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## FIFTEEN PAPERS ON EXTANT AND FOSSIL SPIDERS (ARANEAE)

Joerg Wunderlich (ed.)



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## **FIFTEEN PAPERS ON EXTANT AND FOSSIL SPIDERS (ARANEAE)**

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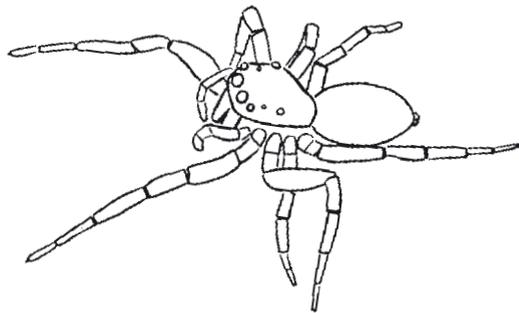
*On the top left:* Male of *Dictyna rufa* n. sp. (Dictynidae), subrecent, in copal from Madagascar, body length 1.65 mm. Note the preservation of the original redbrown colouration.

*On the top right:* Male of the Pirate spider (Mimetidae) *Ero (Succinero) clunis* n. sp. in Eocene Baltic amber, body length ca. 3 mm, anterior aspect. Note the big pedipalpi and the long bristles of the legs.

*At the bottom:* Male of the Combfooted Spider (Theridiidae) *Lasaeola (Phycosoma) inclinata*, subrecent, in copal from Madagascar, body length 1.7 mm. Note the preservation of the original redbrown colouration.

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JOERG WUNDERLICH (ED.)



Editor and author of most papers as well:  
Joