1, 4 and 7-8.  
 B = basitarsus, D = distitarsus, F = femur, T = tibia, X = remains of the basitarsus,  
 1, 2, 3 = teeth of the tibia.

### 3. Order UROPYGI s. l.

Members of the Uropygi – German name: Geisselskorpione – are dwellers of tropical rain forests. Mainly arachnids of the suborder Thelyphonida are similar to scorpions but a thick tail bearing a poisonous sting is absent, a long and thin flagellum exists (a short flagellum in the suborder Schizomida), see the figs. (b) and (c) above and the photos 176, 187.

Mainly because of the existence of the unique opisthosomal defence glands as well as of ommatoids shared by Thelyphonida (fig. b) and Schizomida (fig. c) I regard these taxa as suborders of a single order, the Uropygi; but see DUNLOP & PENNEY (2012). Members of this tropically (mainly) to subtropically distributed order are still unknown in Eocene Baltic amber; they are reported here to the Mid Cretaceous Burmite for the first time.

#### Diagnostic characters of the Uropygi s. l. (external characters and behaviour):

- Existence of opisthosomal defense glands,
- „aggressive posturing“ (raising up strongly the opisthosoma) and spraying the defensory secrete);
- existence of „ommatoids“ on the 12. opisthosomal segment (fig. 5); see HEURTAULT (1984), ROWLAND & COOKE (1973).
- raptorial pedipalpi (used for prey capturing), large, subchelate, with a movable „fang“ (figs. 7-8, photos 176, 187);
- leg I strongly elongated (antenniform), with numerous tarsal pseudoarticles (figs. b, c above) and fig. 2, and no tarsal claws;
- metasoma bearing a flagellum (figs. b, c, photo);
- broodcare behaviour: The female digs a subterraneous „brood chamber“, carries the eggs in a sac on the opisthosoma and later the youngs.

#### Differences between the suborders:

Size and shape: Body and pedipalpi of the Schizomida are smaller than in the Thelyphonida – 3 to 12 mm resp. 25 to 80 mm) – and usually more slender, especially their pedipalpi;

prosoma (peltidium) entire in the Thelyphonida, tripartite in the Schizomida;

eyes: 8 or 12 (in three groups) in the Thelyphonida, no or a single median pair in the Schizomida;

flagellum shorter and frequently enlarged/bulbous distally in the male sex of the Schizomida;

pedipalpi subchelate and articulate more from side to side in the Thelyphonida (fig. 7) but articulate up and down in the Schizomida.

## **Suborder THELYPHONIDA**

**Main diagnostic characters:** See above.

**Material in Burmite:** Besides the taxon described below I know of following Thelyphonida indet. specimens:

- A distal part of a flagellum, 6.5 mm long, about 40 articles, together with a male Schizomida indet. in the same piece of amber, F2780/BU/CJW;
- I saw the photo of an almost 1 cm long specimen, offered at the Scott Market in Rangun, recently sold to China;
- S. ELLENBERGER told me of a large specimen, probably ca. 4 cm long, seen in Myanmar in 2014, which probably has been also sold to China.

### **Burmathelyphonia n. gen.**

**Etymology:** The genus name combines the name of the country (Burma = Myanmar) – the origin of the type material – with the main part of the name of the suborder Thelyphonida.

The gender of the name is feminine.

**Type species** (by monotypy): *Burmathelyphonia prima* n. sp.

**Diagnostic characters** (based on an immature specimen): Prosoma (fig. 1, photo): Probably 8 eyes, prosomal keel and suture of the tergites absent (photos), anterior sternum very large (wide and long), anteriorly-medially not protruding but straight, weakly or probably even undivided (!) in the immature holotype; tarsus of the antenniform leg I (fig. 2) not modified; pedipalpus (figs. 6-8): Trochanter relatively large, femur retrolaterally with few blunt teeth, patellar apophysis large and pointed.

**Remark:** According to its well sclerotized body and legs – as well as its well developed pedipalpi, leg I and flagellum – the present specimen is an older juvenile, and I estimate the body size of adult specimens to be not more than 2 to 4 cm. The body size of extant Thelyphonida is 2.5 – 8 cm.

**Relationships:** The articles of the pedipalpus are similar to other members of the family Thelyphonidae but the shape of the sternum is different: It is prolonged anteriorly-medially to a „triangular point“ and divided (tripartite) in other taxa. Usually the anterior sternum is narrowish, even in older immatures. These characters justify in my opinion the erection of a new genus.

**Distribution:** Mid Cretaceous amber forest of Myanmar (Burma).

***Burmathelyphonia prima* n. gen. n. sp.** (figs. 1-8) photo 187

**Etymology:** The name refers to the first report of a member of the Thelyphonida in Burmese amber, from primum (lat.) = first.

**Material:** Holotype, immature specimen in Mid Cretaceous Burmese amber from N-Myanmar (Burma), Kachin State, locality unknown, F2782/ BU/CJW.

**Preservation and syninclusions** (see the photos): The arachnid is very well preserved in a clear yellow piece of amber which is 11 mm long. Parts of the left leg I, of the right legs I and IV, the left patella IV as well as of the flagellum are cut off. A fissure in the amber runs almost transverse through its anterior part. The right leg I is bent downwards, its distal part is hidden between the pedipalps and the mouth parts. – Few remains of a Diptera: Nematocera are preserved at the margin of the piece of amber behind the arachnid. A tiny Thysanoptera and numerous tiny particles of detritus are also preserved.

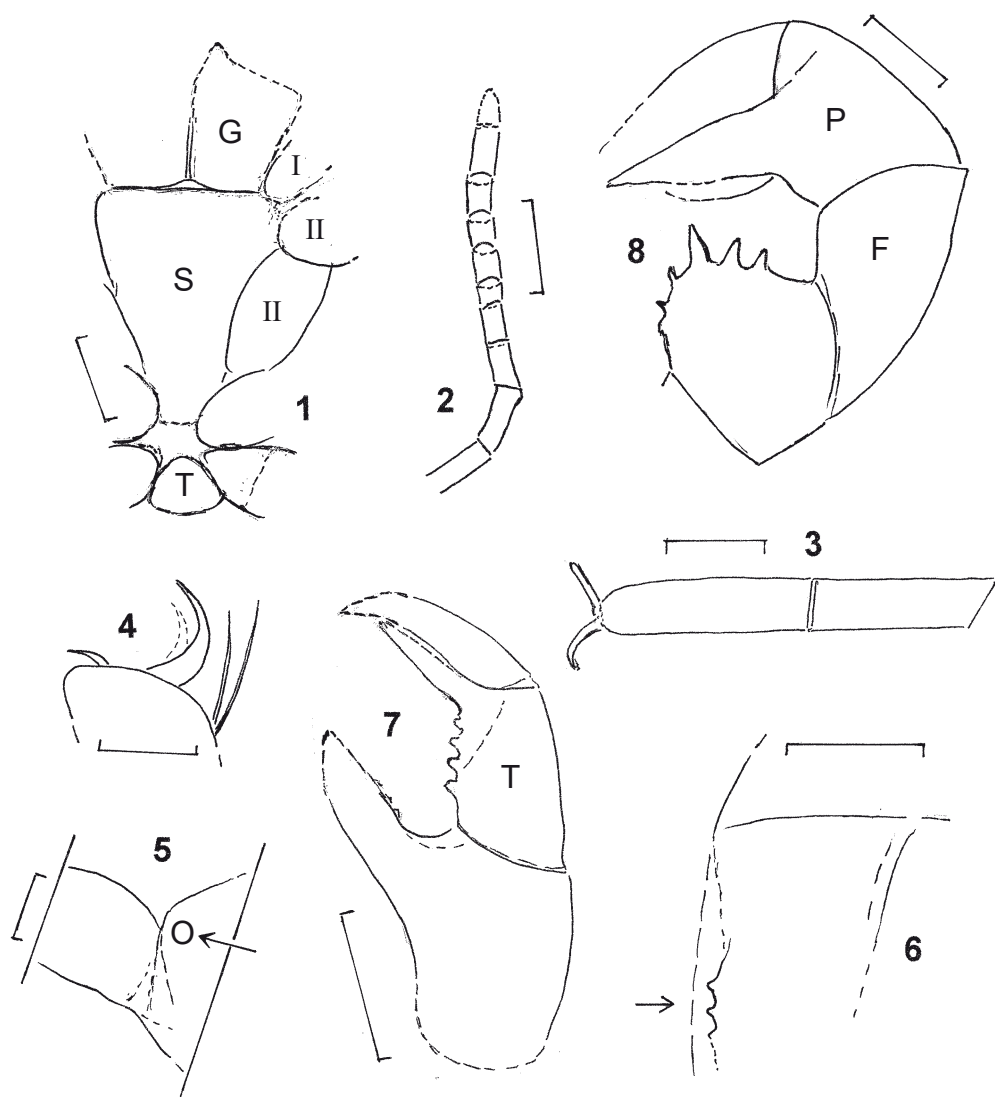
**Diagnosis:** See above.

**Description** (immature):

Measurements (in mm): Body length 6.0; prosoma: Length 2.6, width 1.7; anterior sternum: Length and width almost 1.0; opisthosoma: Length without metasome 3.1, width 1.7; leg I at least 9.0, leg II at least 4.5 (estimations); femur I 1.9, femur III ca. 1.5. Colour medium brown.

Prosoma (fig. 1, photo): 1.53 times longer than wide, cuticula fairly rugose, hairs absent or rubbed off, keel absent, anterior margin convex and not protruding, probably 8 eyes, anterior/median pair (partly hidden) probably large and closely together, on low tubercles, lateral eyes existing but badly observable, probably 3 pairs, chelicerae (partly hidden) small, gnathocoxae large, protruding proapically, sternum wide and long, apparently weakly or even undivided (!), anterior margin straight. – Legs (figs. 2-4, photo) bristleless, hairs short and indistinct, order I/IV/III/II, coxae I and II widely, coxae III and IV distinctly spaced, leg I antenniform, distinctly longer than the body, tarsi with probably 10 pseudosegments, not modified. Tarsi II-IV biarticulate; 3 smooth claws, unpaired claw small. – Opisthosoma (figs. 5, photos) 1.82 times longer than wide, longitudinally undivided; 8 sternites besides the anterior triangular one, metasoma tripartite, the questionable large right „ommatoïd“ is observable; only the basal 8 articles of the flagellum are preserved. – Pedipalpus: See above. The trochanter bears 6 teeth.

**Relationships and distribution:** See above.



Figs. 1-8: *Burmathelyphonia prima* n. gen. n. sp., immature; 1) ventral aspect of the prosoma: Anterior sternum (S), left gnathocoxa, basal articles of the left legs (I, II = legs I and II) and the first – triangular – opisthosomal sternite (T); 2) prolateral aspect of the rarsal articles of the right – tactile – leg I which is partly hidden apically; 3) dorsal aspect of the left tarsus III; 4) retrolateral aspect of the tip of the left leg II; dorsal-right aspect of flagellum and the distal part of the metasoma with the questionable right „ommatoid“ (arrow); 5) dorsal-right aspect of the flagellum and the distal part of the metasoma with the questionable right „ommatoid“ (arrow); 6) dorsal aspect of the left pedipalpal femur (parts are hidden). The arrow points to the retromarginal teeth; 7) prolateral aspect of the right pedipalpus (parts are hidden). T = tibia; 8) prodorsal aspect of the right pedipalpus (the distal part is hidden). F = femur, P = patella. – Scale bars 0.1 mm in figs. 4 and 5, 0.2 in fig. 3, 0.5 in the remaining figs.

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**DESCRIPTIONS OF THE NEW SUBGENERA *PARVIDIPOENA* AND *SIMONOLA* OF THE GENUS *LASAEOLA* SIMON 1881 S. L. WHICH INCLUDE TWO TINY EUROPEAN SPECIES (ARANEAE: THERIDIIDAE)**

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**Abstract:** Two new subgenera of *Lasaeola* SIMON 1881 s. l. are described from European Araneae: Theridiidae (Hadrotarsinae): *Simonola* is erected for *Theridium coracinum* C. L. KOCH 1837 (= *Dipoena coracina* which is transferred to *Lasaeola* (n. comb.) (a junior synonym is *Lasaeola nigrina* SIMON 1881), and *Parvidipoena* for *armona* n. sp. from Portugal. Remarks on European subgenera of *Lasaeola* – which may be elevated to a generic rank in the future – and on tiny European species of *Lasaeola* are added.

**Key words:** Hadrotarsinae, Portugal, spiders, synonymy, taxonomy.

**Acknowledgements:** I thank J. GRUBER (Wien) for hints to the collection of C. L. KOCH, as well as CHRISTOPH HÖRWEG, (Wien), MYKOLA KOVBLYUK (Ukraine), CHRISTINE ROLLARD (Paris) and PETER SCHWENDINGER (Genf) for the loan of material.

**Material** (see also below): CJW = coll. of J. WUNDERLICH, Lab. of Arachnology Hirschberg.

*Lasaeola* in a wide sense is the most diverse genus of the theridiid subfamily Hadrotarsinae. The arrangement in subgenera is still discussed; they are regarded as genera of their own by certain authors like YOSHIDA, but as species-groups by others like LEVI. A worldwide revision of the genera of the Hadrotarsinae is needed, in which the chaetotaxy and the trichobothrotaxy has to be included as well as REM studies of the bulbus structures of tiny species, and the behaviour like the oecobiid leg position or the eggsac-carrying by females in certain taxa.

Most of the species of *Lasaeola* s. l. were previously listed in the genus *Dipoena* THORELL 1869 but in Europe only *melanogaster* (C. L. KOCH 1837) is a true *Dipoena*, see WUNDERLICH (2008: 282). Authors like BÖSENBERG (1902), CHYZER & KULCZYSKI (1894) and SIMON (1881) already regarded certain European species like *coracina* as members of *Lasaeola*.

To my knowledge the two species treated in this paper do not fit in any of the described subgenera or species-groups; therefore I create two new subgenera.

Tiny specimens of *Lasaeola* like *armona* n. sp. and *minutissima* WUNDERLICH 2011 – body length of the males ca. 1.1 mm – are easily overlooked in the field or may be mistaken as juveniles. Therefore I suppose that further undescribed species exist in Southern Europe, probably living on low plants in dunes like the two species in question.

(1) ***Simonola* n. subgen.** of the genus *Lasaeola* s. l.

**Derivatio nominis und etymology:** The name is composed by the surname of the famous arachnologist EUGENE SIMON, who named and described the type species of the new subgenus, and the last three letters of the genus name *Lasaeola*.

The gender of the name is feminine.

**Type species** (by monotypy): *Theridium coracinum* C. L. KOCH 1837.

**Diagnostic characters:** Prosoma (fig. 1) even in the male not distinctly raised (no sexual dimorphism), legs bristleless (fig. 2); ♂-pedipalpus (figs. 3-6): Tip of the cymbium with a bristle-shaped hair (arrow in the figs.), tegulum divided, embolus and conductor short. Vulva (e. g. as in fig. 7 (\*)) with variable introductory ducts which may extend far of the median pair of the receptacula.

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(\*) Compared with vulvae from Portugal and the Ukraine this fig. appears untypical to me: In these females the posterior pair of receptacula is distinctly smaller and thin-walled (weakly scler-

otized), and the position of the ducts of the vulva extend less anteriorly but more laterally of the median pair of receptacula.

Further important characters: Colour of the body completely black, posterior eye row straight, position of the metatarsal I-II trichobothrium in 0.3-0.4, complicated distal structures of the bulbus, see MILLER (1971: t. 31, fig. 16), conductor not fused to the tegulum, introducing opening of the vulva apparently unpaired, small and indistinct.

**Relationships:** In *Yaginumena* YOSHIDA 2002, see also YOSHIDA 2003 from East Asia the legs are bristleless, too, but the prosoma is strongly raised, the conductor is fused to the tegulum and the introductory ducts of the vulva are shorter. To my knowledge *Simonola* is the only west-palaearctic taxon of *Lasaeola* s. l. except *L.* (subgenus?) *inornata* (O. PICKARD-CAMBRIDGE 1861) (see below) in which leg bristles are absent (the leg bristles of *L. minutissima* WUNDERLICH 2011 are unknown). In *inornata* an apical bristle-shaped cymbial hair is absent and the tegulum is undivided.

**Distribution:** Europe.

***Lasaeola (Simonola) coracina* (C. L. KOCH 1837) (Abb. 1-7) (n. comb.)**

1837 *Theridium coracinum* C. L. KOCH, Übersicht des Arachnidensystems, 1: 8 (ad. or subad. ♀).

1881 *Lasaeola nigrina* SIMON, Les Arachn. de France, 5: 144.

1914 *Dipoena coracina* SIMON, -- Les Arachn. de France, 6 (1): 277 und 301.

To my knowledge in this paper *nigrina* is listed as a junior synonym of „*Theridium coracinum* C. KOCH ..., 1841“ (sic!) for the first time.

Remark to further references: See SIMON (1914: 301) and PLATNICK (2012).

Under *Dipoena coracina* (C. L. KOCH) the species is treated by HEIMER & NENTWIG (1991: 286), LOCKET & MILLIDGE (1953: 48-49), MILLER (1947: 36 und 1971: 184), ROBERTS (1985: 176 und 1998: 284) und WIEHLE (1937: 185-186: Subad.). According to the figs. of the epigyne (mainly regarding the distinctly separated introductory openings) I consider the conspecificity of the following specimens as unsure: BÖSENBERG (1902: 123, t. 11, fig. 156 B) (apparently the material has been destroyed during the World War Two) and CHYZER & KULCZYNSKI (1894: 26, t. 1, fig. 22) under *Lasaeola nigrina*.

**Material studied** (CJW = coll. JOERG WUNDERLICH; SMF = Senckenberg Museum Frankfurt a. M.). If not noted otherwise the spiders are kept under *Dipoena coracina*: (a) Germany: Kaiserstuhl, Oberbergen, 2♂, A. ZILCHE leg. in IV 1960, SMF 28462; Hessen, Vogelsberg, 1♂1♀, HEIDT leg. VIII 1983, SMF 32223 und 32224; 1 subad. ♂, 1 subad. ♀, Germany, without locality, coll. H. WIEHLE, SMF 20824. – (b) Portugal: Near Caldas da Rainha N Lissabon, beaten from a bush, 1♂1♀ JW leg. at the end of VII 2012 (under *Lasaeola coracina*), R159/AR/CJW. – (c) France (Mus. Nat. Hist. Nat.

Paris; spiders not designed as type material): „Banyuls“, 1 subad. ♂ (under *Lasaeola nigrina*), AR 10895; „La Nouvelle“, 4 subad. ♀ (under *Lasaeola nigrina*), AR 10897; 1♀ „Mur de Bretagne“, AR 3394; 1♀, „Nrb. – C. L. K.“ (sic!), AR 3455. Note: The meaning of „Nrb. – C. L. Koch“ of the label in this tube is unclear. If it is a ♀ collected by C. L. KOCH near Nürnberg it is apparently not the missing typus-specimen of *coracina*, because the origin of this female is the area of Regensburg. – (d) former Czechoslovakia, 5 tubes with ♂♀ and juv. from the coll. F. MILLER, see KURKA (2003: 134). – (e) Ukraine/Russia, Krim, Opuk Natur Reservation, 1♂1♀ V. A. GNELITZA leg. 20. IV 2005, ex Coll. KOVBLYUK, SMF. (e) Switzerland, Genf and Wadland, 2♀, Mus. d'hist. nat. Genf.

Type material neither in the Naturhistor. Mus. Wien (3. Zool. Abt.) (GRUBER and HÖR- WEG in litt. in X. 2012) (see also below), nor in the Mus. Nat. Hist. London (J. BEC- CALONI) material of *coracina* has been found. The type locality has been published as near Regensburg.

Further material: 2♀ in a single tube, collected in Germany, „*Dipoena coracina* (C. L. KOCH), Fränk. Jura, det. L. Koch, A. D. 1884..., Inv. No. 589“, Naturhistor. Mus. Wien, 3. Zoolog. Abt. – Note: The tube contains females of different species apparently of the genus *Lasaeola*. The larger specimen is an ad. ♀ of *L. tristis* (HAHN 1831), the smaller ♀ is an incomplete subadult spider without legs, the body length is 2.8 mm, the prosomal length is 0.9 mm.

The name of the species treated here – under *Lasaeola nigrina* – has been reported from Germany already more than hundred years ago by BÖSENBERG (1902) but I regard its conspecificity as unsure. Further reports from Germany and Europe (under *Dipoena coracina* (C. L. KOCH 1837): See the World Spider Catalog by PLATNICK.

**Diagnostic characters:** See the diagnosis of *Simonola* n. gen.

Further characters besides characters of the subfamily Hadrotarsinae: Opisthosoma rounded apically, slightly longer than the spinnerets, colulus fairly large, bearing a pair of bristles, claw of the ♀-pedipalpus not studied, metatarsi I-III with a trichobothrium, its position in 0.3-0.4, length of metatarsus I 1.3-1.5 times tarsus I, internal paracymbium (fig. 6) hook-shaped.

Measurements (in mm): Body length ♂ usually (and based on material studied by me) 1.5-1.8, according to Locket & Millidge 1.75-2.0, ♀ usually (and based on material studied by me) 1.9-2.2 (so an egg-bearing female from the Ukraine), according to Locket & Millidge larger: 2.0-2.5; prosomal length 0.7-0.8; the body length of the type specimen of *coracina* is 2.7 mm; tibia I 0.45 (♀) – 0.55 (♂), tibia IV 0.55 (♀) – 0.6 (♂).

Colour: Body black, legs (e. g. as in fig. 2 but quite variable!) frequently annulated, tarsi always yellow or light grey, so usually also the patellae basally and trochantera III-IV, femora I-II black but occasionally light basally and apically, femora III-IV mainly black, frequently yellow in the basal half, tibiae mainly black, at least III-IV may be yellow in the basal half, metatarsi usually yellow, I-II occasionally more or less darkened. According to KOVBLYUK (in litt.) the legs of Ukrainian spiders are mainly dark, the tarsi lighter but not yellow. The variability of the vulva has to be studied more closely in the future. An unpaired introductory opening exists probably medially behind the anterior pair of the receptacula, see fig. 7. The structures regarded as introductory openings regarded by certain authors like LOCKET & MILLIDGE and ROBERTS are more likely internal sclerotized structures of the vulva.

**Relationships:** See the new subgenus.

**Ecology and phenology:** The spiders live on low plants in sunny localities and are adult from early summer to autumn.

**Distribution:** Europe from Portugal to the Ukraine, rare or absent in the north. – Note: Because of erroneous determinations the material in museums and private collections has to be checked.

**Synonymy:** SIMON (1914: 301) regarded *Lasaeola nigrina* SIMON 1881 as younger synonym of *Dipoena coracina* (= *Theridium coracinum* C. L. KOCH 1837 and sensu 1841). The original description of *coracinum* is based on an adult (but probably sub-adult) female. Type material is apparently lost, see above. The body length of the holotype – see C. L. KOCH (1841: 84) – is 2.7 mm; it is larger than of all females known to me, see above. Based on these findings I will regard *Theridium coracinum* C. L. KOCH 1837 with some hesitation in the sense of nomenclatory stability as older synonym of *Lasaeola nigrina* SIMON 1881, following SIMON (1914). The original assignment of *coracina* (under *nigrina*) to *Lasaeola* by SIMON (1881) seems to be correct (**n. comb.** for *coracina*).

(2) ***Parvidipoena* n. subgen.** of the genus *Lasaeola* s. l.

**Etymology:** The name is composed of *parvus* (lat) = small, according to the low body length of the type species, and the name of the related genus *Dipoena*.

The gender of the name is feminine.

**Type species:** *Lasaeola* (*Parvidipoena*) *armona* n. sp.

Further species: I do not want to exclude that *Lasaeola minutissima* WUNDERLICH 2011 (see below) may be congeneric.

**Diagnostic characters** (♂; ♀ unknown): Body length 1.15 mm, prosoma with a wide black median field and without dorsal furrows, legs uniformly yellow, tibia III (fig. 9) with a long dorsal bristle in contrast to the bristleless remaining tibiae (!), position of the metatarsal trichobothrium (fig. 8) in 0.9, pedipalpus (fig. 10) with a long sperm duct and straight embolus and conductor.

**Relationships:** A key to most of the extant and fossil palaeartic subgenera of *Lasaeola* was given by WUNDERLICH (2008:285-286); a revision is needed, and at least some of the subgenera may be elevated to the genus rank in the future. Herewith I add to this key:

- (1) To *Trigonobothrys*: Tibial bristles absent.
- (2) To the last line: Tibial bristles existing or absent.
- (3) To 4(3) (*Yaginumena*): Prosoma very high.
- (4) To 4(3) after *Yaginumena*:

- Tibial bristles also absent, prosoma not strongly raised (fig. 1). Position of the metatarsal trichobothrium in 0.3-0.4. Tip of the cymbium with a bristle-shaped hair (figs. 3-4), tegulum divided (fig. 3). Extant, Europe, *coracina* (= *nigra*). . . . . *Simonola* n. gen.

- Tibial bristles also absent, prosoma and metatarsal trichobothrium similar, apical cymbial hair absent, tegulum undivided. Extant, Europe, *inornata*. (= *Theridion i.*, confused with *Phycosoma*) . . . . . *subgenus* *indet.*

- Only tibia III bears a dorsal bristle, prosoma not strongly raised, position of the metatarsal trichobothrium in 0.9 (fig. 9), apical cymbial hair absent, tegulum undivided (fig. 10), body length (♂) in *armona* ca. 1.1-1.2 mm (in the two taxa above at least 1.5 mm). Extant, Portugal. . . . . *Parvidipoena* n. gen.

Probably *L. inornata* (O. PICKARD-CAMABRIDGE 1861) is related (subgenus? See above); in *inornata* leg bristles are absent and the position of the metatarsal trichobothrium is in 0.3-0.4.

**Distribution:** Portugal.

### ***Lasaeola (Parvidipoena) armona* n. sp. (figs. 8-10)**

**Etymology:** The spider is named after the S-Portuguese island Armona (= Isla de Fuzeta) S Fuzeta, E-Algarve.

**Material:** S-Portugal, E-Algarve, E Faro, island Armona (= Isla de Fuzeta), on low vegetation in the dunes near the southern beach, holotype ♂ JW leg. 25. VI. 2014, R166/AR/CJW.

**Diagnosis:** See the new subgenus.

### **Description (♂):**

Measurements (in mm): Body length 1.15, prosoma: Length 0.6, width 0.52, height above coxae 0.35; opisthosoma: Length 0.9, width 0.58, height 0.58; leg I: Femur 0.48, patella 0.2, tibia 0.27, metatarsus 0.29, tarsus 0.22; tibia II 0.25; leg III: Tibia 0.2, metatarsus 0.2, tarsus 0.21, tibia IV 0.4.

Colour: Prosoma mainly yellow, medially in the anterior two thirds with a wide black field, margin black, sternum mainly yellowish, legs yellow, opisthosoma black.

Prosoma 1.15 times longer than wide, without dorsal furrows as in *L. minutissima* WUNDERLICH 2011, profile fairly convex, thoracic fissure and posterior stridulatory files

absent, eyes large, anterior medians largest, posterior row slightly recurved, clypeus strongly concave, basal cheliceral articles small, teeth on the margins absent, labium distinctly wider than long, with a seam to the sternum, gnathocoxae strongly converging, sternum convex, coxae IV spaced by more than their diameter. – Legs (figs. 8-9) only fairly long, order IV/I/II/III, IV distinctly longest, a long tibial bristle (on both legs) exists only on III, in the basal half, position of the metatarsal trichobothria in 0.9, bothria large absent on IV. Tarsal claws small, unpaired claw thin and strongly bent. Comb of hairs under tarsi IV absent. – Opisthosoma oval, not flattened, posteriorly fairly pointed (a bit similar to *Euryopis*; so in all specimens?), hairs of medium length, epigaster not bulging, 6 spinnerets in an apical position.

**Relationships:** *L. minutissima* WUNDERLICH 2011 (♂) from the same locality in S-Portugal is also tiny, the prosoma is higher and the clypeus is more protruding ventrally, its colour is grey, medially fairly darkened, the position of the metatarsal I-II trichobothrium is in 0.45, the tibial bristles are unknown (absent?), and the structures of the pedipalpus are different.

A key to tiny European members of *Lasaeola* was given by WUNDERLICH (2011: 254-255). Herewith I add two species:

(1) At the beginning of the key (before no. 1):

Position of the metatarsal trichobothrium in 0.3-0.4, tibial bristles absent, tip of the cymbium with a bristle-shaped hair, tegulum divided (figs. 3-4), body length 1.5 (♂) – 2.2 mm (♀). Europe. . . . . *coracina* (= *nigra*)  
In the following species the combination of characters is different.

(2) No. 1 after *minutissima*:

- Tibia III bears a long dorsal bristle, the remaining tibiae are bristleless, position of the metatarsal trichobothrium in 0.9, body length (♂) 1.15 mm. S-Portugal. . . . . *armona*

**Distribution:** S-Portugal.

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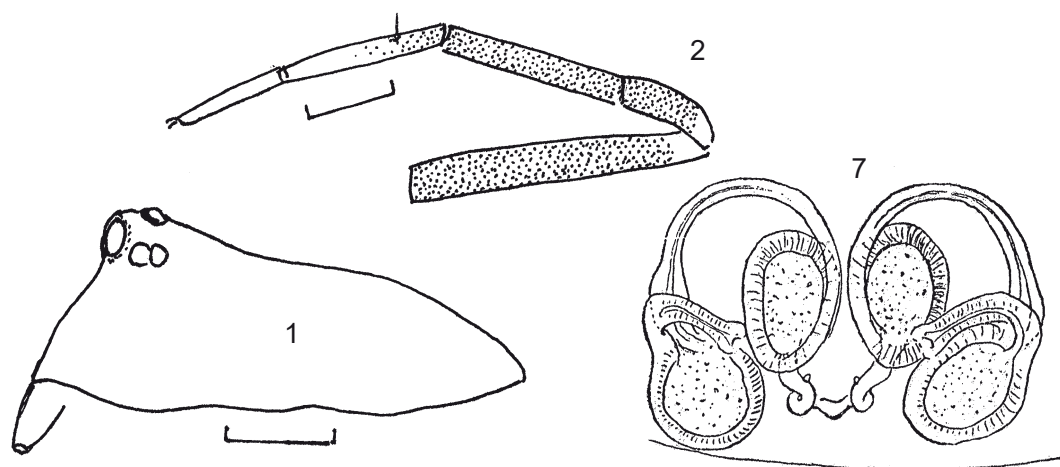
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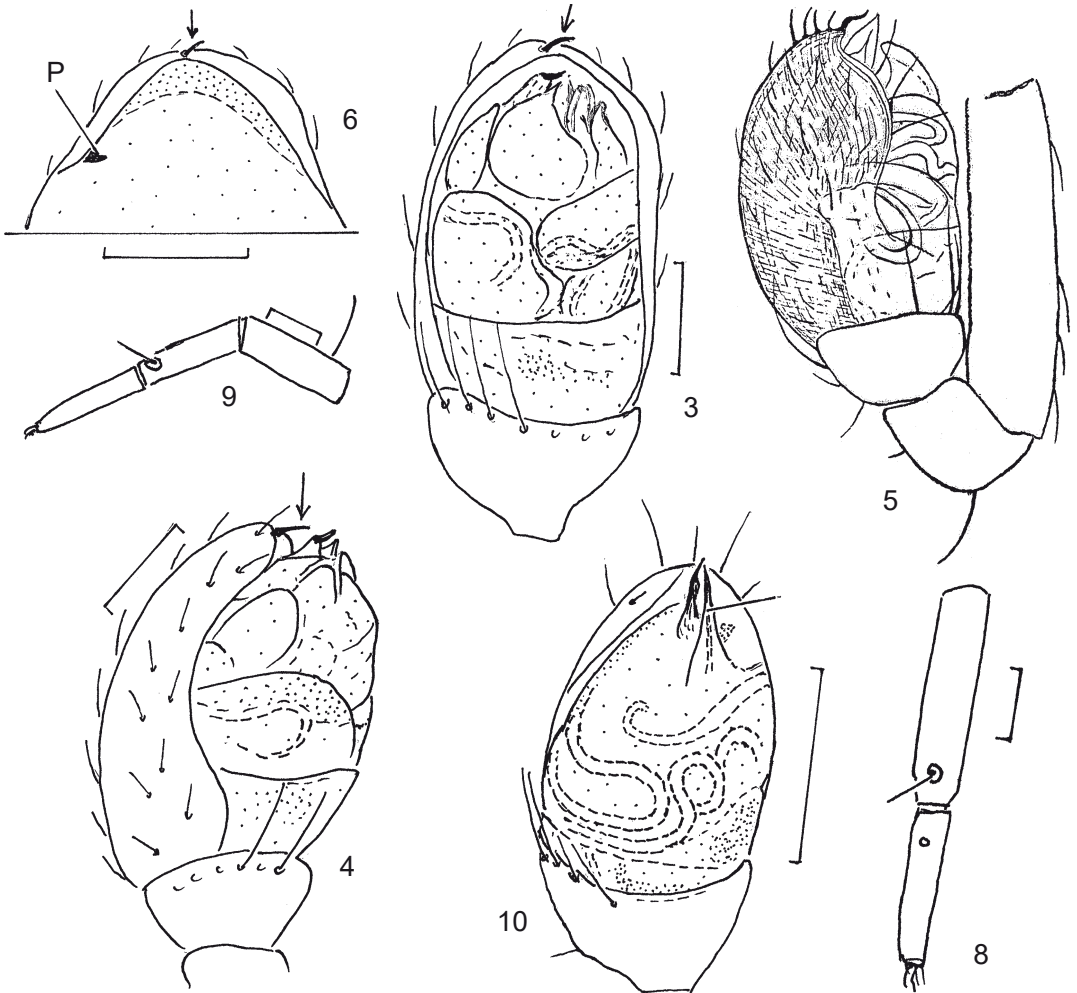
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Figs. 1-7: *Lasaeola (Simonola) coracina* (C. L. KOCH 1837); 1) lateral aspect of the ♂♀-prosoma; 2) lateral aspect of the left ♂♀-leg I. Note: In some specimens the metatarsus is completely darkened. Note the position of the metatarsal trichobothrium in the basal half and the absence of tibial bristles; 3-4) ventral and retrolateral aspect of the right ♂-pedipalpus. The arrow points to the bristle-shaped hair at the tip of the cymbium; 5) retrolateral aspect of the right ♂-pedipalpus; taken from MILLER (1947); 6) distal part of the right cymbium after removing the bulb, ventral aspect, with the paracymbium (P); 7) ♀ from the former Czechoslovakia (probably Mohelno), vulva; taken from MILLER (1947: T. 4, fig. 3, under *Dipoena coracina*). Note: The figs of the vulva are – probably depending on its position – quite variable, see above. – Scale bars: 0.2 mm in figs. 1-2, 0.1 mm in figs. 3-4 and 6, no scale bars in the figs. 5 and 7.

Figs. 8-10: *Lasaeola (Parvidipoena) armona* n. sp., ♂; 8) dorsal aspect of the right tarsus and metatarsus I. Note the large bothrium of the metatarsal trichobothrium. Hairs are not drawn; 9) prolateral aspect of the distal articles of the right leg III. Note the tibial bristle which exists only on tibia III; 10) retroventral aspect of the right pedipalpus. E = embolus. Scale bars 0.1 mm.

**DESCRIPTIONS OF TWO GNAPHOSIDAE (ARANEAE) FROM PORTUGAL: *PHAEOCEDUS MIKHA* LEVY 2009 NEW TO EUROPE, AND *GNAPHOSA MONTESERRA* N. SP.**

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**Abstract:** *Gnaphosa monteserra* n. sp. and *Phaeocedus mikha* LEVY 2009 (new to Europe) (Araneae: Gnaphosidae) are described from Southern Portugal.

**Material:** The spiders are still kept in the collection of the author (CJW) and will probably be given to the Senckenberg Museum in Frankfurt a. M. in the future.

The spider fauna of Southern Portugal is fairly well known. During the last ten years I collected spiders on the Eastern Algarve, mainly near Fuzeta. From a large material (CJW) I described two new species of *Ariadna* (Segestriidae), see WUNDERLICH (2011: 175-198); a new species of *Lasaeola* (Theridiidae) is described in this volume. In this paper I describe two further species from the Algarve, both of the family Gnaphosidae.

Gnaphosidae are frequent in Portugal (15 genera) but members of *Gnaphosa* LATREILLE 1804 are quite rare on the Iberian Peninsula, and this genus is even reported for the first time from Portugal. *Phaeocedus mikha* LEVY 2009 is the second known European species of this genus which is poor in species.

(1) *Gnaphosa monteserra* n. sp. (figs. 1-3)

Derivatio nominis: The species name refers to a hill (Monte Serra) and our holiday home (Monteserra) near the locus typicus of the new species, located north of Fuzeta.

**Material**: Southern Portugal, East Algarve, E of Faro, S of Fuzeta, Ilha de Fuzeta (Armona), on the ground within dunes, holotype ♂ JW leg. in VI 2014, R167/AR/CJW.

Note: Both legs II of the spider are lost.

**Diagnosis** (♂; ♀ unknown): Posterior eye row only slightly recurved (fig. 1), opisthosoma with a small scutum (fig. 1); pedipalpus (figs. 2-3): Tibial apophysis short and slightly bent, cymbium and bulbus slender, embolus very long, slender and winding.

**Description** (♂):

Measurements (in mm): Body length 8.6, prosoma: Length 4.0, width 3.3; opisthosoma: Length 4.6, width 2.7; leg I: Femur 3.1, patella 1.9, tibia 3.0, metatarsus 2.4, tarsus 1.6; tibia III 1.6, tibia IV 2.3, metatarsus IV 3.3.

Colour: Prosoma medium to dark brown, margin black, with a pair of black patches (fig. 1), chelicerae, gnathocoxae and sternum dark brown but gnathocoxae apical-medially white, legs mainly light brown but beyond the femur fairly darkened, opisthosoma grey brown, dorsally with indistinct markings, scutum and sigillae red brown.

Prosoma (fig. 1): Thoracal fissure very long, eyes small, posterior row only slightly recurved, serrated cheliceral keel well developed, anterior margin of the fang furrow with a large medial tooth, fangs fairly stout, labium free, longer than wide, gnathocoxae large and strongly converging, sternum slightly longer than wide, posteriorly not elongated. – Legs only fairly long, order (II is lost) I/IV/III, tarsus I scopulate, metatarsus I with a scopula in the distal half which is more distinct distally and with a ventral-apical brush of hairs. Bristles: Only few on I: Femur with 2 dorsals and a single prodistal one, patella none, tibia with a single ventral-apical bristle, metatarsus a single probasally (broken off near its base), tibia IV bears ca. 10 bristles. – Opisthosoma (fig. 1) dorsally with numerous short and few long hairs as well as a small dorsal-basal scutum and three pairs of sigillae; feathery hairs absent. – Pedipalpus (figs. 2-3): See the diagnosis; femur slender, patella and tibia fairly stout, cymbium with long bristles.

**Relationships**: In contrast to most species of *Gnaphosa* the posterior eye row is only slightly recurved. A long and slender cymbium, bulbus and embolus exist also in *G. modestior* KULCZYNSKI 1894 in which the embolus is almost straight, the posterior eye row is distinctly recurved, most leg articles are darkened, and metatarsus I bears a ventral pair of bristles near the middle.

**Distribution**: South Portugal, E Faro.

(2) *Phaeocedus mikha* LEVY 2009 (figs. 4-6)

**Material:** Southern Portugal, East Algarve, E of Faro, S of Fuzeta, Ilha de Fuzeta (Armona), on the ground within dunes, holotype ♂ JW leg. in VI 2014, R167/AR/CJW.

In the present specimen two pairs of large white dorsal opisthosomal patches exist (fig. 4). The retromarginal cheliceral lobe (not a true tooth) (fig. 5) is typical for the genus *Phaeocedus* SIMON 1893 and has to be added to the generic key in the paper by WUNDERLICH (2011: 40, no. 24 - ). The widened tibial apophysis of the ♂-pedipalpus (fig. 6) is typical for this species and reminds one of similar apophyses in the genus *Haplodrassus*.

**Distribution:** Israel (area typica) and Portugal; new to Portugal and Europe.

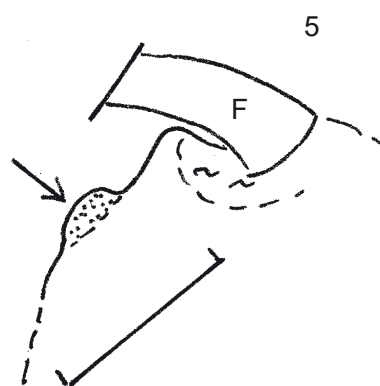
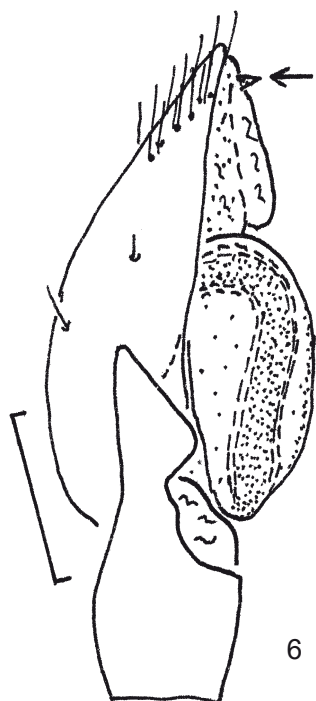
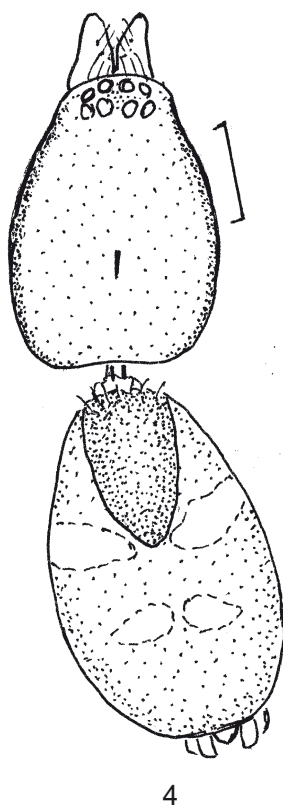
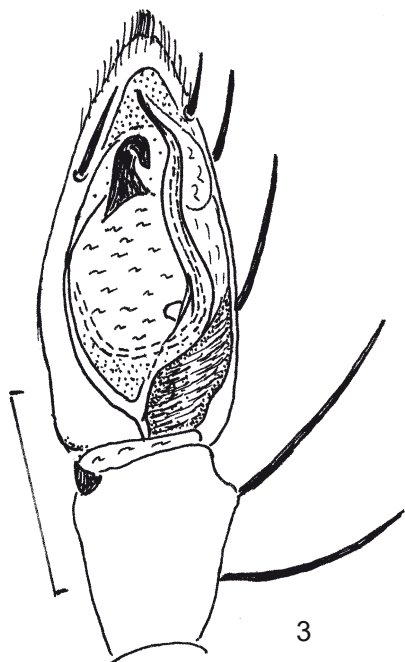
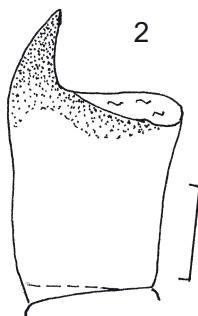
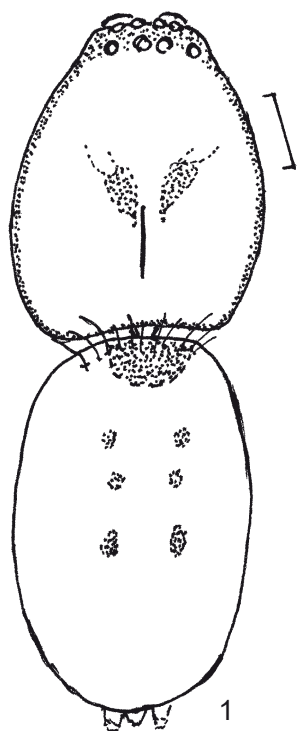
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Figs. 1-3: *Gnaphosoa monteserra* n. sp., ♂; 1) dorsal aspect of the body; 2) retrolateral aspect of the right pedipalpal tibia; 3) ventral aspect of the right pedipalpus. – Scale bars 1.0, 0.2 and 0.5 mm.

Figs. 4-6: *Phaeocedus mikha* LEVY 2009, ♂; 4) dorsal aspect of the body; 5) ventral aspect of the distal part of the left chelicera with the fang (F) and the cheliceral lobe (arrow); 6) retrolateral aspect of the right pedipalpus. The arrow points to the tip of the embolus. – Scale bars 0.5, 0.1 and 0.2 mm.



## ADDITIONS AND CORRECTIONS CONCERNING VOL. 7 OF THE BEITR. ARANEOL. (2012): FIFTEEN PAPERS ON EXTANT AND FOSSIL SPIDERS (ARANEAE)

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*Philodromimus* WUNDERLICH 2012 (p. 36-37): The mature moulting of the type species of this genus, *dispar* (WALCKENAER 1826), is remarkable early in the year, from the Spring on, in contrast to the members of the remaining European genera (usually from the early Summer on). At the end of March 2013 I collected a subadult couple in low herbs at the beach S Bormes des Mimosas in S-France. According to the light colour of the male like the female, the subad. stade apparently just before being adult in the Spring, and the occurrence within herbs – not on trees like *P. dispar* – I do not want to exclude that the specimens in question may be members of a second and unknown species of *Philodromimus*.

The type species of *Pulchellodromus* WUNDERLICH 2012: 38 is *Philodromus pulchellus* LUCAS 1846, see p. 33, and *Philodromus mainlingensis* HU & LI 1987 has to add as no. 12 to the species-list of this genus, see KASTRYGINA & KOVBLIUK (2014: 279), Arthropoda Selecta, 23 (3).

P. 44 (key to the philodromid genera): Within the no. „9“ the fig. 49 of *Pulchellodromus* has to be deleted and has to add to „9 -“ and „10-“.

Material and distribution of *Nomisia gomerensis* WUNDERLICH 2011 (p. 71):

The spiders from the Barranco de Masca and Las Canadas have been collected by J. LISSNER on Tenerife but not on La Gomera. The species is known from La Gomera and Tenerife.

P. 208: The family *Micropalpmimanidae* as well as *Micropalpmimanus poinari* have been described in 2008 but not in 2004.



## **CORRECTIONS CONCERNING VOL. 8 OF THE BEITR. ARANEOL. (2012): THE SPIDER FAMILIES OF EUROPE**

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- P. 31, line 8 from below: Add to Philodromidae: „Aber vordere Tarsen mit Scopula“.
- P. 34: Add after 5(4): „Paarige Tarsal-Krallen breit und mit zwei Reihen von Zähnen im Gegensatz zu den übrigen Familien europäischer Längskieferspinnen“.
- P. 45 and 71, fossil Theridiidae: See Beitr. Araneol., 5: 183-373, 399-402 (2008).
- P. 61: Add after 5(4): „Paired tarsal claws wide and bearing two rows of teeth in contrast to the remaining European mygalomorph families“.
- P. 73 (Clubionidae): „No jumping behaviour“ has to change to „Usually jumping behaviour“. Six lines later after „Gnaphosidae“ has to add „No jumping behaviour“.
- P. 85 (Nemesiidae): To „Further diagnostic characters“ has to add: „Wide paired tarsal claws with TWO rows of teeth (in contrast to other European families).“
- P. 87 (Filistatidae): Under „Main diagnostic character(s)“: Replace „trichobothria“ by „short trichobothria“.
- P. 88 (Segestriidae): Add to „Main diagnostic characters“: „A narrow light (hairless) lateral opisthosomal band exists probably in all extant taxa worldwide; it is indistinct in some specimens, see WUNDERLICH (2011: 632, fig. 81), Beitr. Araneol., 6. See also this volume, extant European spiders and Cretaceous spiders.“
- P. 98-99: Feathery (two-dimensional wide) hairs exist in the Hersiliidae in contrast to the Oecobiidae.
- P. 100: Add to „Further important characters“: Feathery (two-dimensional wide) hairs.
- P. 106 and 179, fig. 151: „L“ points to the base of a muscle (not lung openings).
- P. 114: Fig. 162 has to exchange by the correct fig. 162 p. 181.
- P. 137: Figs. 3 has to be deleted.

**A NEW *MEGALEPHYPHANTES* WUNDERLICH 1994  
(ARANEAE: LINYPHIIDAE FROM A CAVE OF CRETE (GREECE))**

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&

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**Abstract:** A single male of a new spider species, probably belonging to the genus *Megalephyphantes* WUNDERLICH 1994, *M. minotaur* n. sp. (Araneae: Linyphiidae: Micronetinae) is described from a cave of Crete, Greece.

**Acknowledgements:** We are most grateful to Mr. V. BRACHAT and H. MIXANIG for providing material used in this study.

**Introduction:** The Palaearctic genus *Megalephyphantes* WUNDERLICH 1994 at present contains 15 large sized well-coloured species with the centre of diversity in the Mediterranean and Central Asia. Below a strange male with some troglobiont features is regarded with some hesitation as a member of *Megalephyphantes*.

Abbreviations: E = embolus, EP = embolus proper, L = lamella characteristica, MP = membraneous process of the terminal apophysis, R = radix, RA = radix apophysis, SS = special spine, T = tooth of the embolus, Th = thumb.

The terminology of the genital structures follows SAARISTO & TANASEVITCH (1996). The sequence of leg segment measurements is as follows: femur + patella + tibia + metatarsus + tarsus. All measurements in mm.

**?*Megalephyphantes minotaur* n. sp.** (figs. 1-7)

Etymology: The species name, a noun apposition, is taken from the mythical monster, living in a cave of Crete.

**Material**: Greece, Crete, cave, Nida plateau, Tripa, Mithia Kavatura, male holotype leg. HARALD MIXANIG 4. VIII 2000; sent to JW by V. BRACHAT, coll. J. WUNDERLICH R158/AR/CJW, later most probably Senckenberg, Frankfurt a. M. (SMF).

**Diagnosis** (♂; ♀ unknown): The species is well distinguished from other congeners by some troglobiont features, an unmodified pedipalpal patella, the shape of cymbium and paracymbium as well as by the peculiar shape of the embolus.

**Description** (♂): The specimen is in a bad condition: several leg articles and bristles are lost. Body and legs very pale. Body length 2.5; prosoma: Length 1.2, width 1.0, unmodified, cephalic part slightly elevated, bearing several bent bristles. Eight eyes small (reduced), with dark margins. Chelicerae 0.5 long, anterior margin of the fang furrow with three stout teeth. Legs long, thin and pale. Length of leg I 7.9 (2.1 + 0.4 + 2.2 + 2.0 + 1.2), length of leg IV 7.15 (1.95 + 0.3 + 1.95 + 1.9 + 1.05). Chaetotaxy unclear, most bristles lost, metatarsus I-IV with a dorsal bristle, tibiae with lateral bristles and probably without ventral bristles. Position of the metatarsal trichobothria unknown. Pedipalpus (figs. 1-7): patella unmodified, bearing a long and bent dorsal bristle. Cymbium unmodified, without posterodorsal outgrowth. Paracymbium relatively large, toothless, posterior pocket reduced, anterior and apical pockets merged. Lamella characteristica short, wide and strongly sclerotized. Embolus with a hump-like retrolateral outgrowth, and three narrow, long, pointed and spear-shaped apophyses on terminal apophysis side, hidden by one of its narrow and long membraneous process. Thumb very large, with a tooth-like apophysis near its base, T in figs. 1 and 6. Terminal apophysis with a small and well sclerotized part and two flanked membraneous processes, MP 1 and 2 in figs. 1 and 4. Radix boat-shaped, proximal part bearing a short pointed radical apophysis. Fickert's gland large, globular. Opisthosoma 1.4 long, 0.95 wide, white, dorsal pattern absent.

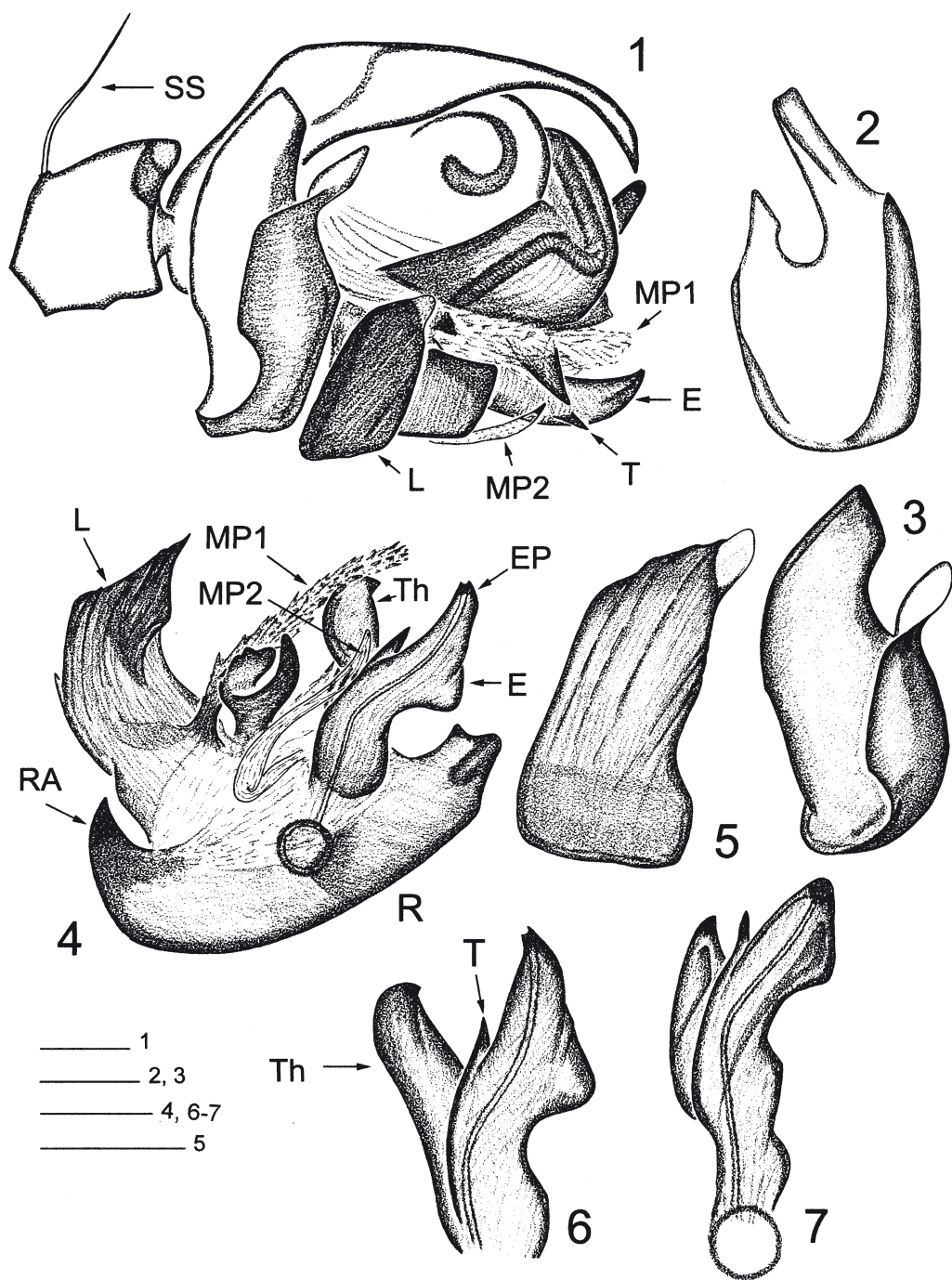
**Relationships**: The pedipalpal conformation is similar in general to that of *Megalephyphantes* but several peculiarities in the structures of the pedipalpus, as well as the absence of the conspecific female makes its taxonomic position unclear; so the species

is placed provisionally in *Megalephyphantes*. It may be regarded as the member of an undescribed genus; the discovery of the unknown female may help to solve this question. In the majority of the species of *Megalephyphantes*, including the type species *nebulosus* (SUNDEVALL 1830), the embolus is peculiar in shape and looks like a sea-horse, see BOSMANS (2006: 182, fig. 21), TANASEVITCH (2009a: 399, fig. 44), TANASEVITCH (2009b: 424, fig. 3). In contrast, in *minotaur* the embolus has a large thumb and is very similar to that of *Mughiphantes* SAARISTO & TANASEVITCH 1999, *Bolyphantes* C. L. KOCH 1837 and *Poeciloneta* KULCZYNSKI 1894, see SAARISTO & TANASEVITCH (1999, 2000). The boat-shaped radix is also similar in the genera mentioned above. Besides this character the new species differs from *Megalephyphantes* congeners by having only a single special spine on an unmodified pedipalpal patella, by the unarmed and simple paracymbium and by the existence of the apophysis of the radix. Furthermore certain troglobiont features distinguishes the new species from congeners: the very pale body and legs, absence of markings of pro- and opisthosoma, reduced eyes as well as long and slender legs.

**Distribution:** Crete (Greece).

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Figs. 1-7: ?*Megalephyphantes minotaur* n. sp., ♂, right pedipalpus; 1) retrolateral aspect; 2-3) different aspects of the paracymbium; 4) embolic division; 5) lamella characteristica, 6-7) different aspects of the embolus. – Scale bars 0.1 mm.

**PFUI SPINNE** – Linguistische „Gendereien“

Dankenswerterweise wurde kürzlich in der Frauenzeitschrift AMME auf die Diskriminierung des weiblichen Geschlechts durch Angst einflößende „Ekeltiere“ wie DIE Spinne hingewiesen (vgl. auch DIE Ziege). „Die spinnt ja“ klingt auch nicht gerade schmeichelhaft. Im Gegensatz dazu stünde das positive Image von Tieren wie DER Adler und DER Elefant. Die Leserinnen wurden aufgefordert, hier über Abhilfe nachzudenken.

Mein Vorschlag zur Anpassung des Artikels: etwa DAS Spinne – entsprechend zu DAS Pferd und DAS Schaf. Die Umstellung wäre möglicherweise lediglich eine Frage der Gewöhnung. Kann schließlich MANN das durchgängig weibliche „die“ im Plural akzeptieren? Aber das ist wohl eine „andere Geschichte“...

Es wäre daran zu denken, die Nationale Kommission zur Geschlechtsneutralen Namensgebung (NKG) anzurufen und diese um eine entsprechende positive Entscheidung zu bitten. Allerdings war bereits in der Vergangenheit zu beobachten, dass auch ohne Einwirkung durch eine Kommission sich in ihrer ursprünglichen Bedeutung abgewandelte Begriffe des NEUSPRECH durchsetzen können; man denke etwa an „Restrisiko“ oder an „Entsorgungspark“ für Atommülldeponie oder an „Friedenseinsatz“ für Krieg. Menschenrechtswidrige und heimtückische autonome Kriegsgeräte werden „Drohnen“ genannt. (Bemerkenswerterweise sind Drohnen ausgerechnet die einzigen „waffenlosen“ Honigbienen, da ihnen ein Giftstachel fehlt!). George Orwell hätte sicher sein Vergnügen an solchen Wortschöpfungen! – Bereits vor einem halben Jahrhundert wurde aus „Gott“ in „Dr. Murkes gesammeltes Schweigen“ von Heinrich Böll (siehe Internet) geschlechtsneutral „Jenes höhere Wesen, das wir verehren“. Genderfreundlich waren bereits die „alten Germanen“: ihr „guoa“ – vielleicht Vorläufer von „Gott“ – war neutrum.

Weitere „artikuläre Ungereimtheiten“ sind schließlich prominente humane Reizorgane: DER Kitzler und DIE Eichel – „pfui Spinne“; wer sowas in den Mund nimmt, dem ist der Klerus sicher SPINNEFEIND. Sollte MitGLIED durch MitKLIT ersetzt werden? Wer weiß linguistischen Rat? AMME oder EMMA? – Nach einem Änderungsantrag zum Bundeswahlprogramm 2013 von BÜNDNIS 90/ DIE GRÜNEN vom (1.?) April 2013 sollen Redewendungen wie „Herr der Lage“ „konsequent in geschlechterspezifische Äquivalente“ umgeschrieben werden. Wie ist nun die (!) Lage? Darf man gespannt sein auf „Frau der Lage“? Oder „HerrIn der Lage“? Oder „Mensch der Lage“? Der Mensch oder das Mensch? HerrIn der Ringe? Beherrschen – befrauschen? Die NKG ist dringend gefordert! Möglicherweise ist sie aber überfordert. Die Realität war in diesem Fall allerdings schneller: Am 1. April (dieses Datum ist verbürgt!) 2013 trat die neu gefasste Straßenverkehrsordnung (StVO) in Kraft, in der der Begriff Fußgänger nicht mehr auftaucht, dafür steht „wer zu Fuß geht“. Wäre – nach NEUSPRECH – „das Fußgänger“ oder schlicht „Fußgänger“ nicht einfacher? Eines ist unklar: Welche Spinnerin – weibliche Spinne = Spinnen-Weibchen ist kein Synonym! – war hier am Werke? Ihr glücklichen Engländer – äh – der englischen Sprache Mächtigen.

Sind derartige „geschlechtsspezifischen Äquivalente“ sprachlich nicht einfach herrlich – pardon – fraulich? Hier erhält „fraulich“ eine überraschend neue Bedeutung! Oder sind sie (irgendwie) menschlich? Waren übrigens „herrlich“ und „fraulich“ je Gegensätze?.

EMANzipation: Ob sprachliche Mittel dieser Art hilfreich sind, das Patriarchat – „die weltweite Diktatur der Männer“ – zu beenden?

JW

## A NEW SUBFAMILY, GENUS AND SPECIES OF FOSSIL SCORPIONS FROM CRETACEOUS BURMESE AMBER (SCORPIONES: PALAEOEUS-CORPIIDAE)

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**Abstract:** A fossil scorpion belonging to a new subfamily, Archaeoscorpioninae **subfam. nov.**, and to a new genus and species, *Archaeoscorpions cretacicus* **gen. n., sp. n.**, is described from the Cretaceous amber of Myanmar (Burma). This is the seventh species and the eighth fossil of scorpions to be described from Burmese amber. In addition to the previously described families and subfamilies (Electrochaerilinae, Chaerilobuthidae and Palaeotilineatidae), the description of the new subfamily Archaeoscorpioninae **subfam. nov.**, provides further evidence about the phylogenetic position of certain Burmese Cretaceous amber scorpions and attests to a considerable degree of diversity in the Burmese amber-producing forests.

**Key-words:** scorpion, fossil, new subfamily genus and species, Cretaceous, Burmese amber, Myanmar.

### Introduction

As already noted in several previous publications, scorpions are rare among the arthropods fossilized in amber (Lourenço, 2009a, 2012a, 2013a; Lourenço & Beigel, 2011). Nevertheless, several specimens have been described since the 1980s, mainly from Dominican and Baltic amber (Lourenço, 2009a,b, 2012b). Cretaceous amber scorpions are even rarer than those found in Tertiary amber. Eight such species have been described or redescribed in recent years, representing distinct new families, subfamilies and genera that can be only approximately associated with extant groups.



The first Cretaceous amber scorpion to be described was *Archaeobuthus estephani* Lourenço 2001, from Lebanon. It was accommodated in a new family, Archaeobuthidae (Lourenço, 2001). This was followed by the description of *Palaeoburmesebuthus grimaldii* Lourenço, 2002 from Burmese amber (Lourenço, 2002). Because of the incompleteness of the specimen used in the description, *P. grimaldii* was placed as incertae familiae. The third Cretaceous amber scorpion to be described was *Palaeoeuscorpius gallicus* Lourenço, 2003, from France. This was also placed in a new family, Palaeoeuscorpiidae (Lourenço, 2003). Subsequently, a second new genus and species of scorpion, *Electrochaerilus buckleyi* Santiago-Blay, Fet, Soleglad & Anderson, 2004, was described from Burmese amber and assigned to a new subfamily, Electrochaerilinae, of the extant family Chaerilidae Pocock, 1893 (Santiago-Blay et al., 2004a). Redescriptions were also published for *Palaeoburmesebuthus grimaldii* Lourenço and *Archaeobuthus estephani* Lourenço, providing some new insights into these taxa (Baptista et al., 2006; Santiago-Blay et al., 2004b). More recently, two new families, Chaerilobuthidae Lourenço & Beigel, 2011, and Palaeotrilineatidae Lourenço, 2012, and two new genera and species, *Chaerilobuthus complexus* Lourenço & Beigel, 2011 and *Palaeotrilineatus ellenbergeri* Lourenço, 2013 were described, from Burmese amber (Lourenço, 2012a; Lourenço & Beigel, 2011). A new species was subsequently added to the genus *Chaerilobuthus* (Lourenço, 2013a).

The specimen described here represents the seventh distinct scorpion species to be found in Burmese amber. It shows taxonomic characteristics allying it to the extant family Euscorpiidae, but also to the Cretaceous family Palaeoeuscorpiidae, described from French amber. For this reason, it is placed in the family Palaeoeuscorpiidae, but attributed to a new subfamily, genus and species, which are described here.

### **Material and methods:**

The specimen investigated was originally preserved in a rather opaque block of reddish amber that measured 37 x 33 x 12 mm. In order to facilitate observations, the piece was cut and polished, being reduced to dimensions of 26 x 20 x 4/5 mm. Only the right pedipalp and leg fragments of the scorpion remain, the latter being unusable. Pedipalps bear some of the most informative morphological characters of scorpions and previous descriptions have also been based on such fragments, as in the case of *Palaeoeuscorpius gallicus* from the Cretaceous amber of France. Many characters, and in particular trichobothria, are clearly visible in both dorsal and ventral views, allowing detailed investigation. The schematic drawings provided here are interpretations of what was observable. Illustrations and measurements were produced with the aid of a Wild M5 stereomicroscope equipped with a drawing tube and an ocular micrometer. Measurements follow Stahnke (1970) and are given in mm. Trichobothrial notations follow Vachon (1974). Trichobothria were definitely recorded only when their bothria (areoles) could be observed. Other trichobothria may be suggested by the presence of transverse hairs.

### **Age of Burmite:**

As discussed previously (Lourenço, 2002, 2012a; Lourenço & Beigel, 2011), there is considerable confusion in the literature concerning the probable age of Burmese amber. Also, confusion exists regarding the precise sites in Myanmar where the amber pieces

were mined. There are five regions in Myanmar where fossil resins have been found; however, Burmite only occurs in the Hukawng Valley (Zherikhin & Ross, 2000). According to Zherikhin & Ross (2000) and Grimaldi et al. (2002), the age of Burmese amber is probably Turonian-Cenomanian (90–100 Mya). More recent age estimates for Burmese amber deposits date them as being from the Lower Cretaceous (Upper Albian), based on ammonites and palynomorphs for at least one amber location (Cruickshank & Ko, 2003; Penney, 2010; Santiago-Blay et al., 2004b).

### **Taxonomic remarks about the extant Asian Euscorpiidae:**

The subfamily Scorpiopinae was first proposed by Kraepelin (1905) as Scorpiopsinae, a subfamily of Vaejovidae. The correct Latinized subfamily name, derived from the type genus *Scorpiops*, is Scorpiopinae, as emended by Fet (2000). Francke (1976) drew attention to the inconvenient classification of Kraepelin (1905) and suggested that Scorpiopsinae should no longer be incorporated in the Vaejovidae. Stockwell (1989) raised Scorpiopsinae to family level (as ‘Scorpiopsidae’), and Lourenço (1998) confirmed this decision. Fet (2000) listed the family Scorpiopidae. Subsequently, Soleglad & Sissom (2001) downgraded Scorpiopidae to a subfamily of Euscorpiidae, grouped its Asian genera into the tribe Scorpiopini, and also included in this subfamily the North American genus *Troglocormus* (tribe Troglocormini). The subfamily currently forms a monophyletic group within Euscorpiidae, and it does not share any synapomorphies with North American Vaejovidae (Soleglad & Sissom, 2001).

Vachon (1980) revised the genus *Scorpiops* and described three new subgenera, *Alloscorpiops*, *Euscorpiops* and *Neoscorpiops*, in addition to the nominotypical subgenus *Scorpiops*. These four subgenera were later elevated to generic rank by Lourenço (1998), who added the monotypic genera *Parascorpiops* Banks 1928 and *Dasyscorpiops* Vachon, 1974, thus bringing the total number of genera to six. With the recent description of *Laoscorpiops* Lourenço, 2013 the tribe Scorpiopini includes seven Asian genera, mainly from the South and Southeast of the continent (Lourenço, 2013b). For detailed diagnoses and geographical distributions of the genera, see Vachon (1980), Stockwell (1989) and the Catalog of the Scorpions of the World (Fet, 2000).

### **Systematic description**

Family Palaeoeuscorpiidae Lourenço, 2003  
Subfamily Archaeoscorpiopinae **subfam. nov.**

Type genus *Archaeoscorpiops* **gen. n.**

**Diagnosis for the new subfamily and the new genus:** Total length probably about 27 to 30 mm, based on the lengths of the pedipalp segments, which are as follow (in mm): chela length 8.5, width 2.4; movable finger length 4.5; patella length 3.9, width 2.0; femur length 4.2, width 1.4. In comparison, an adult female of *Scorpiops oligotrichus* Fage, 1933 (Euscorpiidae) from Laos/Vietnam, with a total length of 30.4 mm, shows

the following values: chela length 8.1, width, 3.1; movable finger length 3.8; patella length 4.3, width 1.9; femur length 3.8, width 1.7.

The general morphology of the pedipalp segments is somewhat similar to that of Scorpipinae, particularly *Scorpiops*. The main differences are the reduced size of the apophysis on the internal aspect of the patella (even if this can be also reduced in some species of *Scorpiops*) and a rather unusual trichobothrial pattern. This pattern is similar to type C of Vachon (1974), defined for the family Euscorpiidae (Vachon, 1980). On the chela hand, trichobothria **Db**, **Dt**, **Est**, **Et<sub>1-5</sub>**, **Eb<sub>1</sub>**, **Eb<sub>3</sub>** and **6 V** can be observed. On the chela fixed finger, trichobothria **eb**, **db**, **dsb**, **esb**, **dst**, **est** and **et** can be observed. Patella shows **d<sub>1</sub>** and **d<sub>2</sub>** on dorsal face; **i** is displaced to the ventral face; on the ventral face only 3 **V** trichobothria are observed. This is a rather reduced number of ventral trichobothria for a patella. According to Vachon (1980), members of the subfamily Scorpipinae always presents a minimum of 6 ventral trichobothria on the patella, and for several species this number is higher. External trichobothria cannot be observed on the patella, but the presence of transverse hairs suggest some are present, which may belong to territories **et**, **est**, **esb** and **eb**. Femur shows one **d** and one **i**, displaced to the ventral side.

Type species: *Archaeoscorpiops cretacicus* sp. n.

### ***Archaeoscorpiops cretacicus* sp. n.** (Figs. 1-7. Photos, 190-191)

Holotype: A possible adult (sex unknown): A pedipalp and remains of legs including claws. - Two pieces of amber were separated from the piece which includes the holotype; the larger piece contains remarkable remains of plants and detritus as well as the small larva of an insect, the smaller piece includes a tiny Acari.

Depository: The type specimen is presently in the collection of Jörg Wunderlich, Hirschberg, Germany, no. F2380/BU/CJW, but will probably later be deposited in the collections of the Senckenberg Museum, Frankfurt.

Type locality and horizon: Myanmar (Burma), Kachin; precise locality unknown; Lower Cretaceous.

Derivatio nominis: The specific name makes reference to the Cretaceous geological horizon.

**Diagnosis:** As for the new subfamily and genus.

### **Description:**

Coloration: The general colour is reddish-yellow. After cutting and polishing of the piece, the amber remains only moderately clear, hampering precise observation of the piece from certain angles.

Morphology of pedipalp: Femur, patella and chela slightly flattened; dentate margins of chelal fingers with a single linear row of granules, separated by larger, rounded, accessory granules. Chela with three dorsal and two ventral carinae; patella with one weakly developed internal apophysis, marked by two slightly spinoid granules (one dorsal, one external), but no ventral carinae. Trichobothriotaxy as described in generic diagnosis.

## Discussion

According to the shape of pedipalp femur, patella and chela, the presence of an apophysis on the internal aspect of patella and, especially the trichobothrial pattern, the specimen is most certainly a member of the euscorpoid lineage, sensu Soleglad & Sissom (2001). Its assignment to any of the extant euscorpoid subfamilies is precluded on account of the very reduced trichobothrial pattern observed (in particular on the ventral aspect of patella), the incompleteness of the specimen and, especially, its geological horizon (Lower Cretaceous). The specimen is therefore assigned to a new subfamily, *Archaeoscorpipinae* subfam. nov., until further material becomes available.

## Acknowledgements

Thanks are due to Jörg Wunderlich (Hirschberg, Germany) for arranging facilities for the study of the specimen, to Mark Judson (MNHN, Paris) for corrections to the manuscript and to Elise-Anne Leguin (MNHN, Paris) for assistance with the preparation of photos and plates.

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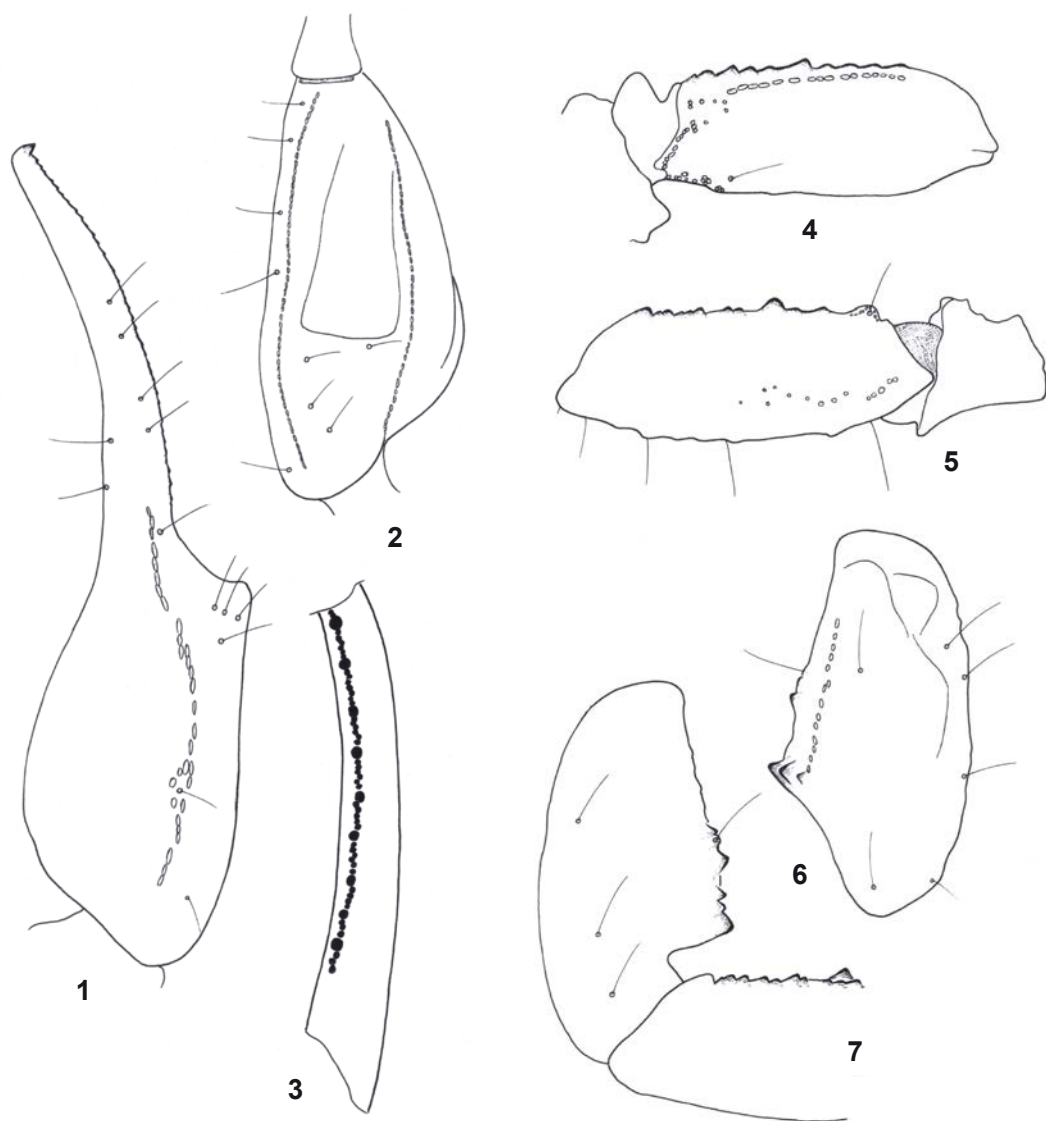
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Figs. 1-3. *Archaeoscorpiops cretaticus* sp. n. 1-2. Trichobothrial pattern of chela, dorso-external and ventral aspects. 3. Dentate margin of basal two-thirds of movable finger, showing rows of granules.

Figs. 4-7. *Archaeoscorpiops cretaticus* sp. n. Trichobothrial pattern. 4-5. Femur, dorsal and ventral aspects. 6-7. Patella, dorsal and ventral aspects.



**CLARIFICATION OF THE FAMILIAR STATUS OF THE GENUS  
*PALAEOBURMESEBUTHUS* LOURENÇO, 2002 FROM CRETACEOUS  
BURMESE AMBER (SCORPIONES: ARCHAEOBUTHIDAE:  
*PALAEOBURMESEBUTHINAE*)**

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**Abstract:** The study of four new scorpion specimens from the Cretaceous amber of Myanmar (Burma) lead to the description of three new species and to the clarification of the status of the genus *Palaeoburmesebuthus* Lourenço, the first scorpion described from Burmese amber. To present, ten species and twelve fossil scorpions have been described from Burmese amber. This attests to a considerable degree of diversity in the Burmese amber-producing forests.

**Key-words:** scorpion, fossil, new subfamily, new species, Cretaceous, Burmese amber, Myanmar.

## **Introduction**

After the conclusion of my previous article (this volume), I had the opportunity to examine four new Burmese amber pieces containing scorpions. Their study leads to the description of three more new species belonging to previously described genera. More significantly, however, are the new taxonomic elements furnish by one of the specimens allowing the clarification of the familial status of the genus *Palaeoburmesebuthus* Lourenço. *Palaeoburmesebuthus grimaldii* Lourenço, 2002 was the first scorpion described from Burmese amber (Lourenço, 2002). However, in account of the incompleteness of the specimen used in the description, *P. grimaldii* was placed as incertae

familiae. A redescription was also published for *Palaeoburmesebuthus grimaldii*, providing some new insights to the taxa (Santiago-Blay et al., 2004). However, the familial status of this genus remained unclear.

The new species of *Palaeoburmesebuthus* described here shows taxonomic characteristics allying it to the extant family Buthidae, but also to the Cretaceous family Archaeobuthidae Lourenço, 2001, described from Lebanon amber (Lourenço, 2001). For this reason, it is placed in the family Archaeobuthidae, but attributed to a new subfamily, which is described here.

### **Material and methods:**

The specimens investigated are originally preserved in rather opaque blocks of reddish amber. Details of each block are supplied together with the description of the specimen. Many characters, and in particular trichobothria, are visible in some specimens, allowing detailed investigation. In other cases, only fragments of the scorpions remain. The schematic drawings provided here are interpretations of what was observable. Illustrations and measurements were produced with the aid of a Wild M5 stereomicroscope equipped with a drawing tube and an ocular micrometer. Measurements follow Stahnke (1970) and are given in mm. Trichobothrial notations follow Vachon (1974). Trichobothria were definitely recorded only when their bothria (areoles) could be observed. Other trichobothria may be suggested by the presence of transverse hairs.

### **Systematic description:**

Family Archaeobuthidae Lourenço, 2001

Subfamily Palaeoburmesebuthinae **subfam. nov.**

### **Diagnosis for the subfamily:**

General morphology shows similarities with Cretaceous Lebanese amber family Archaeobuthidae and also with extant buthid scorpions. The following combination of features can be used to diagnose the new subfamily: Carapace not granulated, smooth; anterior margin with a moderately marked median concavity, as observed in some extant buthids. chelicerae with moderately long distal teeth which do not clearly overlap; fixed and movable fingers with one basal and one median tooth. Vesicle very long, with a pear-like shape, resembling those of some extant buthids; with a very long aculeus. Fixed and movable fingers of pedipalp chela with a series of small rounded granules, without any conspicuous accessory granules. Trichobothrial pattern with elements resembling those of extant buthid type A (Vachon, 1974): at least 1 to 3 internal, 3-4 dorsal and 2 external trichobothria on the femur; dorsal trichobothria disposed in alpha ( $\alpha$ ) configuration (Vachon, 1975); 1 internal, 3-4 dorsal and no ventral trichobothria on patella; some external trichobothria can be suggested on patella by the presence of fine setae; 4-5 dorso-external and 2 ventral on chelal hand; 3 on fixed finger. Tibial spurs present on legs III and IV.

Type genus *Palaeoburmesebuthus* Lourenço, 2002.

Type species: *Palaeoburmesebuthus grimaldii* Lourenço, 2002.

***Palaeoburmesebuthus ohlhoffi* sp. n.** (Figs. 1-4, 6. Photos, 192-193)

Holotype: A juvenile. Sex cannot be determined. Rather opaque block of reddish amber that measured 53 x 44 x 12 mm. Type locality and horizon: Myanmar (Burma), Kachin; precise locality unknown; Lower Cretaceous.

Patronym: The specific name honours Mr. Rainer Ohlhoff, Saarbrücken, Germany who arranged facilities for the study of the holotype.

Depository: The type specimen is deposited in the personal collection of Rainer Ohlhoff, Saarbrücken, Germany.

***Diagnosis***: As for the new subfamily.

**Description**:

Coloration: the scorpion is yellow to reddish-yellow; carapace and tergites yellow; metasomal segments I to IV yellow; segment V and telson reddish-yellow; pedipalps and legs yellow. The ventral aspect of the specimen is destroyed.

Morphology. Carapace not granulated, smooth; anterior margin with a moderately marked median concavity, as observed in some extant buthids. Carinae and furrows absent. Median ocular tubercle clearly anterior to the centre of carapace; median eyes moderate to small in size. Three inconspicuous lateral eyes. Sternum unknown. Mesosomal tergites weakly granular, with one median carina; VII with five weakly marked carinae. Pectines unknown. Sternites unknown. Spiracles unknown. Metasomal segment I to IV rounded with 10-8-8-8 carinae; segment V slender with five carinae; dorsal carinae of segments I-IV without spinoid granules; dorsal aspect of segments I to V weakly depressed; setation on all segments moderately marked. Telson with a very long pear-shaped vesicle, flattened laterally, as in some extant buthids; weakly granular to smooth; aculeus extremely long and moderately curved. Cheliceral dentition only partially visible; fixed and movable fingers with one basal and one median tooth observable; distal teeth moderately long (see Vachon, 1963 as reference). Pedipalp femur pentacarinat; patella with dorso-internal, ventro-internal, dorso-external and external carinae; internal face with some minor spinoid granules. Chela with moderately marked carinae and one spinoid granule on internal face; all faces weakly granular. Fixed and movable fingers each with one series of small rounded granules; conspicuous accessory granules not observable; extremity of fingers with stronger spinoid granules; setation of pedipalps inconspicuous. Trichobothriotaxy recalling type A (Vachon, 1974) of extants buthids (see diagnosis of subfamily): at least 1 to 3 internal, 3-4 dorsal and 2 external trichobothria on the femur; dorsal trichobothria disposed in alpha ( $\alpha$ )

configuration (Vachon, 1975); 1 internal, 3-4 dorsal and no ventral trichobothria on patella; some external trichobothria can be suggested on patella by the presence of fine setae; 4-5 dorso-external and 2 ventral on chelal hand; 3 on fixed finger.

Morphometric values (in mm) of juvenile holotype of *Palaeoburmesebuthus ohlhoffi* sp. n.

Total length 12.28 (including telson). Carapace: length 1.21, anterior width 0.93, posterior width 1.46. Mesosoma length 2.06. Metasomal segments. I: length 0.66, width 0.66; II: length 0.87, width 0.66; III: length 1.06, depth 0.80; IV: length 1.33, depth 0.73; V: length 1.93, depth 0.46. Telson length 3.16. Vesicle: depth 0.34. Right pedipalp: femur length 1.23, width 0.34; patella length 2.45, width 0.35; chela length 2.26, width 0.34, depth 0.33; movable finger length 1.53.

*Palaeoburmesebuthus* sp. (fig. 12)

A juvenile specimen, slightly larger than the previously described species with 19.1 mm in total length. Sex cannot be determined but the very slender morphology of the body and appendages may suggest a male. In a very opaque block of reddish amber that measured 43 x 27 x 14 mm. Most characters are not observable mainly because the specimen suffered an important dissection process within the resin. The structure of metasoma and telson clearly associates this scorpion to the genus *Palaeoburmesebuthus*.

Syninclusion are numerous; the most important one is the holotype of a plant (Pentapetalae, family unknown): *Micropetasos burmenis* Poinar, Chambers & Wunderlich 2013.

Type locality and horizon: Myanmar (Burma), Kachin; precise locality unknown; Lower Cretaceous.

Depository: The specimen is deposited in the personal collection of Jörg Wunderlich, Hirschberg, Germany, no. F2469/BU/CJW.

## **Other taxa described:**

Family Chaerilobuthidae Lourenço & Beigel, 2011

Genus *Chaerilobuthus* Lourenço & Beigel, 2011

### ***Chaerilobuthus birmanicus* sp. n. (figs. 8-11)**

Holotype is a juvenile specimen, slightly larger than *C. complexus*, the first species described for this genus (Lourenço & Beigel, 2011) with 8.69 mm in total length. Sex cannot be determined but the morphology of the body and appendages may suggest a female. The block of amber is very clear, pale yellow and measured 21 x 18 x 5 mm. However, most characters are not observable because the specimen suffered an important dissection process within the resin and is located in a zone of fracture. The structure of the prosoma carapace, with absence of eyes, clearly associates this scorpion to the genus *Chaerilobuthus*.

Several syninclusions like a Coleoptera and some Acari.

Type locality and horizon: Myanmar (Burma), Kachin; precise locality unknown; Lower Cretaceous.

Depository: The type specimen is deposited in the personal collection of Jörg Wunderlich, Hirschberg, Germany, coll. no. 2471/BU/CJW.

The specific name refers to Burma, the country where the new species was found.

**Diagnosis:** General morphology shows similarities with both buthid and chaerilid scorpions and the specimen can clearly be associated to the genus *Chaerilobuthus*. The following combination of features can be used to diagnose the new species: Carapace smooth with the absence of eyes; a few trichobothria observed which can relate it to the pattern previously observed for *Chaerilobuthus*; at least 2 dorsal and one internal trichobothria on the patella; 3-4 trichobothria on the dorso-external aspect of chela hand and 2 trichobothria at the base of fixed finger; Fixed and movable fingers each with one series of small rounded granules; conspicuous accessory granules not observable. Telson with a more or less bulbous vesicle; aculeus very long and moderately curved; base of aculeus enlarged. Tibial spurs present on legs III and IV, moderately marked.

**Description:** Coloration: the scorpion is reddish-brown to dark brown, probably due to the process of dissection suffered by the specimen. The ventral aspect of the specimen cannot be clearly observed since it is located in the zone of fracture of the piece. Morphology. Carapace smooth, not granular; anterior margin almost straight. Carinae and furrows absent. Median ocular tubercle indistinct; probably absent; median eyes, if present, are so small that they cannot be distinguished from bubbles in amber that

hamper observation. Lateral eyes not observable. Sternum not observable. Mesosomal tergites not granular and acarinate. Ventral aspect not observable. Metasomal segments I to IV with eight or ten carinae; the precise numbers cannot be counted; segment V with five carinae; all carinae inconspicuous; dorsal carinae of segments I-IV without any spinoid granule; dorsal aspect of segments I-V only weakly depressed; setation on segments I to V moderately marked. Telson with a more or less bulbous vesicle, not flattened dorso-ventrally; weakly granular to smooth; aculeus very long and moderately curved. Cheliceral dentition not visible. Pedipalp femur probably pentacarinata; no spinoid granules on internal face; patella with 5-6 carinae; internal face with only inconspicuous granules. Chela with moderately marked carinae; all faces almost smooth. Fixed and movable fingers with a longitudinal row of small, rounded granules, without accessory granules; extremity of fingers with one stronger spinoid granule. Trichobothriotaxy: trichobothrial pattern only partially observed (see diagnosis). Leg: tibial spurs present and but moderately marked.

Morphometric values (in mm) of the juvenile holotype of *Chaerilobuthus birmanicus* sp. n.

Total length 8.69 (including telson). Carapace: length 1.21, posterior width 0.81. Mesosoma length 2.67. Metasoma length 3.67. Telson length 1.14. Pedipalp: femur length 1.27, width 0.27; patella length 1.40, width 0.41; chela length 2.07, width 0.61; movable finger length 1.07.

### ***Chaerilobuthus bruckschi* sp. n.** (Figs. 13-18. Photos, 194-196)

Holotype is a juvenile specimen, also slightly larger than *C. complexus*, the first species described for this genus (Lourenço & Beigel, 2011) with 8.75 mm in total length. Sex cannot be determined but the morphology of the body and appendages may suggest a male. The block of amber is very clear, pale yellow and measured 22 x 14 x 7 mm. However, most characters are not observable because the specimen suffered with the dissection process within the resin, is twisted and located in a zone of fracture. The general morphology of the scorpion clearly associates it to the genus *Chaerilobuthus*.

Type locality and horizon: Myanmar (Burma), Kachin; precise locality unknown; Lower Cretaceous.

Patronym: The specific name honours Mr Klaus-Peter Brucksch, Kuranda, Australia, who arranged facilities for the study of the holotype.

Depository: The type specimen is deposited in the personal collection of Mr. Klaus-Peter Brucksch, Kuranda, Australia.

**Diagnosis**: General morphology shows similarities with both buthid and chaerilid scorpions and the specimen can be associated to the genus *Chaerilobuthus*. The following combination of features can be used to diagnose the new species: Carapace smooth, apparently with inconspicuous median eyes; a few trichobothria observed which can relate it to the pattern previously observed for *Chaerilobuthus*; at least 2 external trichobothria on the patella; 3-4 trichobothria on the dorso-external aspect

of chela hand, two trichobothria at the base of fixed finger and two trichobothria on fixed finger. Fixed and movable fingers of pedipalp chela each with 6/7 series of small rounded granules separated by conspicuous accessory granules. Telson with a bulbous vesicle: aculeus moderately long and curved; base of aculeus not enlarged. Tibial spurs absent from legs III and IV.

**Description:** Coloration: the scorpion is reddish-brown to dark brown, probably due to the process of dissection suffered by the specimen. The ventral aspect of the specimen cannot be clearly observed since it is located in the zone of fracture of the piece.

Morphology. Carapace apparently smooth, not granular; anterior margin almost straight. Carinae and furrows absent. Median ocular tubercle more or less distinct; median eyes, if present, are very small. Lateral eyes not observable. Sternum not observable. Mesosomal tergites not granular and acarinate. Ventral aspect not well observable. Metasomal segments I to IV with 10-8-8-8 carinae; segment V with five carinae; all carinae conspicuous; dorsal carinae of segments I-IV with a series of spinoid granules; dorsal aspect of segments I-V strongly depressed; setation on segments I to V moderately to strongly marked. Telson with a bulbous vesicle, not flattened dorso-ventrally; weakly granular to smooth; aculeus moderately long and curved. Cheliceral dentition not visible. Pedipalp femur probably pentacarinata; patella with 5-6 carinae. Chela with moderately marked carinae; all faces almost smooth. Fixed and movable fingers with 6-7 rows of small, rounded granules, separated by strong spinoid accessory granules; extremity of fingers without any stronger spinoid granule. Trichobothriotaxy: trichobothrial pattern only partially observed (see diagnosis). Leg: tibial spurs absent.

Morphometric values (in mm): Total length 8.75 (including telson). Carapace: length 1.03, posterior width -. Mesosoma length 3.11. Metasomal segments length/width: I 0.40/0.33; II 0.47/0.27; III 0.53/0.27; IV 0.67/0.27; V 1.20/0.25. Telson length/width/height: 1.34/0.42/0.47. Pedipalp: patella length 1.46, width 0.52; chela length 1.87, height 0.34; movable finger length 0.93.

## Acknowledgements

Thanks are due to Mr Rainer Ohlhoff, Saarbrücken, Germany, Mr. Klaus-Peter Brucksch, Kuranda, Australia and to Jörg Wunderlich, Hirschberg, Germany for arranging facilities for the study of the specimens, to Elise-Anne Leguin (MNHN, Paris) for assistance with the preparation of plates.



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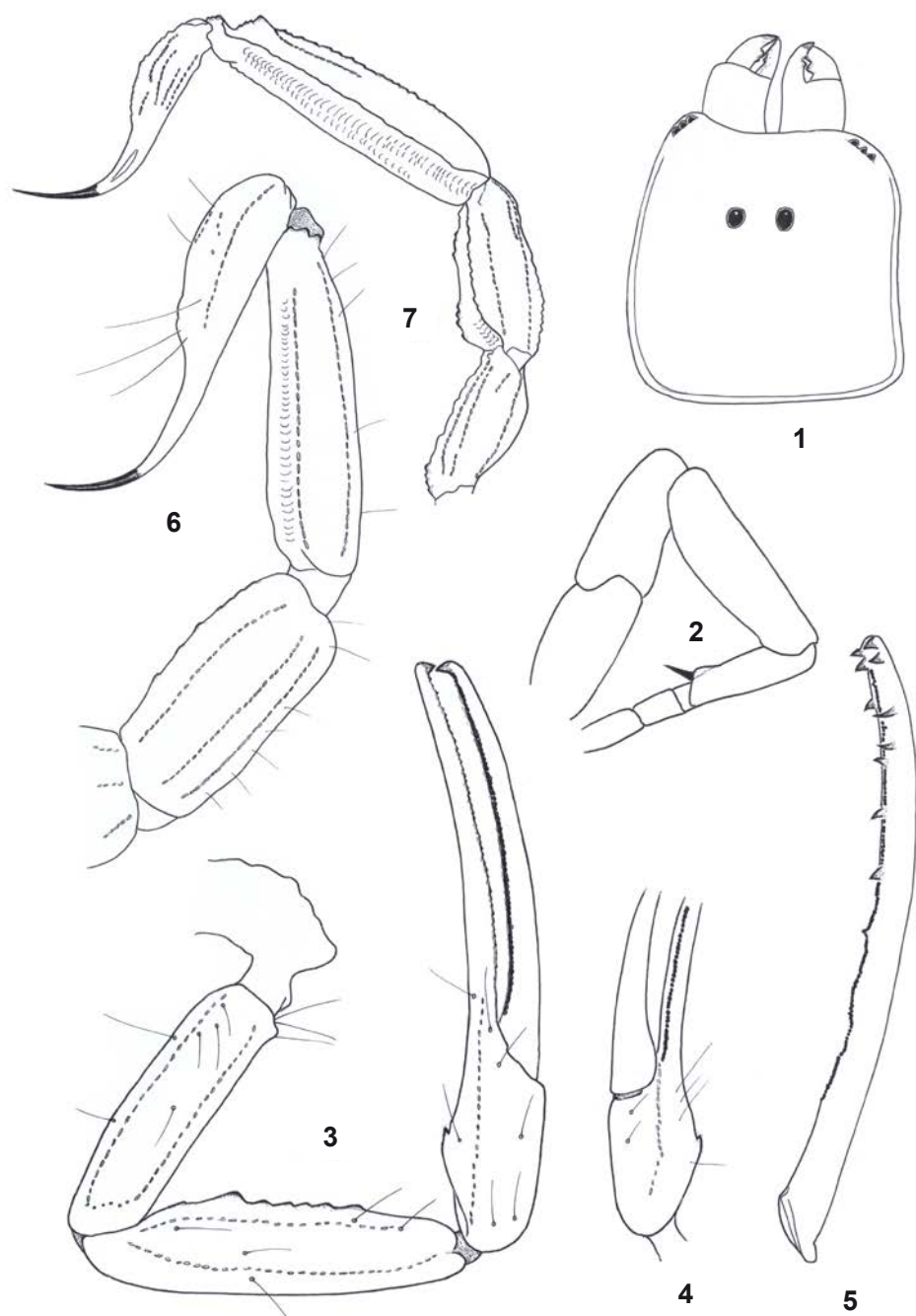
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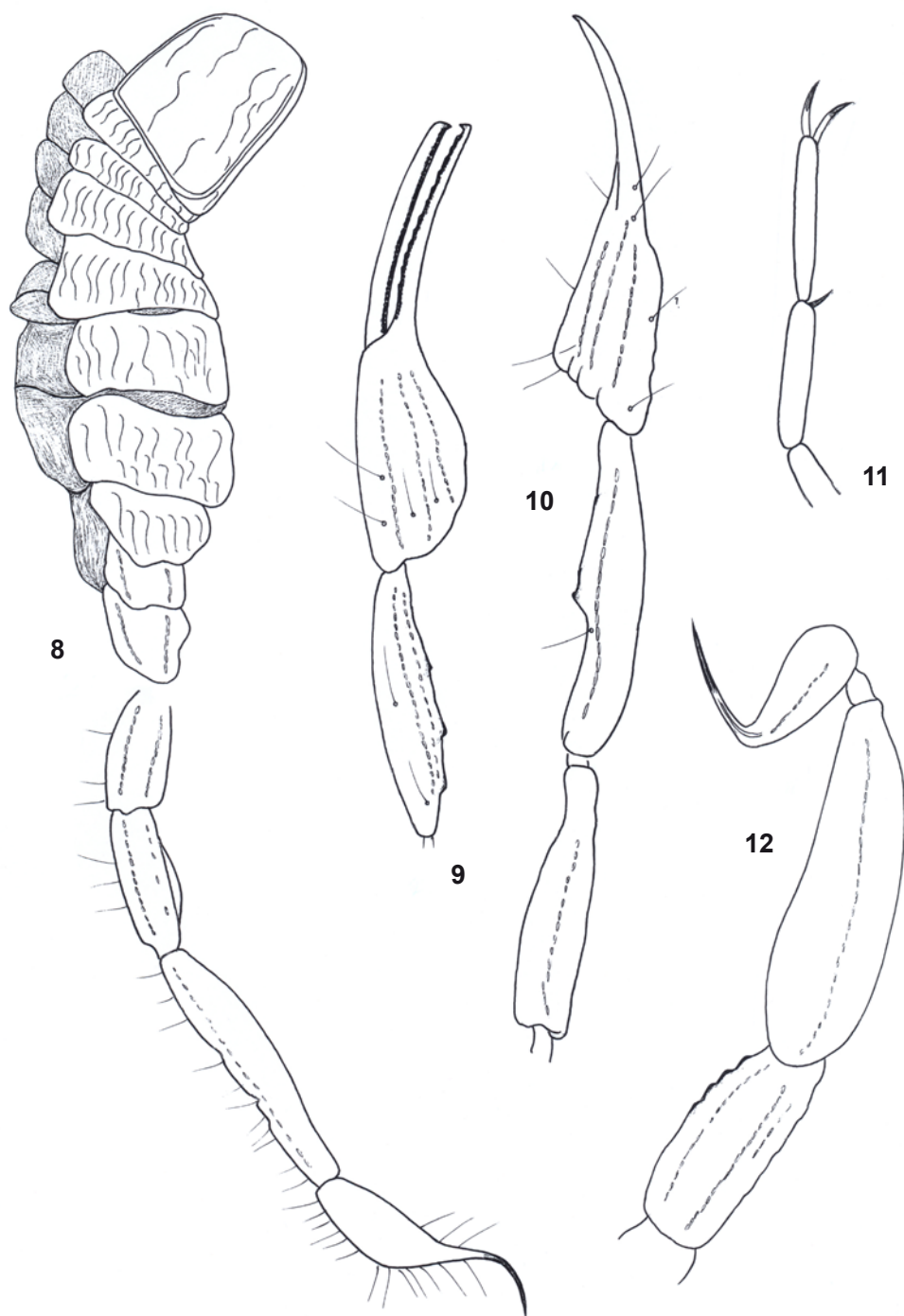
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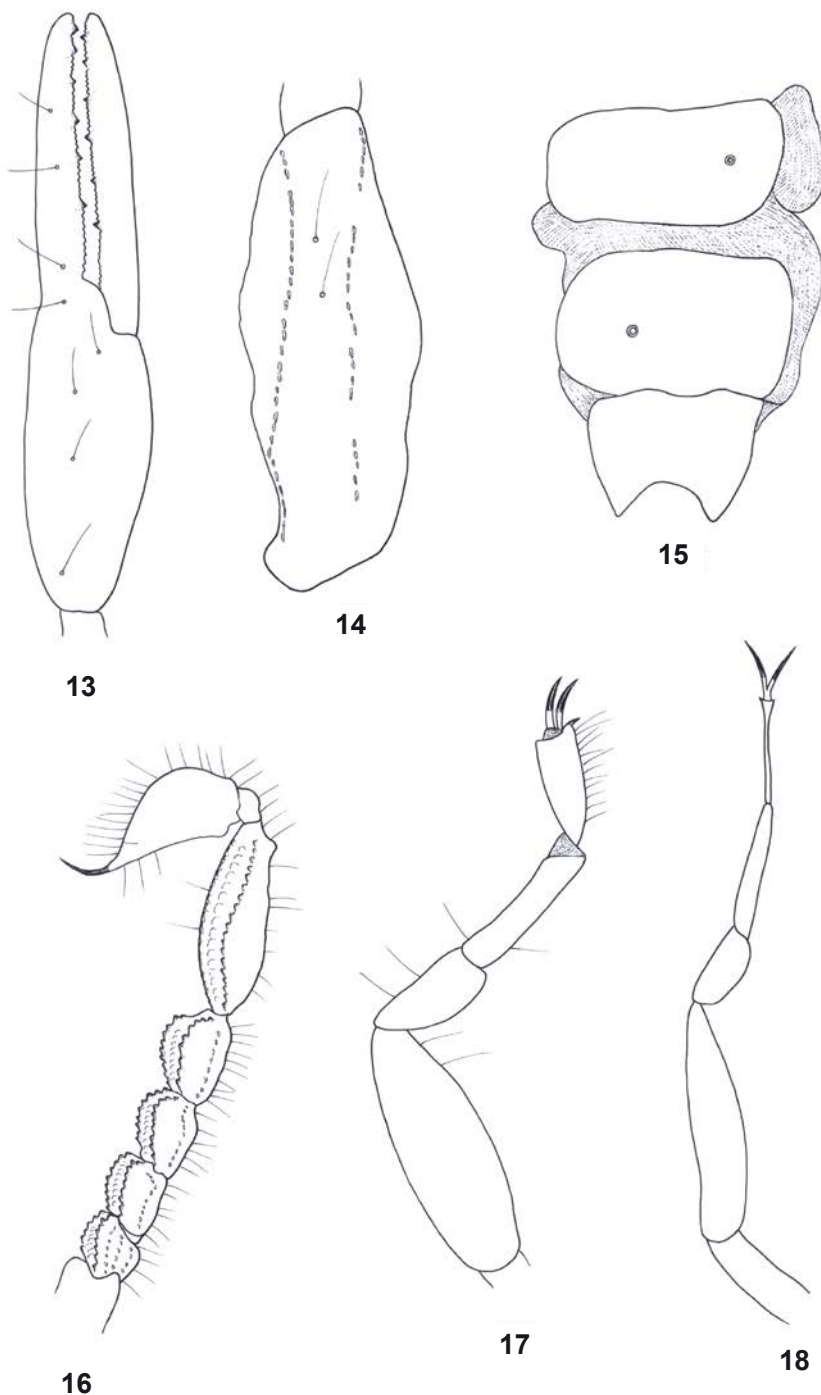
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Figs. 1-4, 6. *Palaeoburmesebuthus ohlhoffi* **sp. n.** Holotype. 1. Carapace, 2. Leg IV showing tibial spur. 3. Right pedipalp showing trichobothria and granulations on movable finger. 4. Chela, ventral aspect, showing trichobothria. Fig. 5: For comparison, movable finger of *Archaeobuthus estephani* from Cretaceous amber of Lebanon. 6. Metasomal segments IV-V and telson, lateral aspect. Fig. 7: Idem for *Palaeoburmesebuthus grimaldii*.



Figs. 8-11. *Chaerilobuthus birmanicus* **sp. n.** Holotype. 8. Dorsal aspect showing carapace, tergites, metasoma and telson. 9-10. Left and right pedipalps showing trichobothria and granulations on fixed and movable fingers. 11. Leg IV, showing tibial spur. Fig. 12. *Palaeoburmesebuthus* sp. Metasomal segments IV-V and telson, lateral aspect.



Figs. 13-18. *Chaerilobuthus bruckschi* **sp. n.** Holotype. 13. Chela, dorso-external aspect, showing trichobothria. 14. Patella, external aspect, showing trichobothria. 15. Sternites V-VII, showing round spiracles. 16. Metasoma and telson, lateral aspect. 17-18. Leg IV, lateral and ventral aspects, showing absence of tibial spur.

## **A NEW GENUS AND SPECIES OF PALAEOBURMESEBUTHINAE LOURENÇO, 2015 (SCORPIONES: ARCHAEOBUTHIDAE) FROM CRETACEOUS AMBER OF MYANMAR**

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**Abstract:** The study of a new scorpion specimen from the Cretaceous amber of Myanmar (Burma) lead to the description of one new genus and species belonging to the subfamily Palaeoburmesebuthinae Lourenço, 2015. The new descriptions bring also further elements to the clarification of the status of this subfamily, proposed in the previous note of this volume. The new descriptions attest once again to the considerable degree of diversity in the Burmese amber-producing forests.

Key-words: scorpion, fossil, new genus, new species, Cretaceous, Burmese amber, Myanmar.

### **Introduction**

After the conclusion of the two previous articles in this volume (Lourenço, 2015a,b), we had the opportunity to examine one new Burmese amber piece containing a remarkable scorpion. Its study leads to the description of one new genus and species belonging to the subfamily Palaeoburmesebuthinae Lourenço, 2015 (see Lourenço, 2015b). The new descriptions bring also further elements to the clarification of the status of the

subfamily Palaeoburmesebuthinae, proposed in the previous note of this volume. For historical details about the scorpions found in Burmese amber, readers can refer to the two previous articles by Lourenço (2015a, b [this volume]).

### **Material and methods:**

The specimen investigated is preserved in very clear block of pale yellow amber. Details of the block are supplied together with the description of the specimen. Many characters, and in particular several trichobothria, are visible in this specimen, allowing detailed investigation. Some characters, however, are not totally observable mainly because the specimen suffered a certain degree of dissection process within the resin. The schematic drawings provided here are interpretations of what was observable. Illustrations and measurements were produced with the aid of a Wild M5 stereomicroscope equipped with a drawing tube and an ocular micrometer. Measurements follow Stahnke (1970) and are given in mm. Trichobothrial notations follow Vachon (1974). Trichobothria were definitely recorded only when their bothria (areoles) could be observed. Other trichobothria may be suggested by the presence of transverse hairs.

### **Systematic description:**

Family Archaeobuthidae Lourenço, 2001

Subfamily Palaeoburmesebuthinae Lourenço, 2015

***Betaburmesebuthus*** Lourenço, **gen. n.**

**Diagnosis:** General morphology shows similarities with Cretaceous Burmese amber genus *Palaeoburmesebuthus* Lourenço, 2002 and also with extant buthid scorpions. The following combination of features can be used to diagnose the new genus: Carapace weakly to moderately granulated. Fixed and movable fingers of pedipalp chela with a series of small rounded granules and a few conspicuous spinoid accessory granules. Trichobothrial pattern with elements resembling those of extant buthid type A (Vachon, 1974): at least 1 to 3 internal, 4 dorsal and 2 external trichobothria on the femur; dorsal trichobothria disposed in beta ( $\beta$ ) configuration (Vachon, 1975); 1 internal, 4-5 dorsal and no ventral trichobothria on patella; 6-7 external trichobothria can be suggested on patella by the presence of fine setae; 4-5 dorso-external and apparently only one ventral on chelal hand; 5 (maybe 6) on fixed finger. Tibial spurs absent from legs III and IV.

The generic name refers to the beta configuration of dorsal trichobothria of femur.

Type species: *Betaburmesebuthus kobberti* Lourenço, sp. n.

***Betaburmesebuthus kobberti*** Lourenço, sp. n. (Figs. 1-9. Photos, 197-198)

Holotype: A juvenile, most certainly a male. Very clear block of pale yellow amber that measured 19 x 9 x 2 mm. Type locality and horizon: Myanmar (Burma), Kachin; precise locality unknown; Lower Cretaceous.

Patronym: The specific name honours Dr. Max Kobbert, Muenster, Germany who arranged facilities for the study of the holotype.

Depository: The type specimen is deposited in the personal collection of Dr. Max Kobbert, Muenster, Germany.

**Diagnosis**: as for the new genus.

### **Description:**

Coloration: the scorpion is yellow to reddish-yellow; carapace and tergites yellow; metasomal segments and telson reddish-yellow; pedipalps and legs yellow. Ventral aspect slightly darker than dorsal aspect.

Morphology. Carapace weakly to moderately granular; anterior margin with a weakly to moderately marked median concavity, as observed in some extant buthids. Carinae inconspicuous; furrows weak to moderate. Median ocular tubercle clearly anterior to the centre of carapace; median eyes moderate in size. Three lateral eyes of moderate size. Sternum pentagonal. Mesosomal tergites weakly to moderately granular, with one median carina and two lateral inconspicuous carinae; VII with five strongly marked carinae. Pectines large, with 20-20(?) teeth; fulcra absent. Sternites weakly granular, with small rounded spiracles. Metasomal segment I to IV rounded with 10-8-8-8 carinae; segment V slender with five carinae; dorsal carinae of segments I–IV without spinoid granules; dorsal aspect of segments I to V weakly depressed; setation on all segments moderately marked. Metasomal segments IV and V are partially destroyed. Telson with a very long pear-shaped vesicle, flattened laterally, as in some extant buthids; weakly granular to smooth; aculeus extremely long and moderately curved; setation strongly marked. Cheliceral dentition only partially visible; fixed and movable fingers with one basal tooth observable; distal teeth moderately long (see Vachon, 1963 as reference). Pedipalp femur pentacarinat; patella with dorso-internal, ventro-internal and dorso-external carinae; internal face with 6-7 spinoid granules. Chela with weakly marked carinae; all faces not granular, smooth. Fixed and movable fingers each with one series of small rounded granules and a few conspicuous spinoid accessory granules; extremity of fingers with stronger spinoid granules; setation of pedipalps moderately marked. Trichobothriotaxy recalling type A (Vachon, 1974) of extants buthids: at least 1 to 3 internal, 4 dorsal and 2 external trichobothria on the femur; dorsal trichobothria disposed in beta ( $\beta$ ) configuration (Vachon, 1975); 1 internal, 4-5 dorsal and no ventral trichobothria on patella; 6-7 external trichobothria can be suggested on patella by the presence of fine setae; 4-5 dorso-external and 1 ventral on chelal hand; 5 or 6 on fixed finger.

Morphometric values (in mm) of male juvenile holotype of *Betaburmesebuthus kobberti* Lourenço, sp. n.



Total length 10.41 (including telson). Carapace: length 1.40, anterior width 0.93, posterior width 1.34. Mesosoma length 2.20. Metasomal segments. I: length 0.80, width 0.54; II: length 0.93, width 0.47; III: length 1.00, depth 0.47; IV: length 1.14, depth 0.47; V: length 1.47, depth 0.46. Telson length 1.47. Vesicle: depth 0.30. Right pedipalp: femur length 1.27, width 0.34; patella length 1.40, width 0.80; chela length 2.14, width 0.34, depth 0.33; movable finger length 1.54.

### **Acknowledgements:**

Thanks are due to Jörg Wunderlich, Hirschberg, Germany for arranging facilities for the publication of this note. To Elise-Anne Leguin (MNHN, Paris) for assistance with the preparation of plates.

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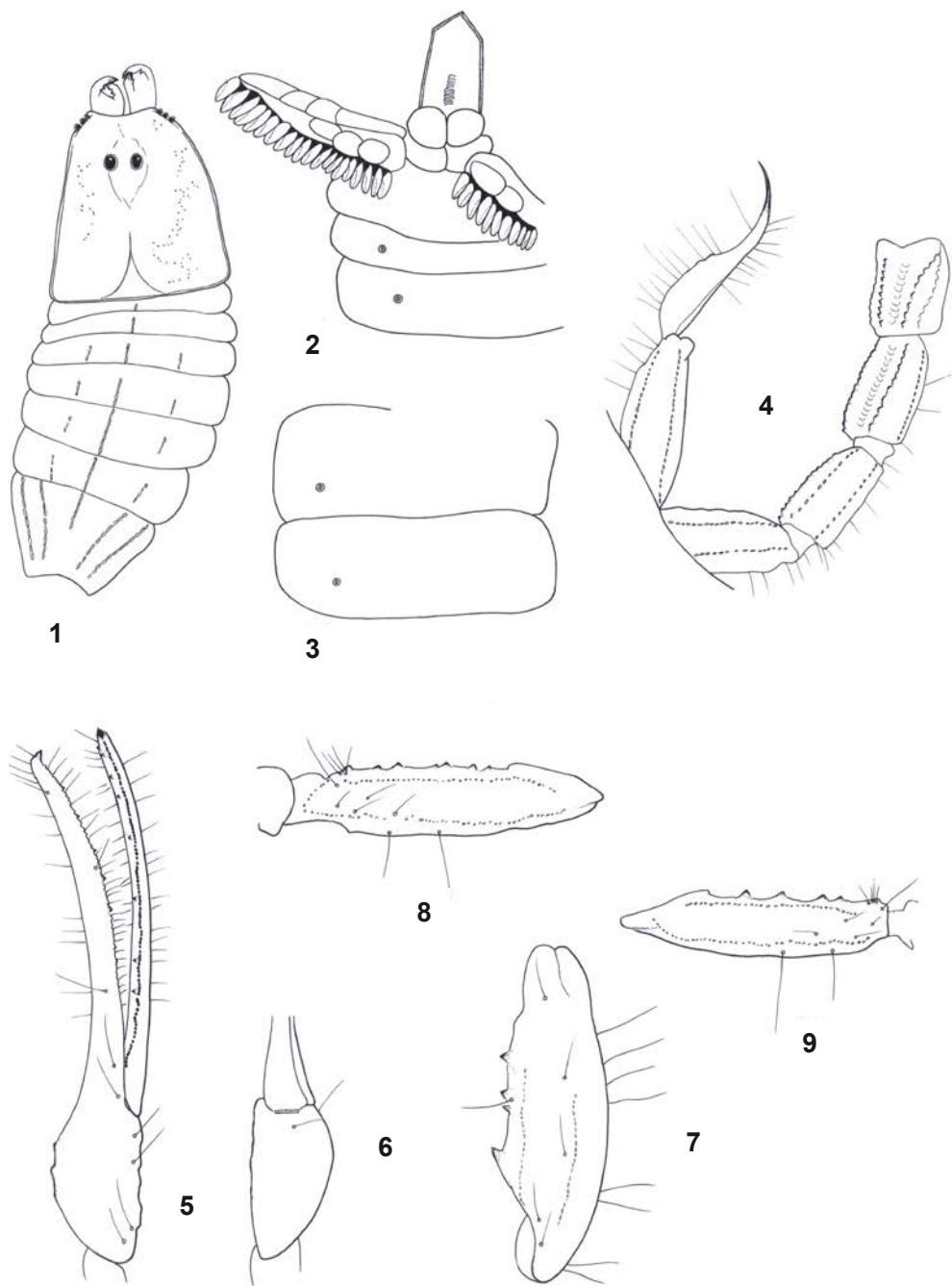
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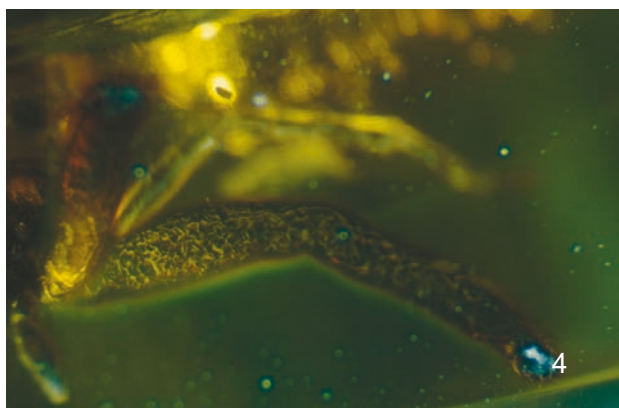
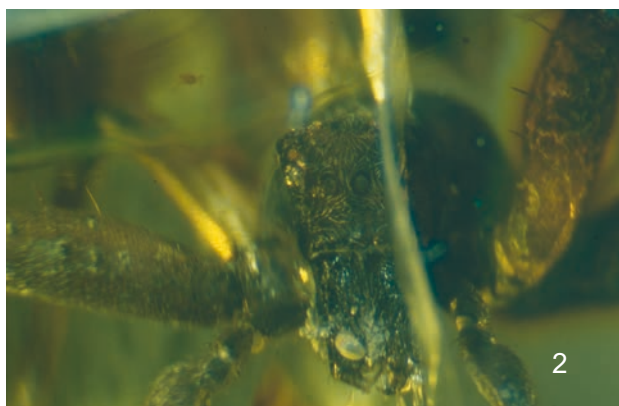
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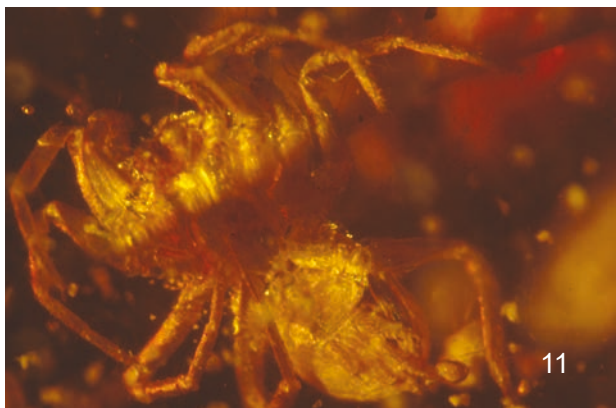
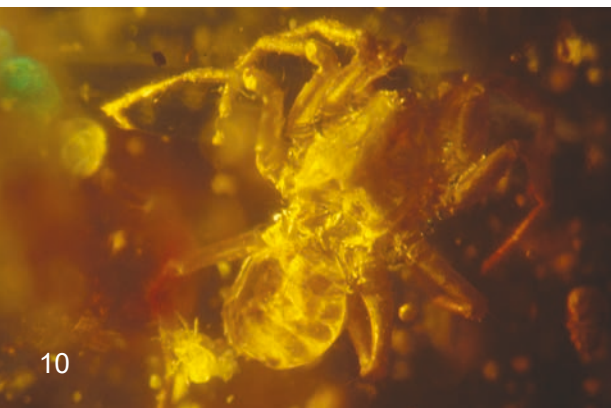
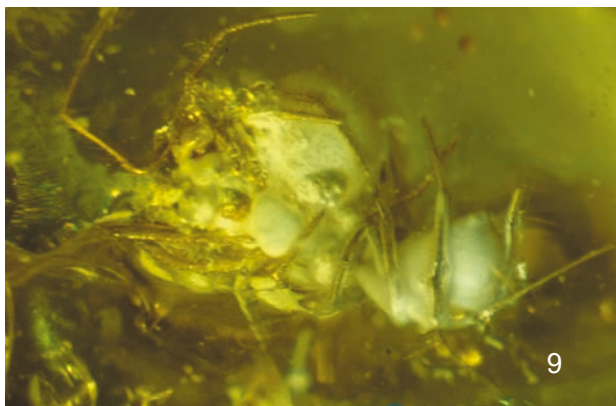
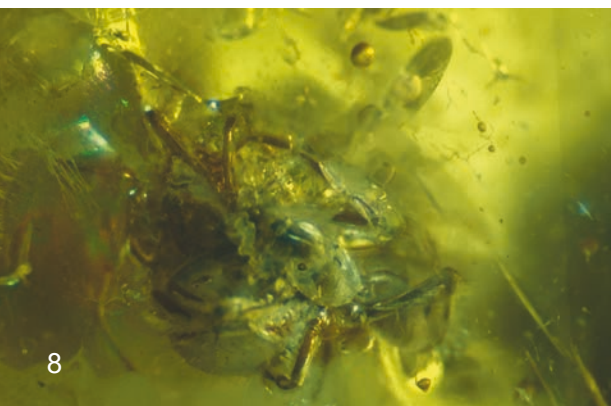
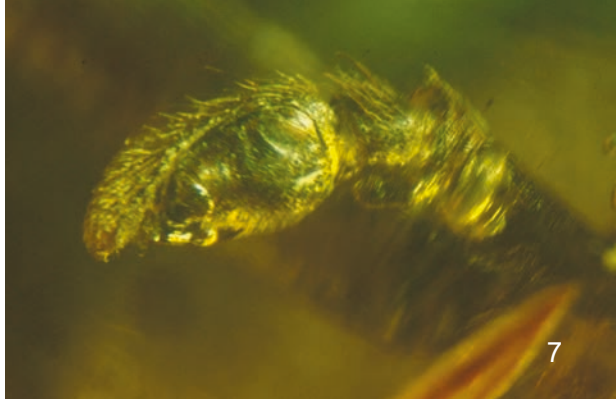
Figs. 1-9. *Betaburmesebuthus kobberti* Lourenço, **sp. n.** Male holotype. 1. Chelicera, carapace and tergites, dorsal aspect. 2. Ventral aspect, showing Sternum, genital operculum pectines and sternites with spiracles. 3. Idem, Sternites V and VI with spiracles. 4. Metasomal segments I to V and telson, lateral aspect; to notice that segments IV and V are cutted. 5-9. Trichobothrial pattern. 5-6. Chela dorso-external and ventral aspects. 7. Patella, dorsal aspect. 8-9. Femurs of right and left pedipalps, dorsal aspect.

## The photos



Photos 1-9: Fossils in Eocene Baltic amber; the remaining photos in Cretaceous ambers, usually from Myanmar (Burma) (Burmite), but photos 62-63 in stone from Liaoning (China).

1-7: *Syphax secedens* n. sp. (THOMISIDAE), holotype ♂ in Eocene Baltic amber, body length 6.5 mm; 1) dorsal aspect of the spider. Note the fissure in the wide piece of amber; 2) anterior aspect of the spider; 3) dorsal aspect of the spider; 4) anterior aspect of the left leg II which cuticula is crumbled by oxidation; 5) prolateral aspect of the right tarsus and metatarsus (part) II;



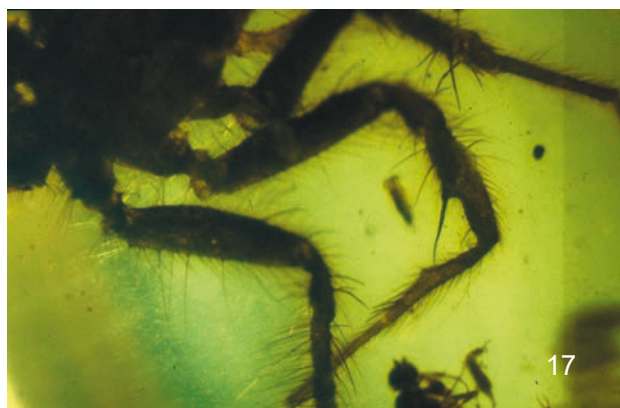
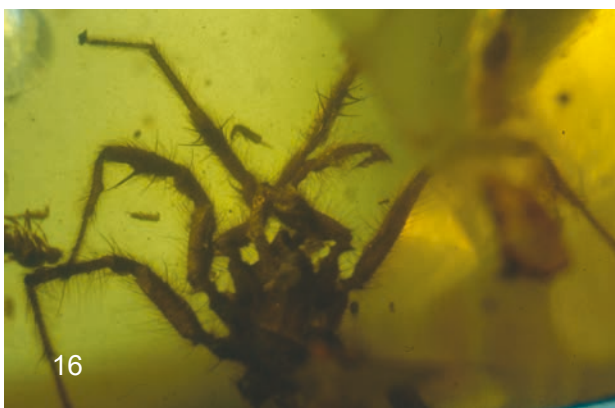
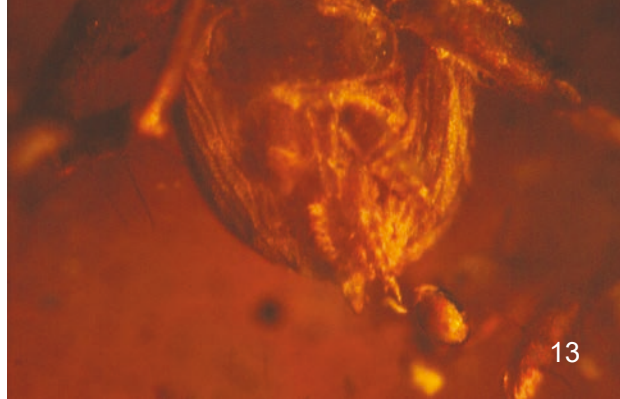
6) ventral aspect of the right tarsus and metatarsus (part) I; 7) prolateral aspect of the right pedipalpus.

8-9: *Spatiator* sp. indet. (SPATIATORIDAE), juvenile F2566/BB/CJW in Eocene Baltic amber, body length 1.25 mm, with its spider prey, *Acrometa* sp. indet. (Synotaxidae), dorsal and ventral aspects. The animals are partly covered with a white emulsion which is typical for Baltic amber inclusions. The extinct Spatiatoridae is a family of the superfamily Archaeoidea (= Palpimanoidea) which members mainly feed on spiders.

10-13: *Cretaceothele lata* n. gen. n. sp. (MESOTHELAÆ: LIPHISTIIDAE), holotype juv. F2447/BU/CJW in Mid Cretaceous Burmite, body length 1.5 mm; 10-11) dorsal and ventral aspects of the spider; 12) prolateral aspect of the right legs I-II and the right pedipalpus; 13) ventral aspect of the spinnerets.

14) *Fossilcalcar praeteritus* n. gen. n. sp. (MYGALOMORPHA: FOSSILCALCARIDAE n. fam.), holotype ♂ in Burmite, body length 6.7 mm, dorsal aspect of the spider which is preserved in a muddy piece of amber.

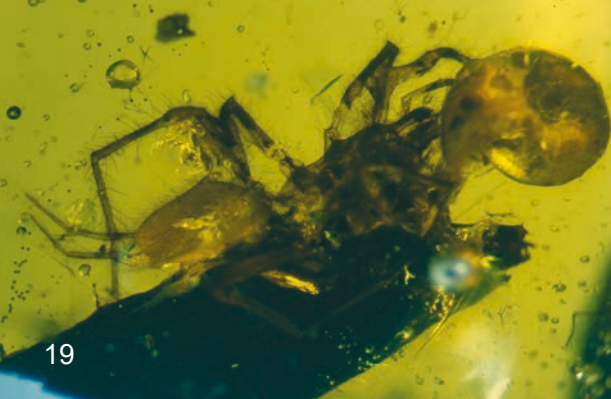




15-17: *Phyxoschemoides collembola* n. gen. n. sp. (MYGALOMORPHA: DIPLURIDAE), holotype ♂ in Burmite, body length ca. 4.5 mm, opisthosoma partly cut off; 15) dorsal aspect of the spider. Note the large „clasping spine“ ventrally on the right tibia II; 16) ventral aspect; 17) dorsal aspect of the right legs, enlarged.

18) *Dipluridae* indet., juv. F2629/BU/CJW in Burmite, body length almost 3.5 mm, dorsal aspect. Note the long spinnerets on the left.





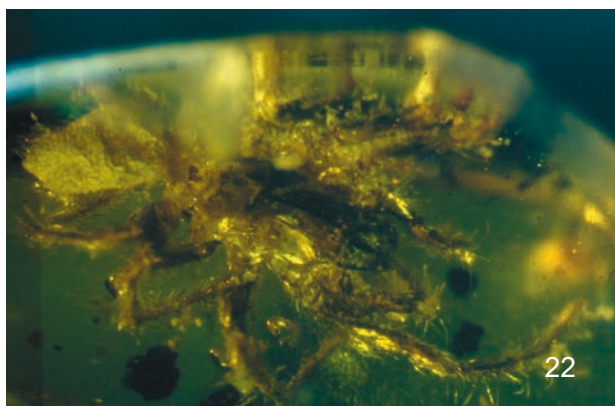
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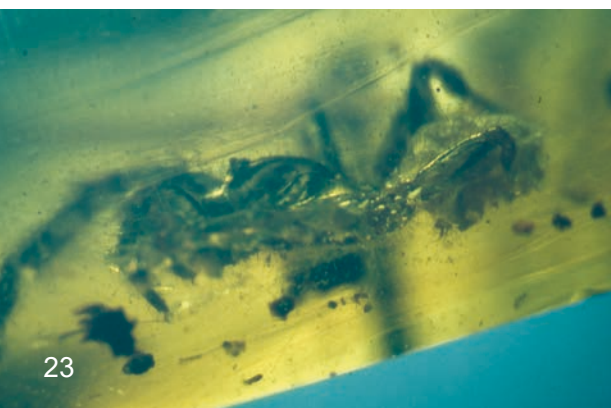
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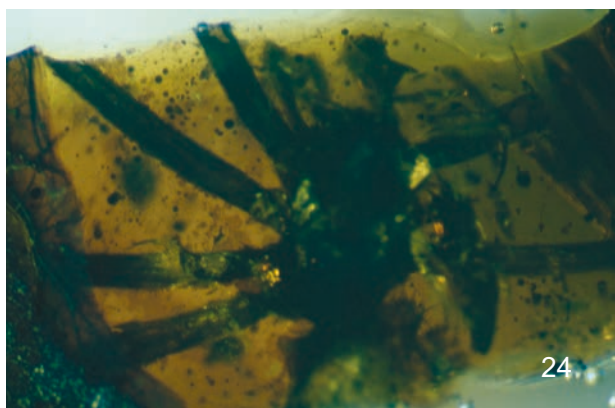
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19) *Dipluridae* indet., juv. F2718/BU/CJW in Burmite, body length 4 mm, dorsal aspect. Note the long spinnerets on the left and the small shell on the right.

20) *Mygalomorpha* indet. (??*Atypidae*), juv. F2608/BU/CJW in Burmite, body length 2.2 mm, dorsal aspect.

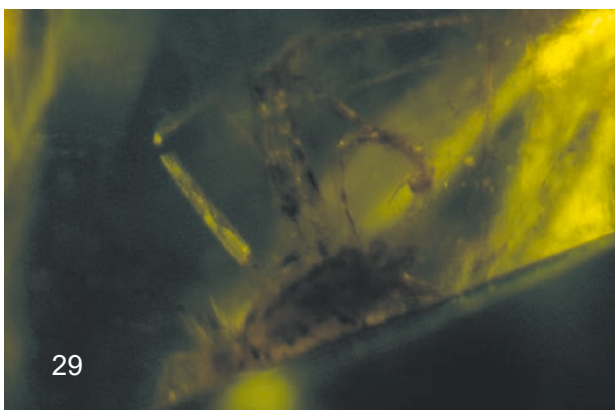
21) Insecta: ?*Mantispida* larva F2608/BU/CjW near a questionable juv. *Atypidae* (see the previous photo), body length 2.2 mm, ventral aspect.

22-23: *Mygalomorpha* indet., juv. F2610/BU/CJW in Burmite, body length 3.7 mm, dorsal and lateral-left aspect.

24) *Jordansegestria detruneo* n. gen. n. sp. (SEGESTRIIDAE), holotype ♂ in Cretaceous Jordanian amber, body length almost 3.5 mm, incompletely and strongly darkened preserved, embedded now in artificial resin.

25-26: *Denticulseggestria rugosa* n. gen. n. sp. (SEGESTRIIDAE), holotype ♂ in Burmite, body length 2.2 mm, dorsal and ventral aspect.





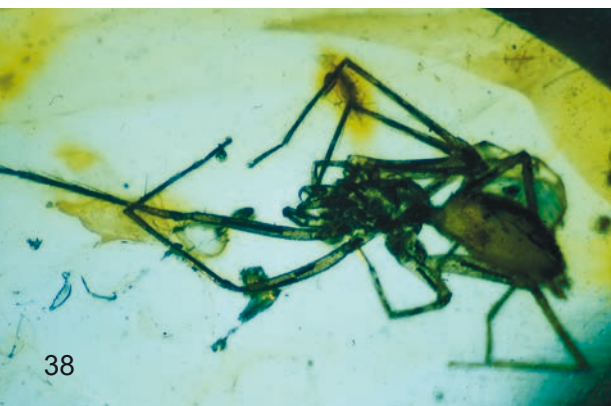
27) *Myansegestria caederens* n. gen. n. sp. (SEGESTRIIDAE), holotype ♂ in Burmite, body length 2.5 mm, dorsal aspect.

28) *Myansegestria engin* n. gen. n. sp. (SEGESTRIIDAE), holotype ♂ in Burmite, body length 3.1 mm, lateral aspect.

29) *Parvosegestria longitibialis* n. gen. n. sp. (SEGESTRIIDAE), holotype, incomplete ♂ in Burmite, body length 2 mm, lateral aspect.

30-31: *Parvosegestria obscura* n. gen. n. sp. (SEGESTRIIDAE), ♂ in Burmite; 30) holotype, body length 2.2 mm, dorsal aspect; 31) paratype, body length 2.2 mm, lateral aspect.

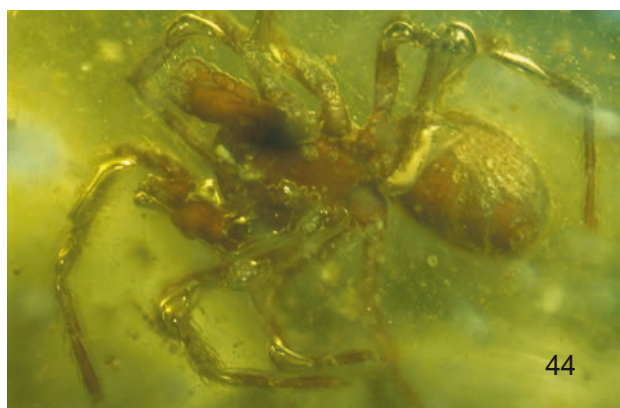




32-34: *Parvosegestria pintgu* n. gen. n. sp. (SEGESTRIIDAE), holotype ♂ in Burmite, body length 2.0 mm; 32) dorsal aspect of the spider; 33) anterior-dorsal aspect of the anterior part of the spider; 34) anterior aspect of the spider.

35) *Parvosegestria triplex* n. gen. n. sp. (SEGESTRIIDAE), holotype ♂ in Burmite, body length 3.2 mm, dorsal aspect of the injured spider.

36) *Burmorchestina pulcher* WUNDERLICH 2008 (OONOPIDAE: ORCHESTININAE), ♀ F2689/BU/CJW in Burmite, dorsal-lateral aspect.



37) *Burmorsolus crassus* n. gen. n. sp. (PLUMORSOLIDAE), holotype ?ad. ♀ in Burmite, body length ca. 4.5 mm, left aspect of the partly decomposed spider.

38-41: *Burmorsolus nonplumosus* n. gen. n. sp. (PLUMORSOLIDAE); 38-39) paratype F2733/BU/CJW, body length 3 mm, dorsal and ventral aspect; 40) paratype F2656/BU/CJW, body length 2.4 mm, dorsal; 41) holotype, body length ca. 2.4 mm, lateral.

42) *Burmorsolus* sp. indet. (PLUMORSOLIDAE), ?ad. ♀ in Burmite, prosoma length 2 mm, dorsal-right aspect, coll. HUANG-HP-B-1277.

43-44: *Bicornoculus levis* n. gen. n. sp. (TETRABLEMMIDAE), holotype ♂ in Burmite, body length 1.9 mm, dorsal and ventral aspect.





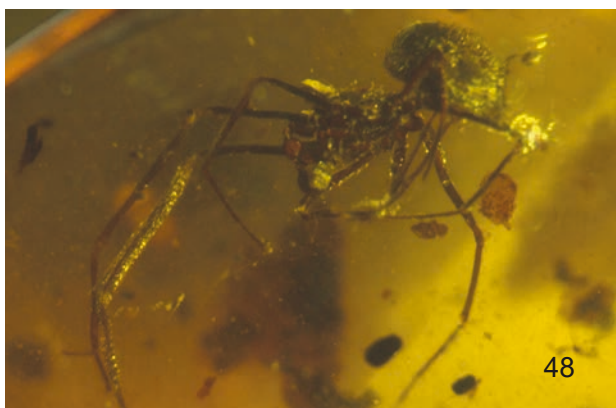
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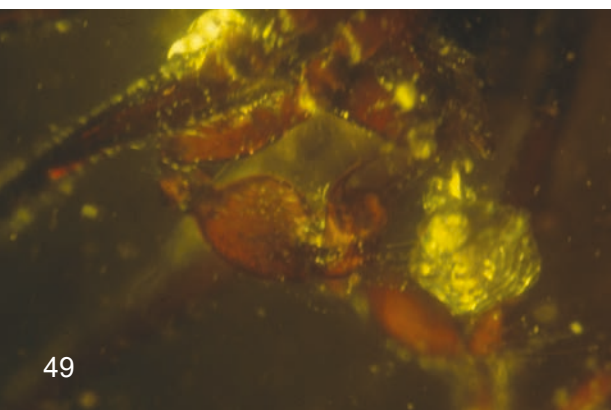
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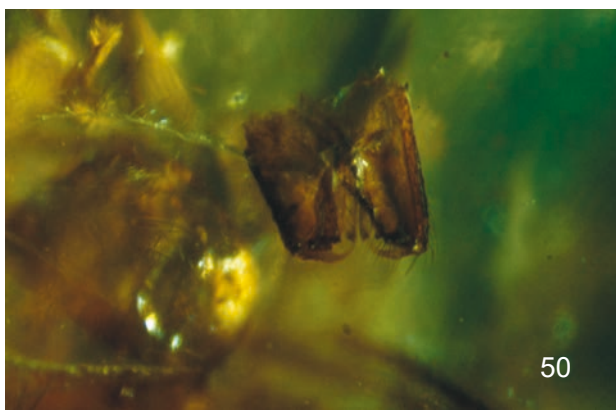
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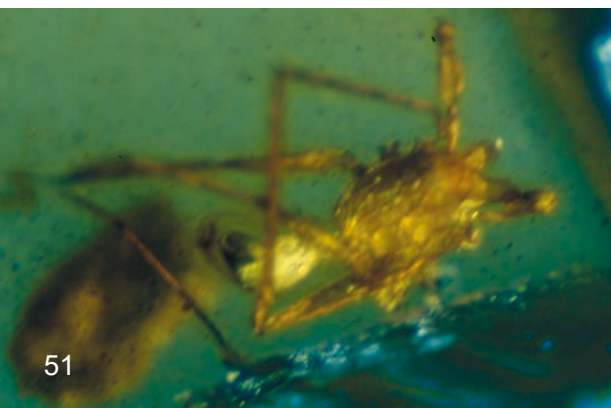
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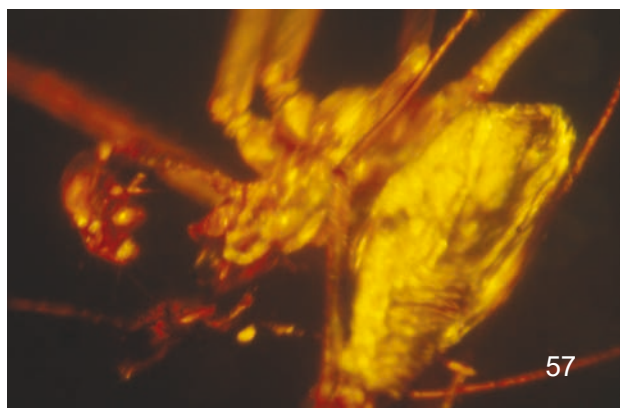
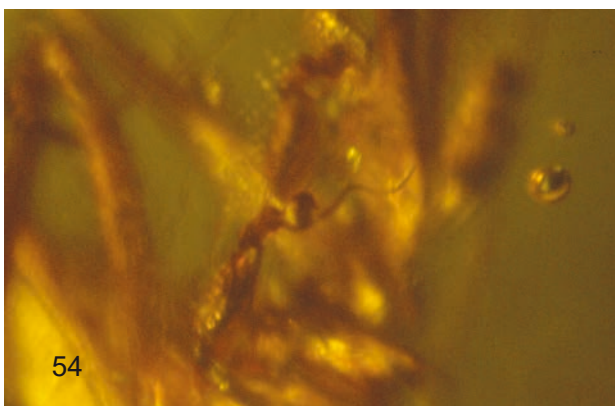
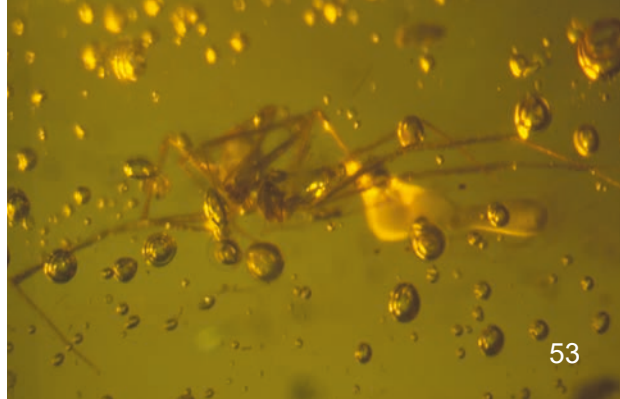
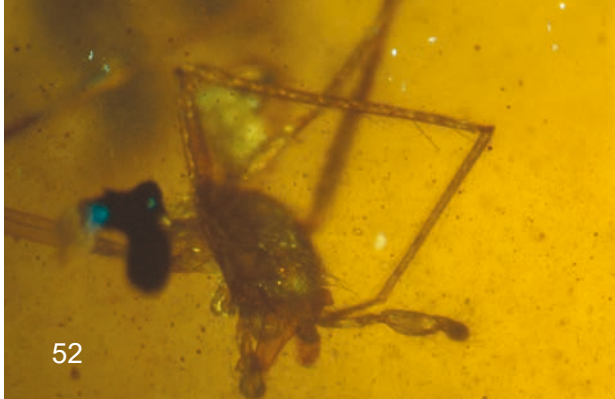


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45) *Eogamasomorpha clara* n. sp. (TETRABLEMMIDAE), holotype ♂ in Burmite, body length 1.1 mm, ventral-lateral aspect.

46) *Praeterpaculla armatura* n. gen. n. sp. (TETRABLEMMIDAE), holotype ♂ in Burmite, body length 3.2 mm, dorsal aspect.

47) *Praeterpaculla biacuta* n. gen. n. sp. (TETRABLEMMIDAE), holotype ♂ in Burmite, body length 3.2 mm, ventral-lateral aspect.



48-49: *Praeterpaculla equester* n. gen. n. sp. (TETRABLEMIDAE), holotype ♂ in Burmite, body length 3.2 mm; 48) lateral aspect of the spider; 49) ventral aspect of the left pedipalpus.

50) *Uniscutosoma aberrans* n. gen. n. sp. (TETRABLEMIDAE), holotype ♂ in Burmite, posterior aspect of the chelicerae.

51-52: *Eopsiloderces serenitas* n. sp. (EOPSILODERCIDAE), holotype ♂ in Burmite, body length 1.25 mm, different dorsal aspects of the spider in a muddy piece of amber.

53-54: *Eopsiloderces* sp. indet. (EOPSILODERCIDAE), ♂ F2634/BU/CJW in Burmite; 53) anterior aspect of the spider; 54) retrolateral aspect of the right pedipalpus in the middle.

55-57: *Leclercera ellenbergeri* n. sp. (PSILODERCIDAE), holotype ♂ in Burmite, body length 1.5 mm, lateral aspect (enlarged in fig. 55; note the well preserved left pedipalpal structures).





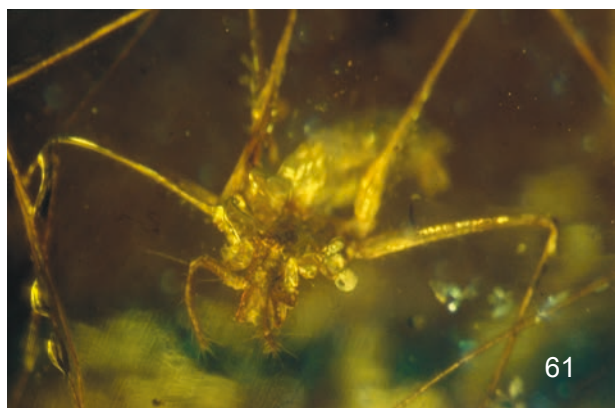
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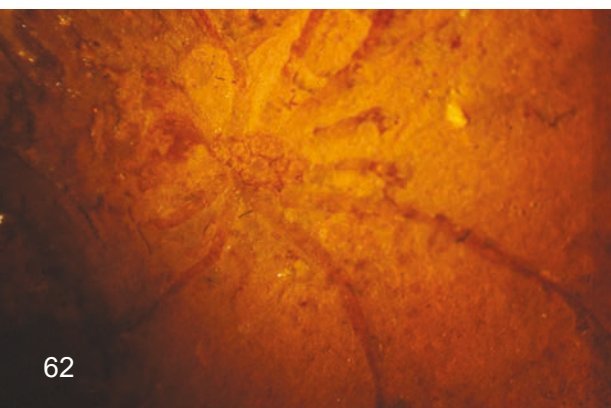
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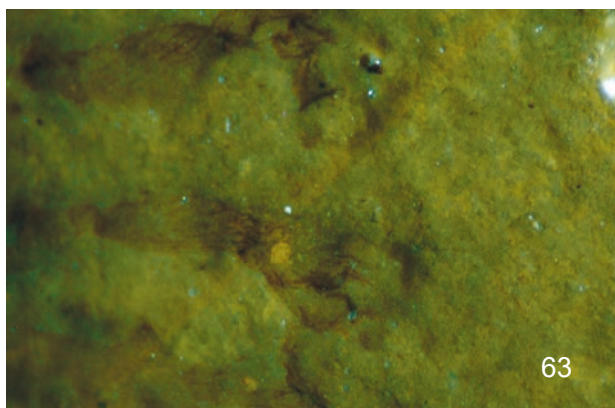
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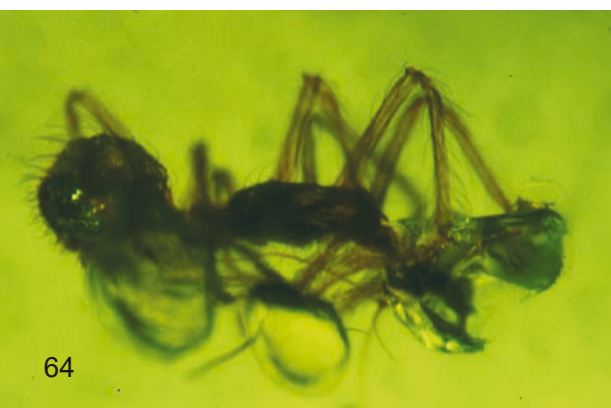
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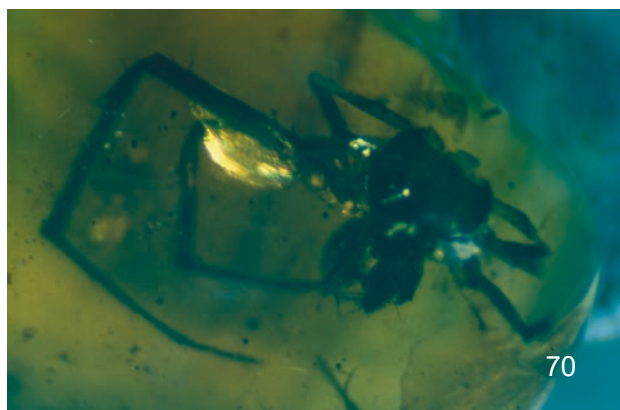
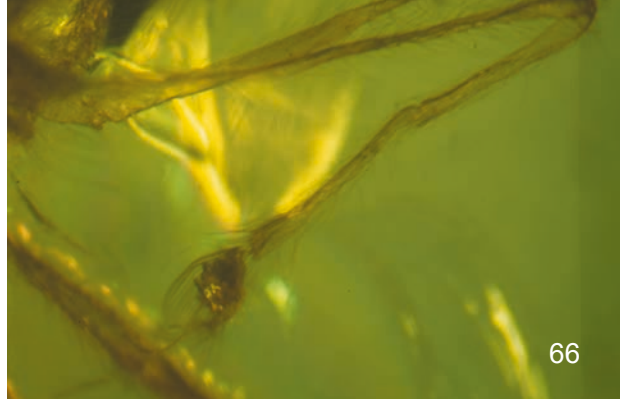


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58) *Leclercera sexoculata* n. sp. (PSILODERCIDAЕ), holotype ♂ in Burmite, body length 1.5 mm, ventral aspect.

59-60: *Leclercera* sp. indet. (PSILODERCIDAЕ), ♂ in Burmite, body length 1.5 mm, ventral and dorsal aspect, unnamed coll.

61) *Leclercera* sp. indet. (PSILODERCIDAЕ), ♀ F2631/BU/CJW in Burmite, body length ca. 1.5 mm, anterior aspect of the spider. Note the long clypeus.



62-63: ?Pholcoidea / ?Leptonetoidea / ?Oecobioidea indet., ♂ F 2454/LI/CJW in stone from Liaoning, China; 62) dorsal aspect of the spider; 63) dorsal aspect of both pedipalpi which bulbi are depressed.

64) Pholcoidea indet., ?ad. ♀ F2633/BU/CJW in Burmite, body length 1.0 mm, lateral aspect of the spider which body is strongly deformed.

65-66: *Longissipalpus minor* n. gen. n. sp. (MONGOLARACHNIDAE), paratype ♂ in Burmite, body length 2.2 mm; 65) lateral aspect of the body; 66) retrolateral aspect of the right pedipalpus. Note the

extremely long pedipalpal articles and the small cymbium and bulbus.

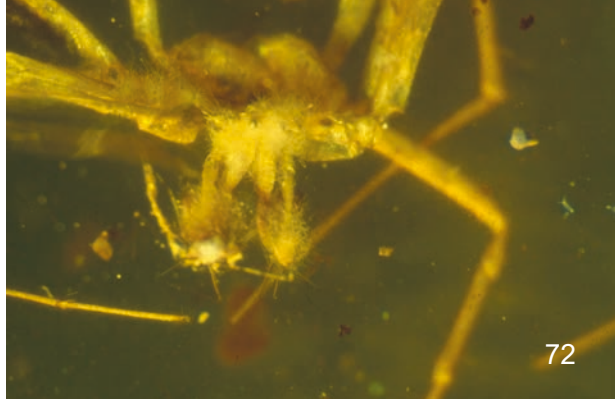
67-69: *Pedipalparaneus seldeni* n. gen. n. sp. (MONGOLARACHNIDAE), holotype ♂ in Burmite, body length ca. 4 mm, dorsal, posterior-lateral and anterior aspects of the spider. Note the opisthosomal humps which are well observable in fig. 68.

70) *Spinicreber antiquus* n. gen. n. sp. (PHOLCOCHYROCERIDAE), holotype ♂ in Burmite, body length 2.5 mm, anterior-dorsal aspect, the opisthosoma is missing.

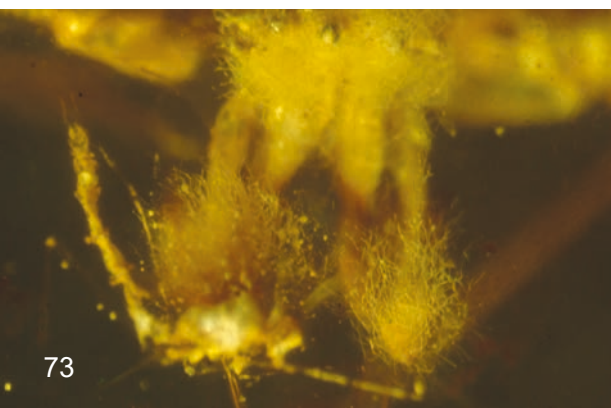




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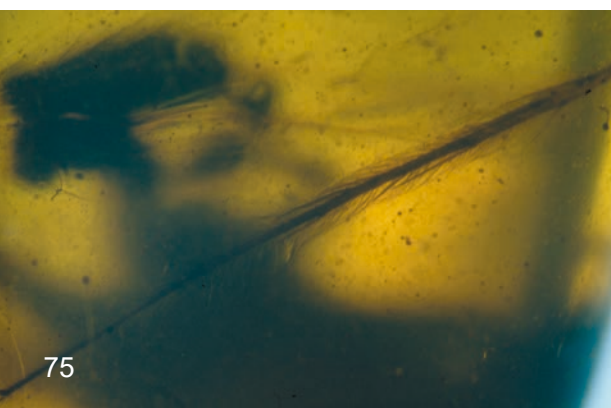
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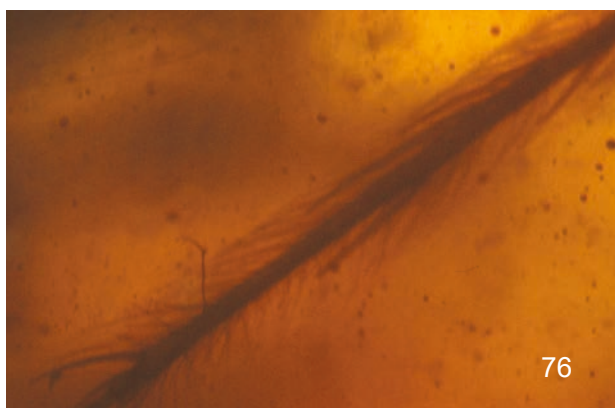
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71-73: *Spinipalpus vetus* n. gen. n. sp. (PHOLCOCHYROCERIDAE), holotype ♂ in Burmite, body length 2.5 mm, partly decomposed, anterior aspect, enlarged in figs. 72-73). Note the numerous hyphae and remain of a small Diptera left below, probably remains of a prey.

74-76: *Autotomiana hirsutipes* n. gen. n. sp. (PRAETERLEPTONETIDAE), holotype ♂, preserved in a muddy piece of Burmite, body length ca. 7 mm; 74) anterior dorsal-right aspect; note the patellar stump (autotomy) below the middle left of remains of 2 insect's excrement; 75-76) dorsal

aspect of the hairy right tarsus and metatarsus I, enlarged in fig. 76).

77) *Autotomiana* sp. 1 (PRAETERLEPTONETIDAE), ?juv. ♀ in a muddy piece of Burmite, body length 3.15 mm, dorsal aspect.

78) ?*Autotomiana* sp. 2 (PRAETERLEPTONETIDAE), ?juv. ♀, body length 3.7 mm, dorsal aspect.

79) *Biapophysys beate* n. gen. n. sp. (PRAETERLEPTONETIDAE), holotype ♂ in Burmite, body length 2 mm, dorsal aspect.

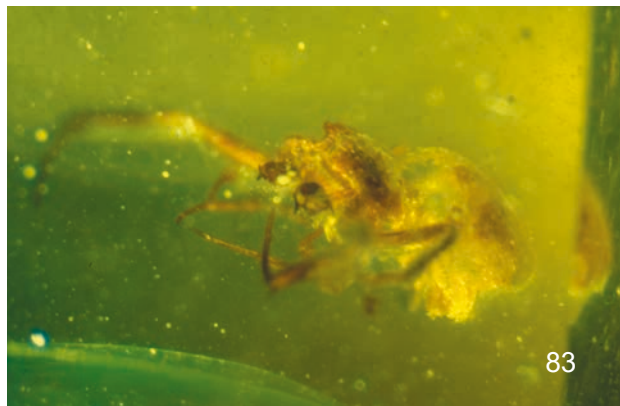




80) *Praeterleptoneta tibialis* WUNDERLICH 2011 (PRAETERLEPTONETIDAE), ♂ F2453/ BU/CJW in Burmite, body length 1.8 mm, dorsal aspect. Note the numerous droplets in the amber.

81) *Bicalamistrum mixtum* n. gen. n. sp. (PRAETERLEPTONETIDAE), holotype subad. ♂ in Burmite, body length 3 mm, lateral aspect of the anterior part of the spider.

82-83: *Crassitibia tenuimana* n. gen. n. sp. (PRAETERLEPTONETIDAE), holotype ♂ in Burmite, body length 1.6 mm, dorsal and anterior-lateral aspect of the spider.





84



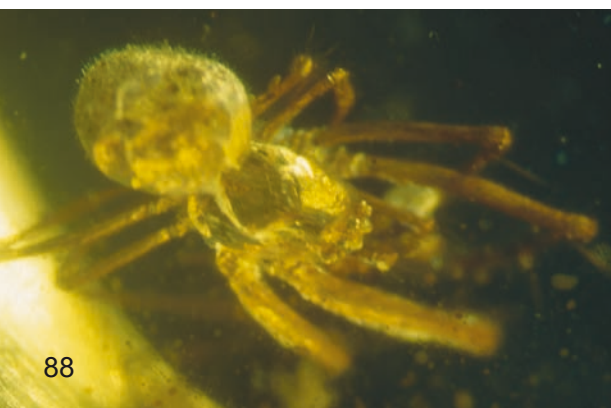
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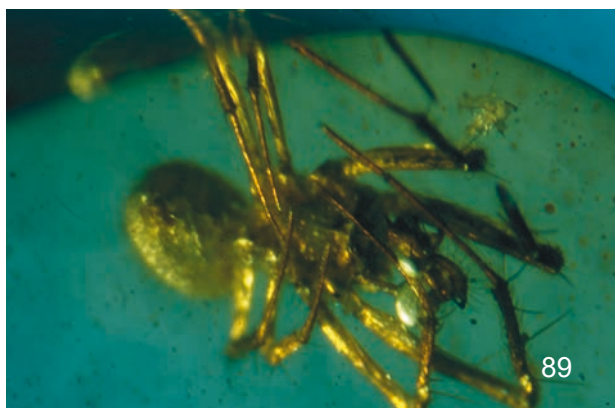
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88



89

84) *Crassitibia longispina* n. gen. n. sp. (PRAETERLEPTONETIDAE), holotype ♂ in Burmite, body length 1.3 mm, anterior aspect of the spider.

85-86: *Curvitibia curimana* n. gen. n. sp. (PRAETERLEPTONETIDAE), holotype ♂ in Burmite, body length 1.2 mm, dorsal and ventral aspect of the spider.

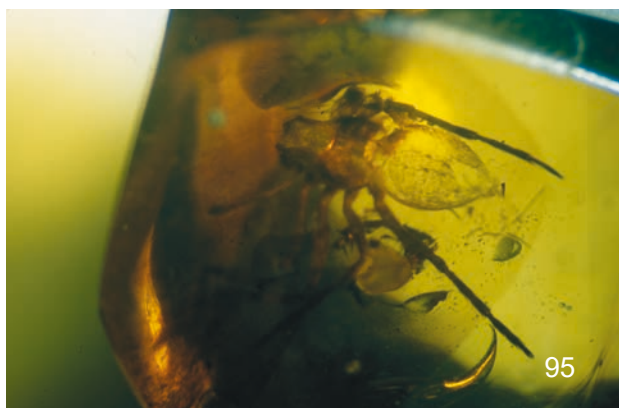
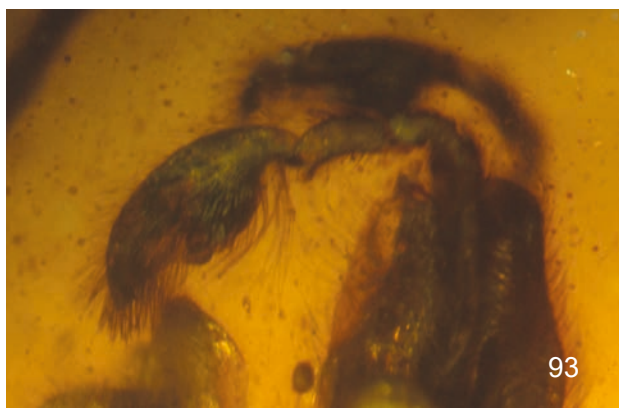
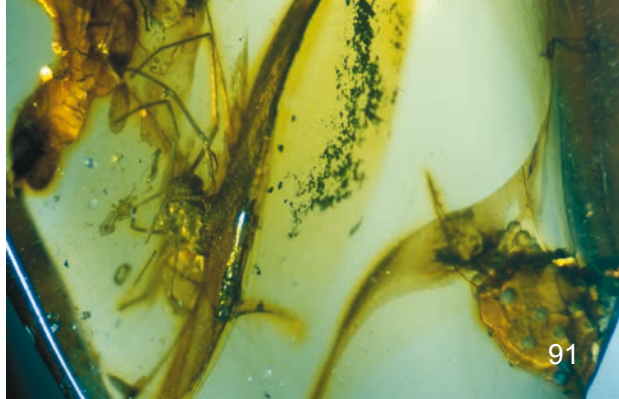
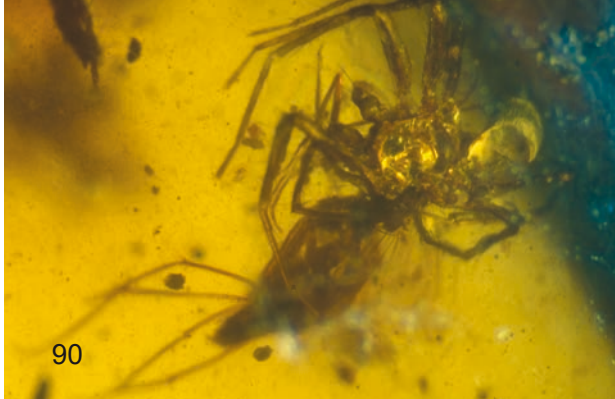
87) *Groehnianus burmensis* n. gen. n. sp. (PRAETERLEPTONETIDAE), holotype ♂ in Burmite, body length 1.25 mm, dorsal aspect of the spider. Note the bubbles on the legs.

88-89: *Hypotheridiosoma falcata* n. sp. (PRAETERLEPTONETIDAE), holotype ♂ in Burmite, body length 1.1 mm, dorsal and ventral aspect of the spider.

90) *Spinipalpitibia maior* n. gen. n. sp. (PRAETERLEPTONETIDAE), holotype ♂ in Burmite, body length 1.8 mm, dorsal aspect, with its questionable prey, a Diptera.

91) ?*Praeterleptonetidae* indet., ♀ F2735/BU/CJW in Burmite, left of the middle, body length 2.5 mm, with two lumps of blue eggs near the left and the right margin of the photo.





92-93: *Archaelagonops propinquus* **n. sp.** (LAGONOMEGOPIDAE), holotype ♂ in Burmite, body length 3.5 mm; 92) lateral aspect of the spider; 93) left aspect of the pedipalpi.

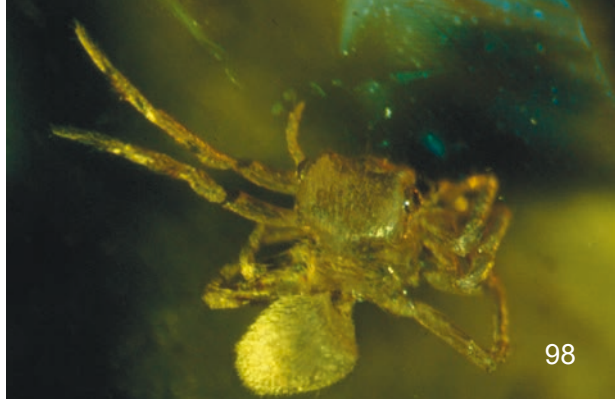
94) *Archaelagonops scorsum* **n. sp.** (LAGONOMEGOPIDAE), holotype ♂ in Burmite, body length 3.8 mm, dorsal-lateral aspect of the spider.

95-97: *Archaelagonops* **sp. indet.** (LAGONOMEGOPIDAE), ♀ F2605/BU/CJW, body length 4.1 mm, dorsal, anterior and lateral aspects. Note the indistinct markings on the translucent opisthosoma in fig. 95.

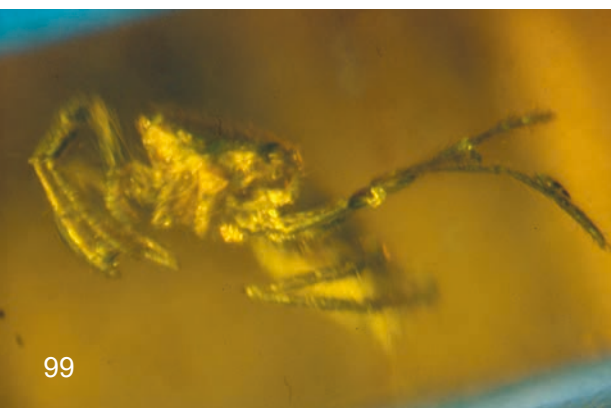




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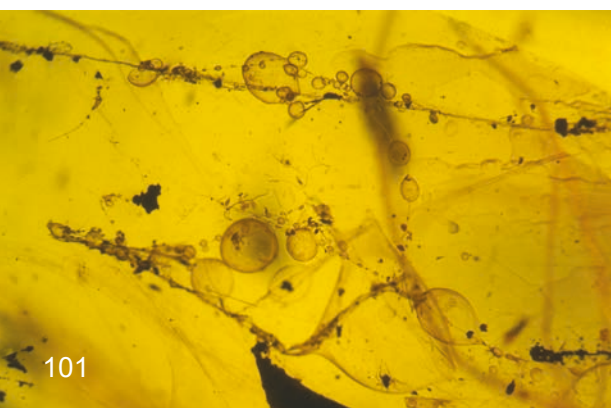
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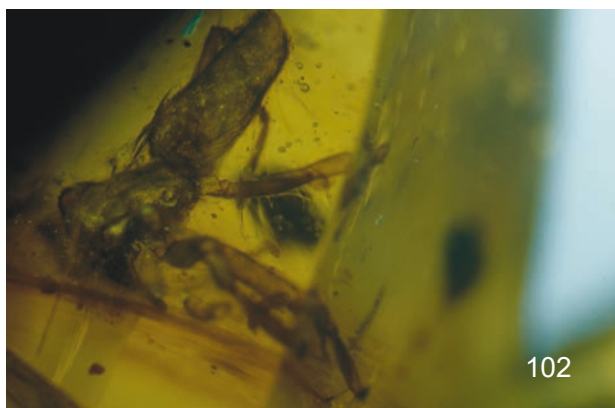
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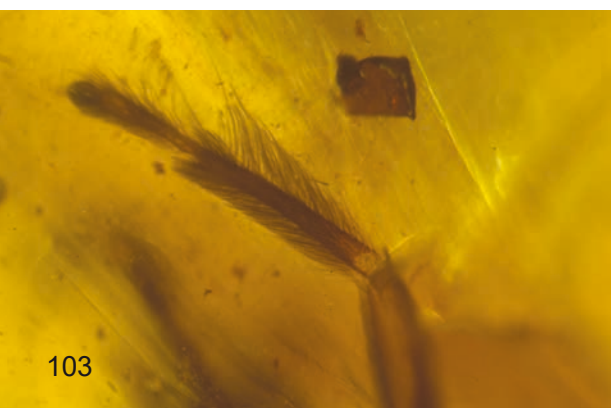
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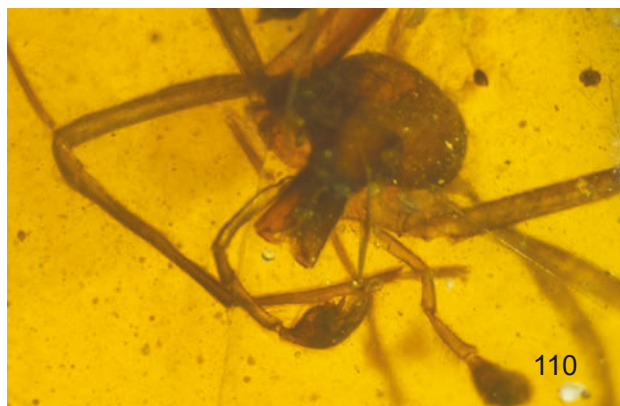
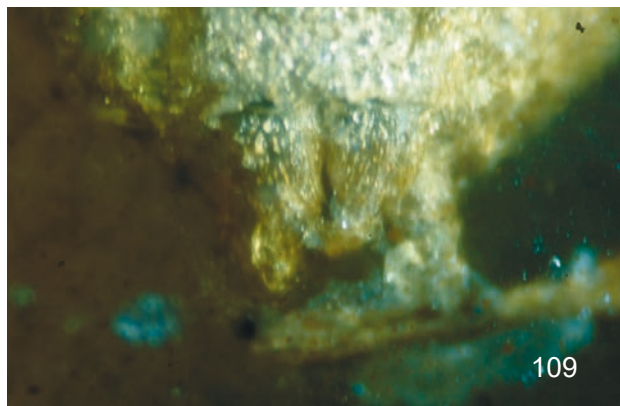
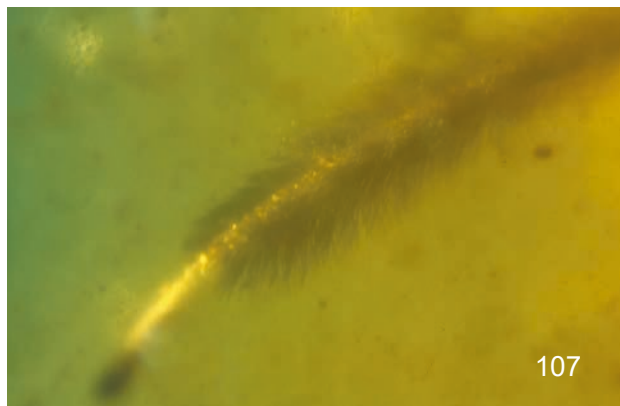
98-99: ?*Lagonomegops tuber* n. sp. (LAGONOMEGOPIDAE), holotype juv. in Burmite, body length 1.2 mm, dorsal and anterior aspect of the spider.

100) *Cymbiolagonops cambiocalcar* n. gen. n. sp. (LAGONOMEGOPIDAE), holotype ♂ in Burmite, body length ca. 4 mm, lateral aspect.

101) Large (1.5 cm wide) part of a capture web with sticky droplets which probably originated from a member of the superfamily Araneoidea, preserved near the holotype of *Cymbiolagonops cambiocalcar*, F2687/BU/CJW.

102-103: *Lagonomegopidae* indet., ♀ F2628/BU/CJW, body length 5 mm; 102) dorsal-lateral aspect of the spider; 103) dorsal aspect of the left tarsus and metatarsus III.





104-105: *Lineaburmops beigeli* n. gen. n. sp. (LAGONOMEGOPIDAE), holotype ♂ in Burmite, body length 3 mm, left and anterior right aspects.

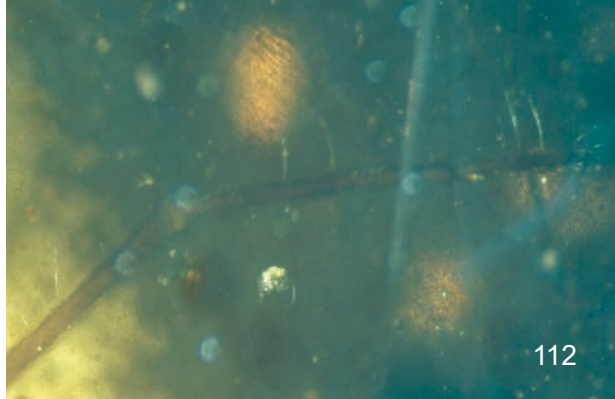
106-107: *Lineaburmops hirsutipes* n. gen. n. sp. (LAGONOMEGOPIDAE), holotype ♂ in Burmite, body length 5 mm; 106) dorsal aspect of the spider; 107) ventral aspect of the right tarsus and metatarsus I in muddy amber.

108-109: *Parviburmops brevipalpus* n. gen. n. sp. (LAGONOMEGOPIDAE), holotype ♂ in Burmite, body length 3.2 mm; 108) ventral aspect of the spider; 109) spinnerets.

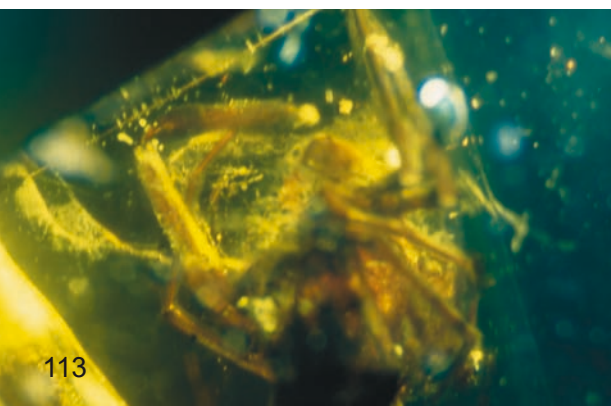
110-112: *Paxillomegops longipes* n. gen. n. sp. (LAGONOMEGOPIDAE), holotype ♂ in Burmite,



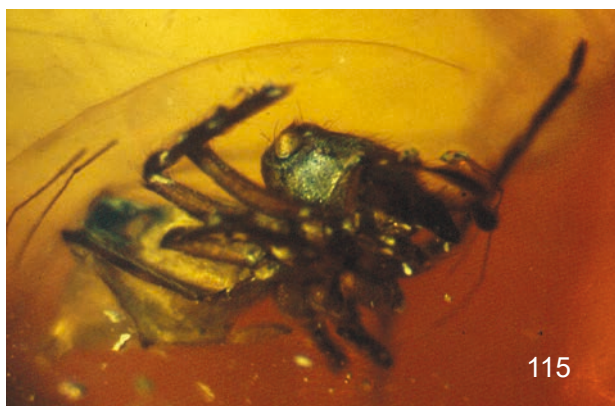
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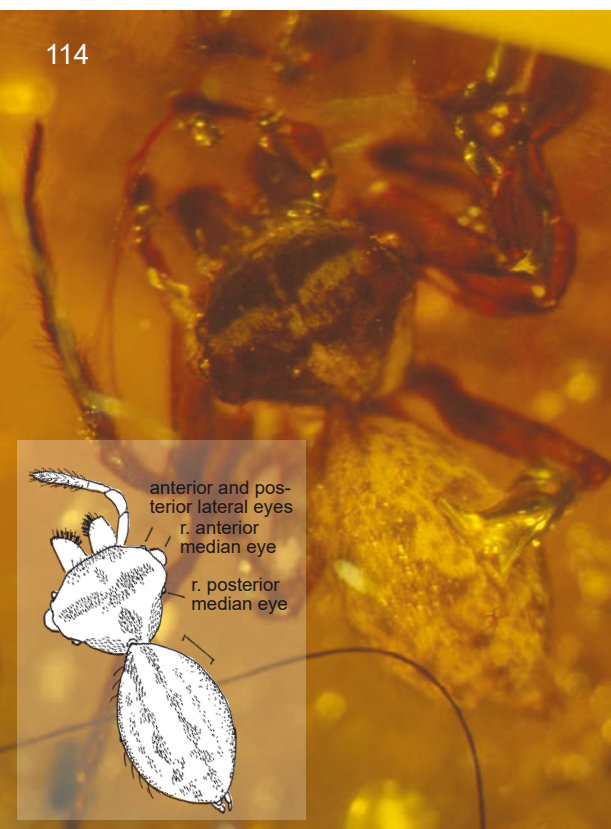
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113



115



114

anterior and posterior lateral eyes  
r. anterior median eye  
r. posterior median eye



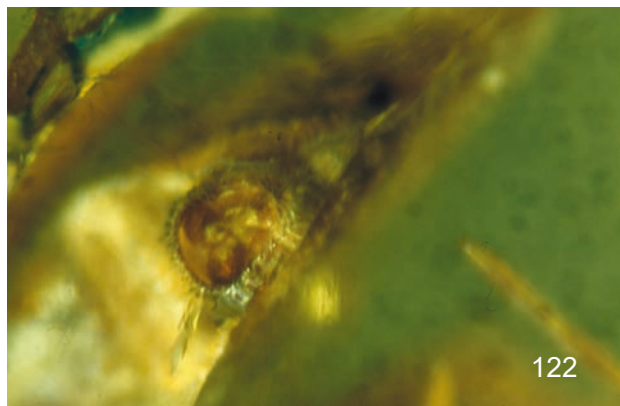
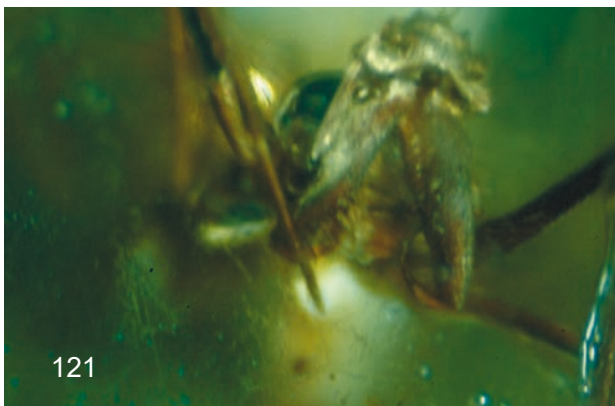
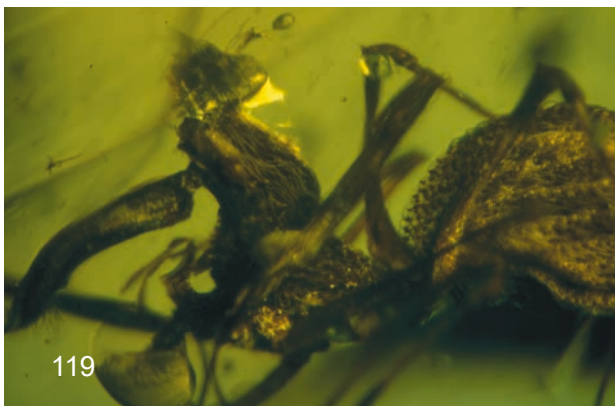
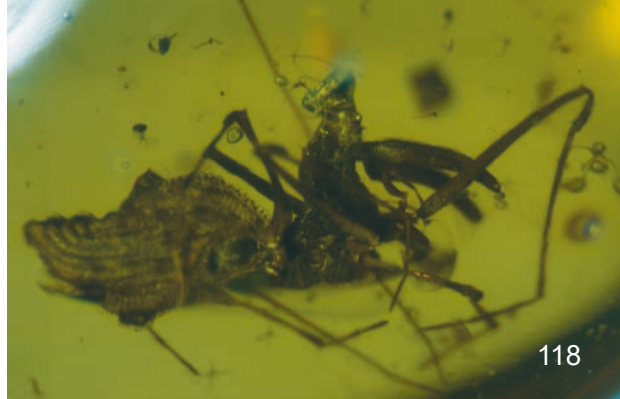
116

body length 4 mm; 110) anterior-dorsal aspect of the spider; 111) anterior aspect; 112) prolateral aspect of the right tarsus and metatarsus I. Note the long dorsal trichobothria!

113) *?Paxillomegops brevipes* **n. gen. n. sp.** (LAGONOMEGOPIDAE), holotype ♂ in Burmite, body length 4 mm. The spider is spun in by threads and has been the prey of a spider.

114-117: *Picturmegops signatus* **n. gen. n. sp.** (LAGONOMEGOPIDAE), holotype ♀ in Burmite, body length 3.6 mm; 114) dorsal aspect of the spider. Note the coloured hairs of the body and the

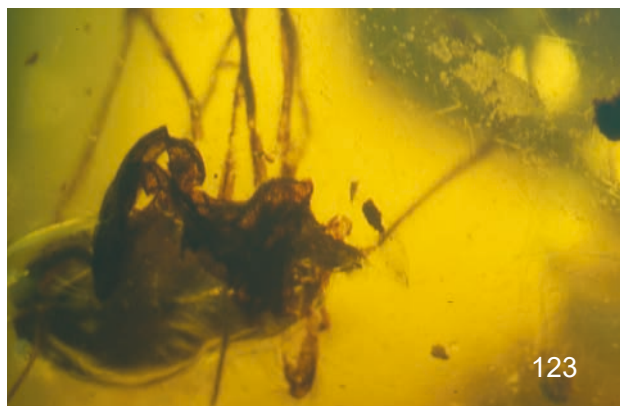




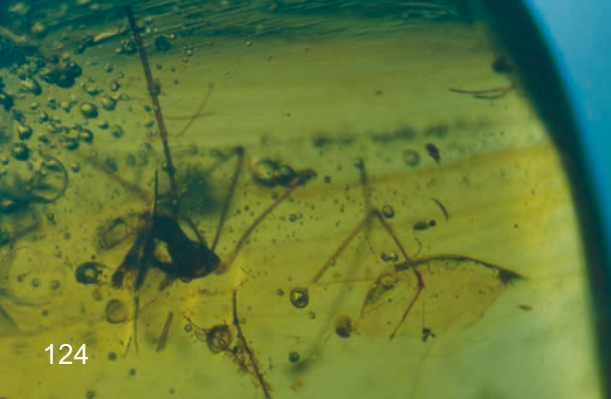
large eyes in the lateral position! 115) lateral (right) position; 116) enlarged; note the large anterior median eye and the tiny lateral eyes! 117) left leg I, prodorsal aspect.

118-122: *Burmesarchaea grimaldii* (PENNEY 2003) (ARCHAEIDAE), ♀ in Burmite, determination not quite sure in figs. 120-122 (F2521); 118-119: F2709, lateral aspects of the spider, body length 2.8 mm; 120-121) dorsal and anterior aspects of the spider; 122) spinnerets.

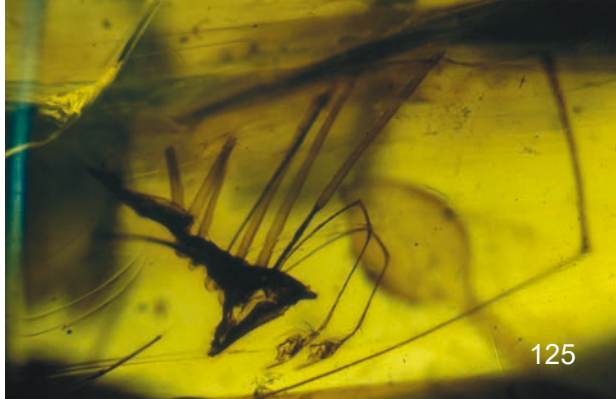
123) *Archaeidae* indet., ♂ F2441/BU/CJW in Burmite, body length almost 2 mm, lateral aspect of the strongly deformed spider.



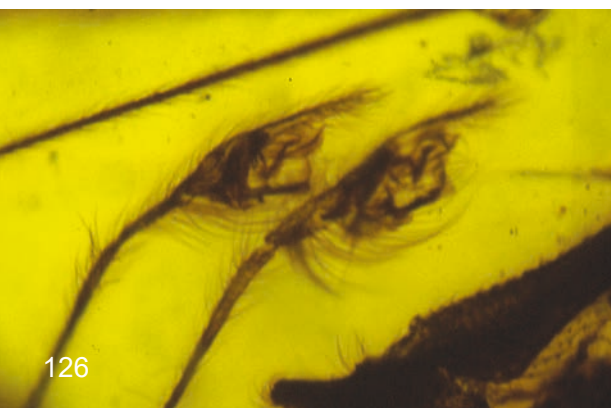




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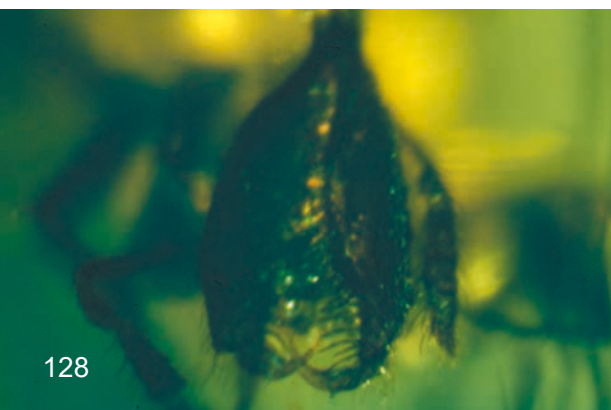
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126



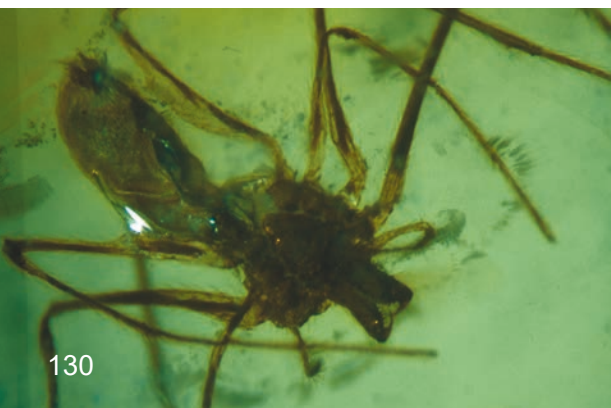
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128



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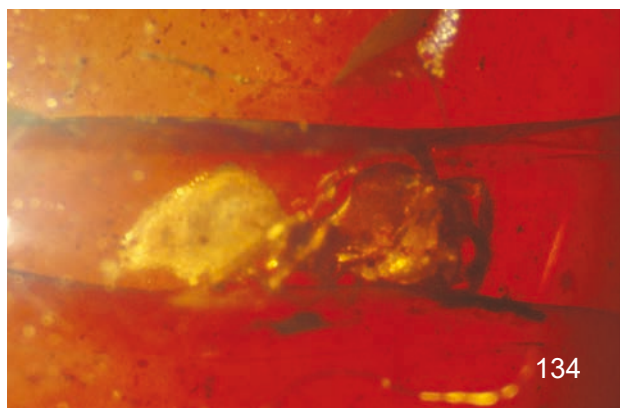
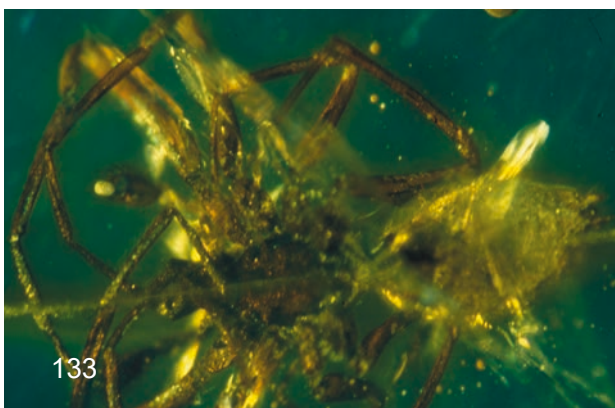


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124) *Lacunauchenius longissipes* **n. sp.** (ARCHAEIDAE), holotype ♂ in Burmite, body length at least 2 mm, lateral (left) aspect. Note the long and slender neck!

125-126: *Lacunauchenius pilosus* **n. sp.** (ARCHAEIDAE), holotype ♂ in Burmite, body length 3.5 mm; 125) lateral aspect of the body (in the background a sticky droplet); 126) pedipalpi.

127-128: *Lacunauchenius* sp. indet. (ARCHAEIDAE), ♀ F2627/BU/CJW in Burmite, body length 2.1 mm; 127) lateral aspect; 128) anterior aspect. Note the large cheliceral peg teeth.



129-130: *Planarchaea kopp* **n. gen. n. sp.** (ARCHAEIDAE), holotype ?ad. ♀, body length 1.65 mm, dorsal and ventral aspect of the spider.

131) *Spatiator putescens* **n. sp.** (SPATIATORIDAE: SPATIATORINAE), holotype ♂ in Burmite, body length 3 mm, dorsal aspect of the spider. Note the strongly wrinkled prosoma.

132-133: *Vetiator gracilipes* **n. gen. n. sp.** (SPATIATORIDAE: VETIATORINAE), holotype ♂ in Burmite, body length 1.8 mm, dorsal and ventral aspects of the spider.

134-135: *Micropalpimanus? poinari* WUNDERLICH 2008 (MICROPALPIMANIDAE), ♂; 134) F2512/BU/CJW, body length 1.9 mm, spider preserved between two layers of the amber; 135) F2511/BU/CJW, body length 1.5 mm, dorsal-anterior aspect.

136) *Micropalpimanus* **sp. indet.** (MICROPALPIMANIDAE), ♀ in Burmite, body length 2.4 mm, dorsal-right aspect. Unnamed institution.





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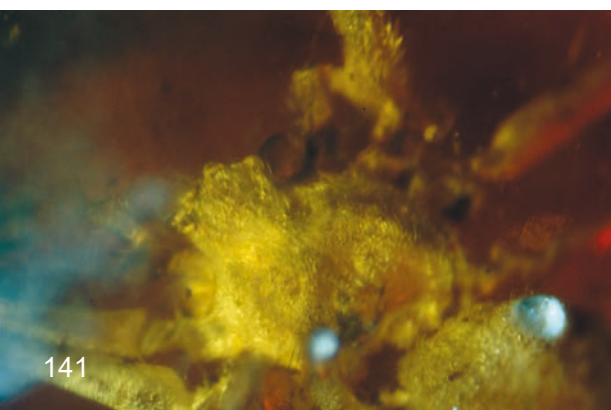
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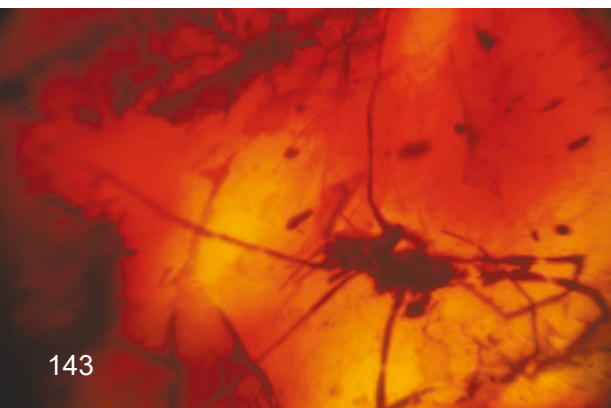
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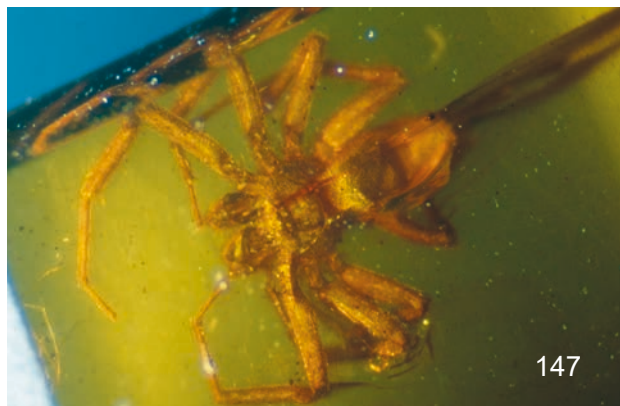
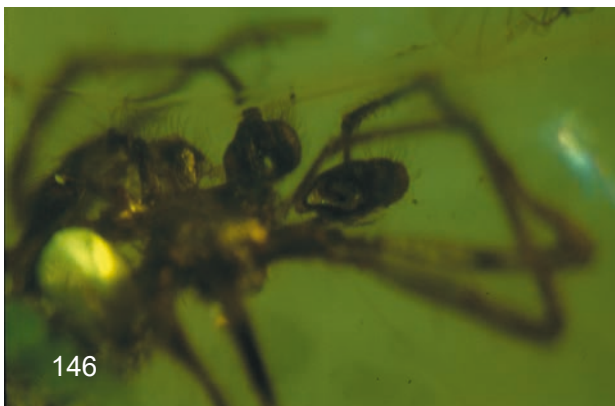
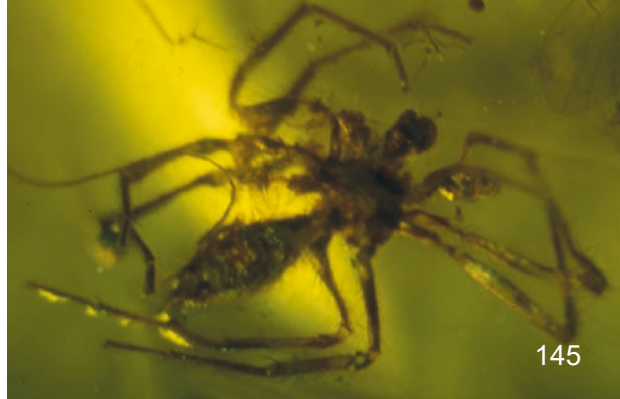
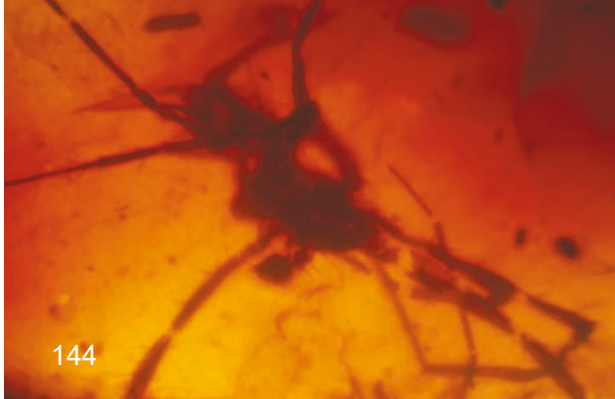


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137) *Micropalpimanus* sp. indet. (MICROPALPI-  
MANIDAE), ♂ in Burmite, body length 1.9 mm, la-  
teral aspect. Unnamed institution.

138) *Micropalpimanus* sp. indet. (MICROPALPI-  
MANIDAE), ♂ in Burmite, body length 1.5 mm, an-  
terior aspect. Unnamed institution.

139) ?*HUTTONIIDAE* indet., ?juv. ♀ F2464/NJ/  
CJW in Cretaceous amber from New Jersey, body  
length 1.5 mm, lateral aspect.



140-142: *Burmesiola daviesi* **n. gen. n. sp.** (HERSILIIDAE), holotype ?juv. ♀ in Burmite, body length 2.2 mm; 140-141: dorsal aspects of the body and the prosoma (enlarged); 142) dorsal aspect of the spinnerets and the right leg IV, note its tibial & metatarsal trichobothria!

143-144: *Spinasilia dissoluta* **n. gen. n. sp.** (HERSILIIDAE), holotype ♂ in Burmite, body length 4 mm, partly dissected body, enlarged in fig. 144).

145-146: *Zamilia aculeopectens* **n. sp.** (OECOBIIDAE), holotype ♂ in Burmite, body length 1.9 mm;

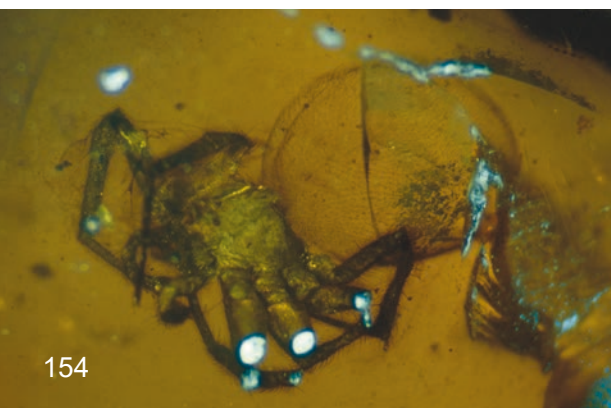
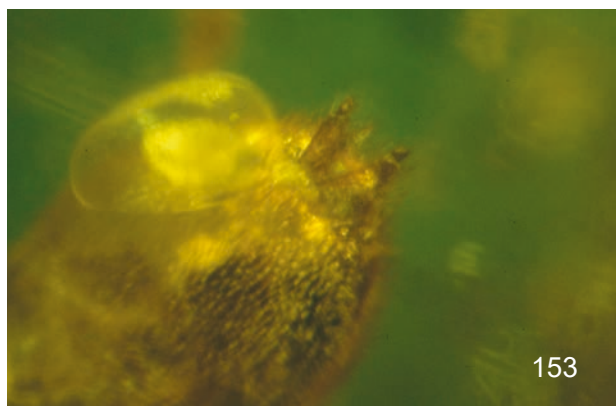
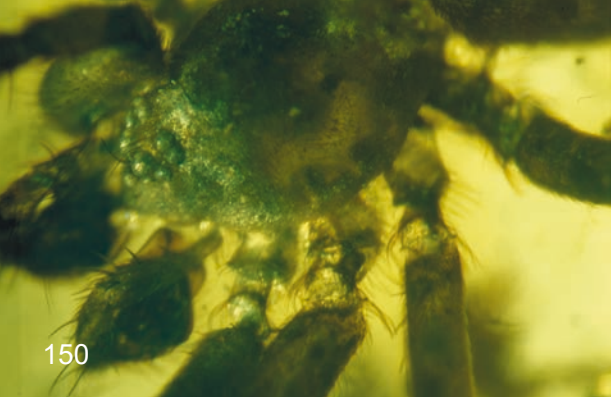
145) ventral aspect of the spider; 146) enlarged: prosoma and pedipalpi.

147) ?*Zamilia quattuormammillae* **n. sp.** (OECOBIIDAE), holotype ♂ in Burmite, body length 2.6 mm, dorsal aspect of the spider.

148) ?*Zamilia* sp. (OECOBIIDAE), ♂ F2672/BU/CJW, body length 3.5 mm, ventral aspect of the pyritized spider.

149-153: *Retrooecobius chomskyi* **n. gen. n. sp.** (OECOBIIDAE), holotype ♂ in Burmite, body length



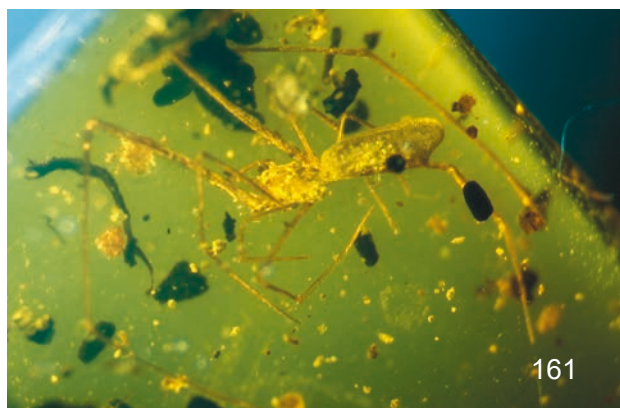
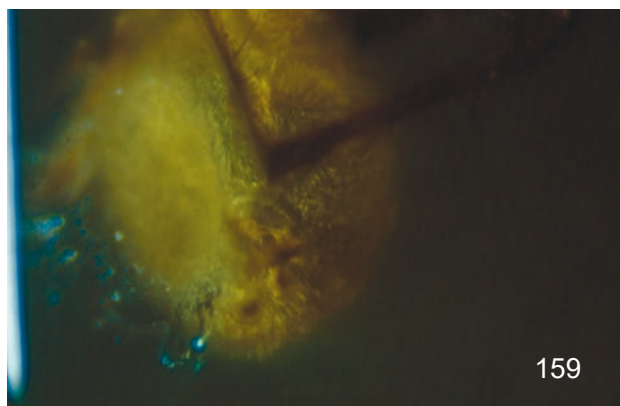
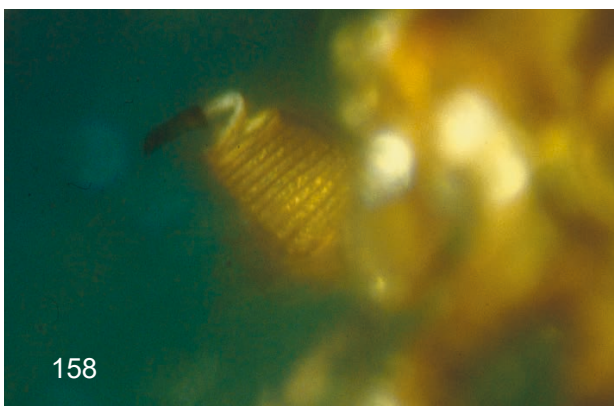


3.5 mm; 149-150: dorsal aspect of the spider, enlarged in fig. 150); 151) lateral aspect of the spider; 152) posterior aspect of the spider; note the secretion below the spinnerets; 153) ventral aspect of the opisthosoma with the spinnerets and the secretion.

154) *Retrooecobius convexus* n. gen. n. sp. (OECOBIIDAE), holotype ♀ in Burmite, body length 5 mm, dorsal-left aspect. Note the large and probably egg-bearing opisthosoma.

155) *Burmadictyna clava* n. sp. (SALTICOIDIDAE), holotype ♂ in Burmite, body length ca. 2.5 mm, lateral aspect of the spider.

156-159: *Burmadictyna excavata* n. sp. (SALTICOIDIDAE), holotype ♂ in Burmite, body length 2.8 mm; 156) dorsal aspect of the spider; 157) ventral aspect of the spider; 158) ventral aspect of the right pedipalpus; note the spirals of the embolus; 159) spinnerets.



160) *Bicalamistrum mixtum* n. gen. n. sp. (ULOBORIDAE), holotype subad. ♂ in Burmite, body length 3 mm, lateral aspect.

161) ?*Burmuloborus antefixus* n. sp. (ULOBORIDAE), holotype ♂ in Burmite, body length 3.2 mm, lateral aspect.

162: ?*Burmuloborus prolongatus* n. sp. (ULOBORIDAE), holotype juv. ♀ in Burmite, body length 2.3 mm, dorsal and ventral aspect of the spider.



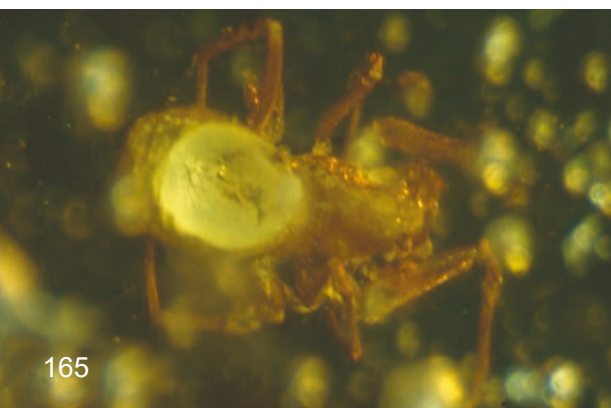




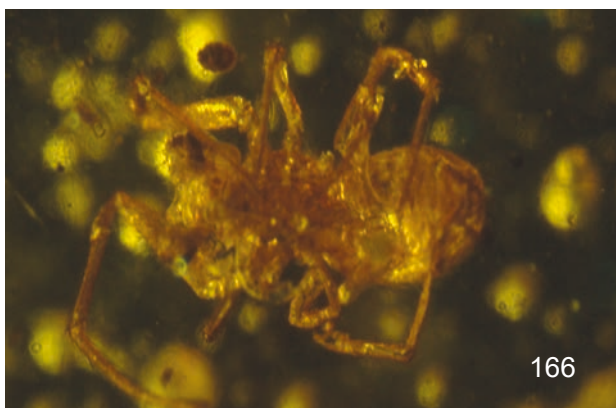
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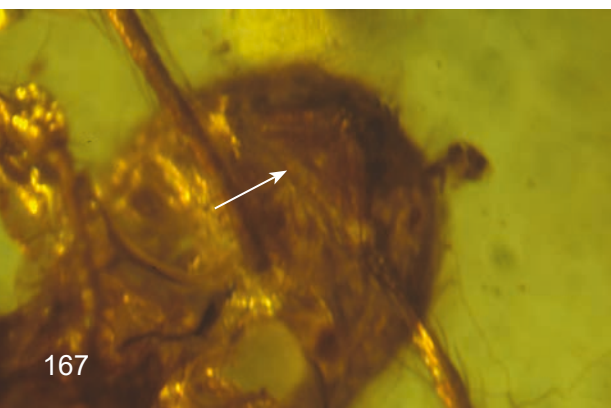
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163: ?*Burmuloborus prolongatus* n. sp. (ULOBORIDAE), holotype juv. ♀ in Burmite, body length 2.3 mm, dorsal aspect of the spider.

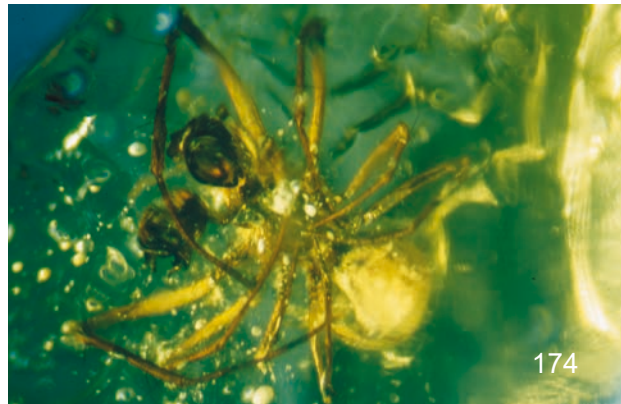
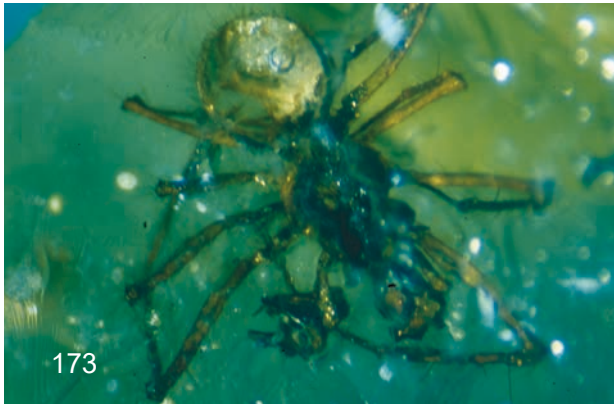
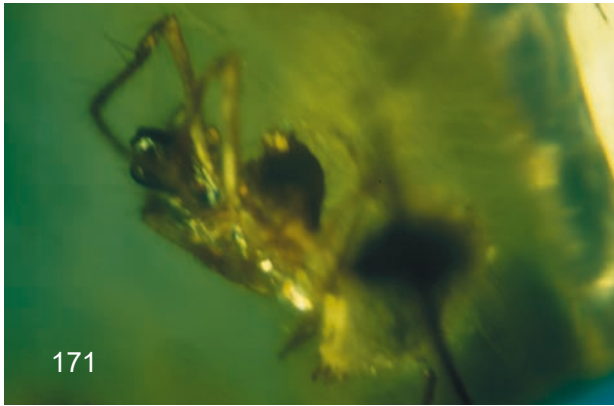
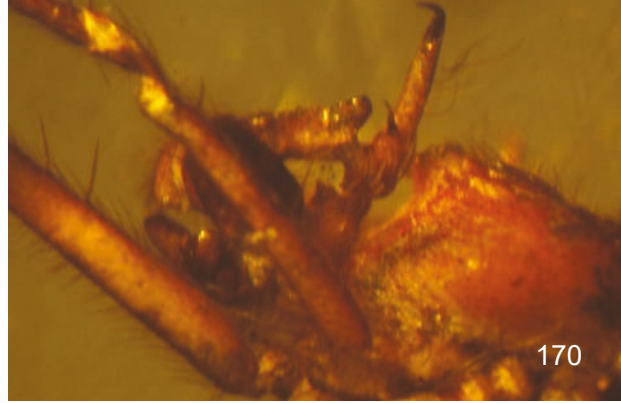
164) ?*Burmuloborus* sp. indet. (ULOBORIDAE), ♀-exuvia F2448 in Burmite, left metatarsus IV with calamistrum. Note its deep and long inclination!

165-167: *Microuloborus birmanicus* n. gen. n. sp. (ULOBORIDAE), holotype ♂ in Burmite, body

length 0.9 mm; 165-166: dorsal and ventral aspects of the spider; 167) ventral aspect of the opisthosoma with the spinnerets and the cribellum (arrow).

168-170: *Paramiagrammopes patellidens* n. sp. (ULOBORIDAE), holotype ♂ in Burmite, body length 2.2 mm; 168-169: lateral and dorsal-lateral aspects of the spider; 170) left aspect of the anterior part of the spider. Note the long erect outgrowth of the right patella!

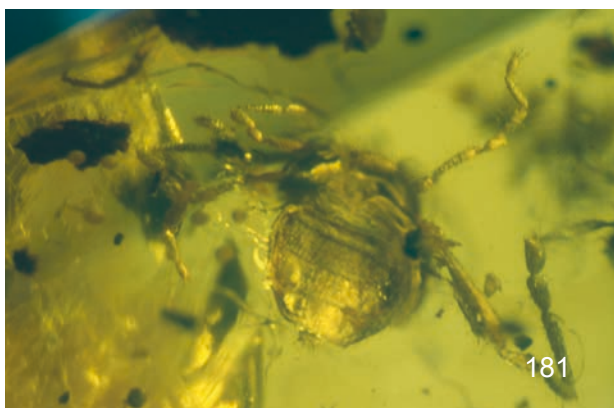
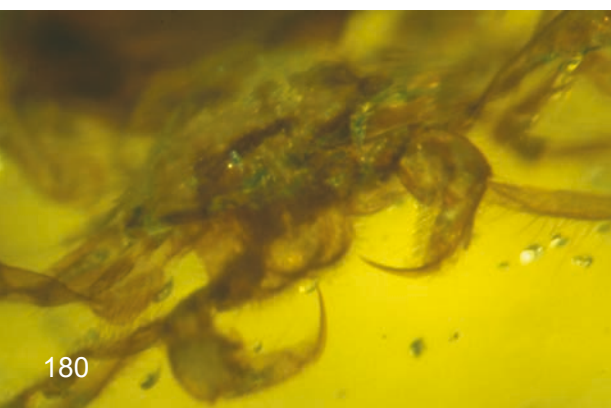
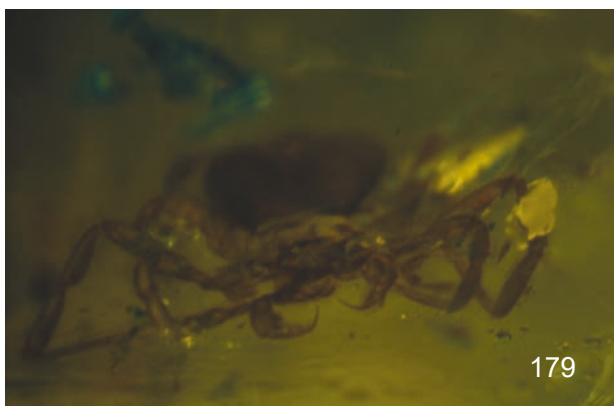
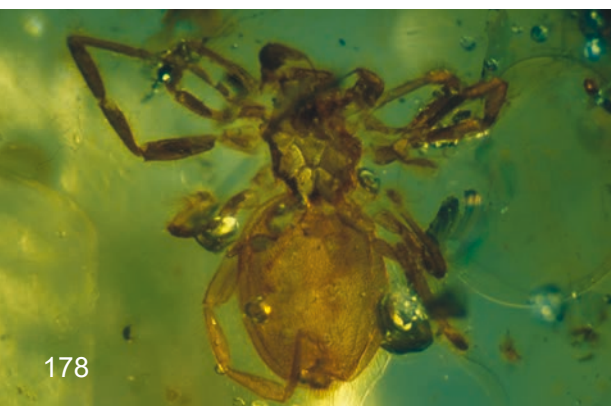
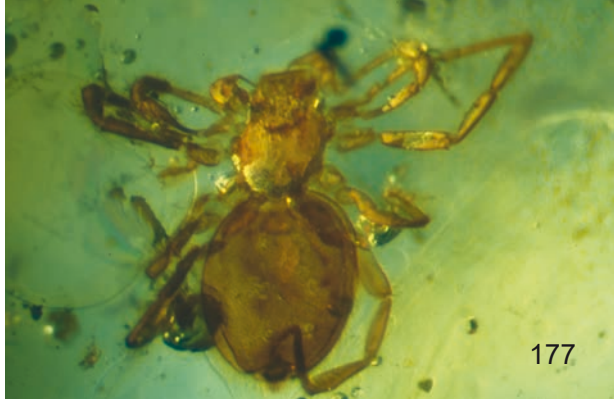




171-174: *Leviunguis ?bruckschi* WUNDERLICH 2012 (THERIDIOSOMATIDAE), ♂ in Burmite, body length 1.1 and 1.0 mm; 171-172: F2777/BU/CJW, lateral and dorsal aspects; 173-174: F2785/BU/CJW, dorsal and ventral aspects.

175) *Cretotheridion inopinatum* n. gen. n. sp. (THERIDIIDAE) (?), holotype ♂ in Burmite, body length 1.6 mm, ventral aspect. Note the prey (Diptera) in front of the spider above the middle!





176) SCHIZOMIDA indet., ♂ F2780/BU/CJW in Burmite, body length 3.4 mm, dorsal aspect.

177-180: RICINULEI: *Primorcinuleus pugio* n. gen. n. sp., holotype nymph in Burmite, body length 1.8 mm; 177-178: dorsal and ventral aspects; 179-180: anterior-dorsal aspect, enlarged in fig. 180.

181-182: RICINULEI: ?*Poliochera* sp. indet., nymph F2781/BU/CJW in Burmite, body length 1.4 mm, dorsal and ventral aspects. Most legs are lost.

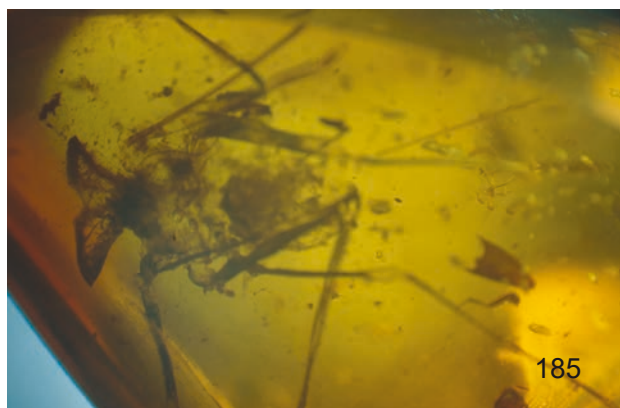
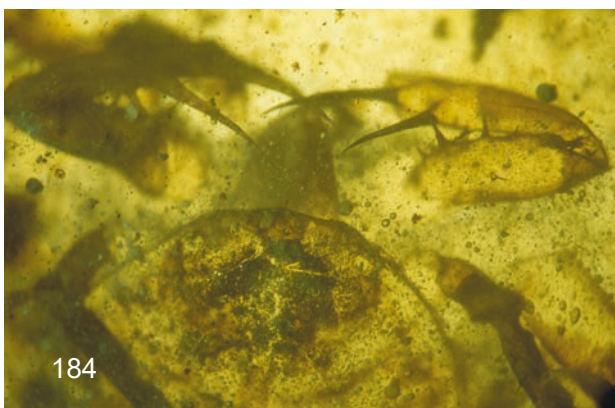
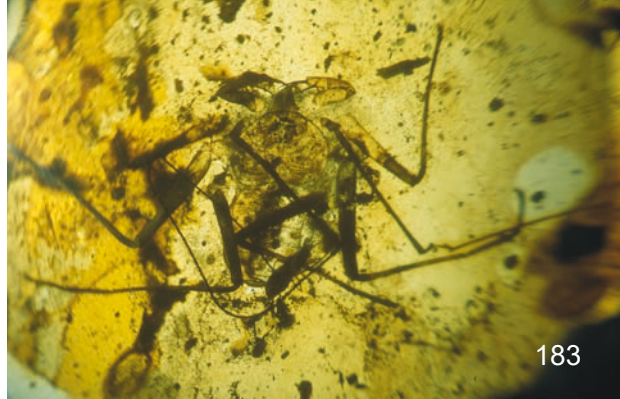
183-184: AMBLYPYGI: *Kronacharon engeli* n. sp., holotype ♀ in Burmite, body length 6.3 mm, dorsal aspects, enlarged anterior part in fig. 184.

185-186: AMBLYPYGI: *Kronacharon longicalcaris* n. sp., decomposed holotype ♀ in Burmite, body length 5.8 mm, dorsal aspects, enlarged anterior part in fig. 186.

187) UROPYGI: THELYPHONIDA: *Burmathelyphonia prima* n. gen. n. sp., immature holotype in Burmite, body length 6 mm, dorsal aspect.

188) SOLIFUGAE indet. specimen in Burmite.





## A TALE ON A SPIDER AT PINDAYA CAVE, MYANMAR (BURMA)

Retold by ENGIN NI, Myanmar. See the photo below.

Pindaya Cave is located in Southern Shan, a state in Myanmar. Why is it called „Pindaya“? Because Pin = Pintgu, which means „spider“, Da = Da Gaung, which means „one“, Ya = got, so that Pindaya means „one spider got here“. This spider is unique and huge.

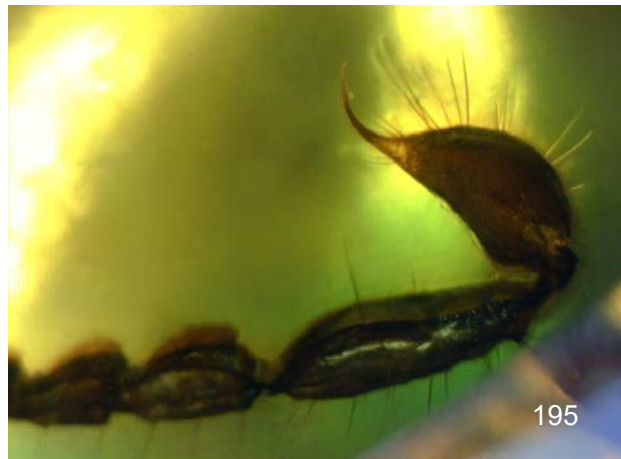
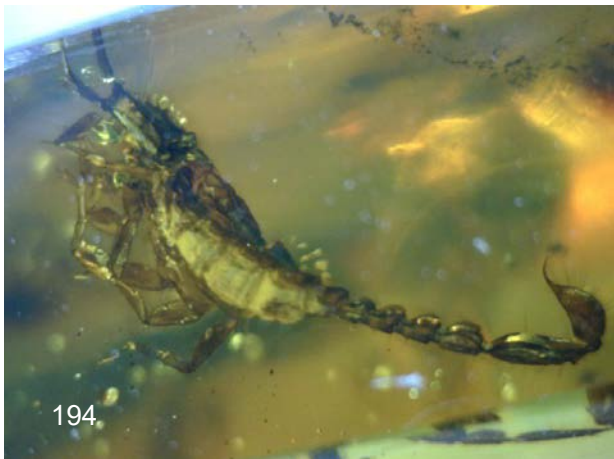
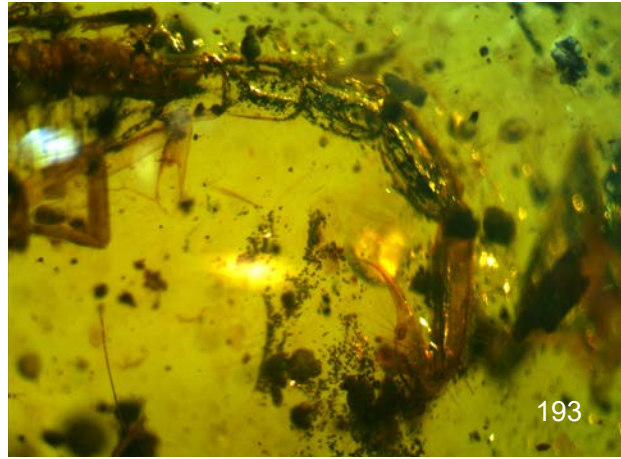
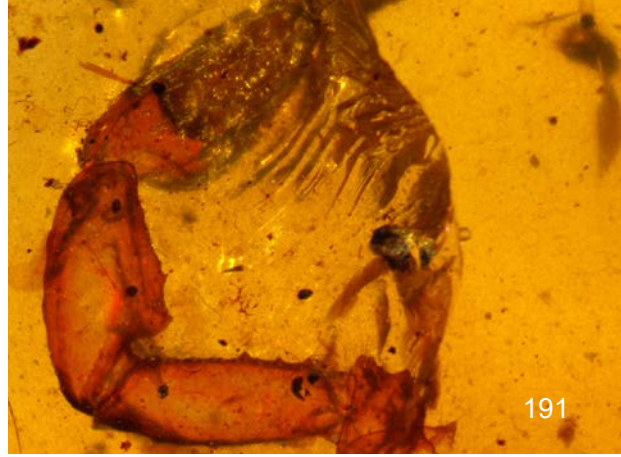
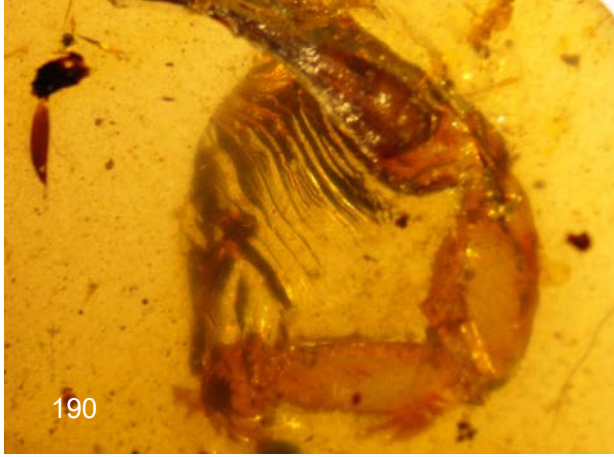
Once upon a time seven sisters lived in Pindaya village, who loved to play in the water of a big lake – Botaloke Lake. One day the hours at the lake went by so quickly that evening overtook them. At the same time a prince was hunting in the forest of Pindaya. The sisters were very tired and the way home was too long. So they went to Pindaya Cave, early in the morning, they would go home later, was their idea. But – alas – a huge spider came into the cave and blocked the entrance, so that the sisters could not escape. They were frightened and didn't know what to do. So they started to shout loudly for help. Finally the prince heard their shouting and came quickly to the cave. He aimed at the spider with his arrows again and again. So in the end the spider was dead and the prince could successfully free the sisters.

When he saw the youngest one he fell in love with her and they soon married in Pindaya village. The prince and the princess lived together happily ever after.

Their romance was always linked to the huge spider at Pindaya Cave. When you arrive there you will see the spider in front of the cave, photo below.







Photos 190-191: *Archaeoscorpiops cretacus* **sp. n.** Left pedipalp: femur, patella and chela, dorsal and ventral aspects.

Photos 192-193: *Palaeoburmesebuthus ohlhoffi* **sp. n.** Holotype. 1. Habitus, dorsal

aspect. 2. Metasoma and telson, lateral aspect.

Photos 194-196: *Chaerilobuthus bruckschi* **sp. n.** Holotype. 194. Habitus, lateral aspect. 195. Detail of metasoma, lateral aspect.

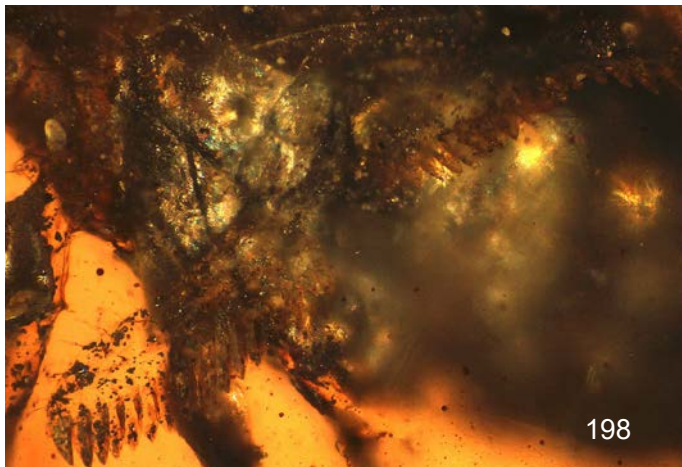
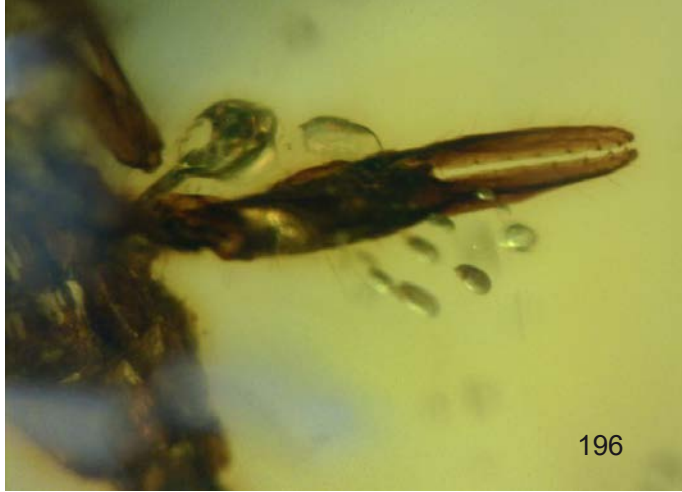


Photo 196. Chela, internal aspect.

Photos 197-198: *Betaburmesebuthus kobberti* Lourenço, **sp. n.** Male holotype. 1. Habitus, dorsal aspect. 2. Ventral aspect showing sternum, genital operculum and pectines.

# MESOZOIC SPIDERS

BEITR. ARANEOL., 9 (2015)

## SPINNEN DES ERDMITTELALTERS

Joerg Wunderlich (ed.)

We do not have a time machine to look backwards on earth but we have fossils which can tell us something about life millions of years ago.

In this volume different aspects of spider evolution are treated, and a provisional detailed overview over the Mesozoic fauna of one of the most diverse "megaorders" of arthropods – the spiders (Araneae) – is given for the first time. Based mainly on fossils from Myanmar (Burma) it includes a list and provides keys to the taxa known up to the beginning of 2015, which are documented by numerous coloured photos and drawings. Certain behavioural, biogeographical, ecological and phylogenetic aspects are also treated. Few papers by other authors are included in this volume.

Today the amber from Myanmar (Burmite) represents the most important and fascinating "window" to Cretaceous arthropods. The study of the 100 million year old fossil spiders provides a tiny puzzle piece to reconstruct a small part of a fascinating and strange vanished world.

The enigma of the first spiders (Araneae): How many million years ago did animals of this order exist? What did they look like at the beginning in the Palaeozoicum? Which important new characters – innovations – did spiders evolve during their existence of 400 million years? Did the first spiders already have poison glands and build capture webs similar to today's spiders? Hopefully, in Cretaceous resins we will find the roots of diverse "modern" spider families like Jumping spiders (Salticidae), Daddy-long-legs Spiders (Pholcidae), Wolf Spiders (Lycosidae) and Crab Spiders (Thomisidae) which are all unknown from the whole Mesozoic period like the whole very diverse spider branch of the Dionycha.

The faunas of ancient spiders (Araneae): How was the spider fauna composed in the middle ages of the Earth (the Mesozoicum)? The order of spiders is one of the largest and most diverse orders of animals on Earth; I assume that several hundred thousand living and extinct species altogether exist (more than 42000 species are known today, about 1200 fossil species). Thanks to the frequently excellent preservation (see the photos!), and the intensive studies of fossils during the last decade the spider faunas of the Cretaceous (65 to 145 million years ago) – the main age of the Dinosaurs! – supplies a surprising insight into selected ancient spider faunas of the Northern Hemisphere, which are quite strange compared to faunas of today, and which consist predominantly of ancient and even extinct families.

Orders of this book [directly to the author:](#)

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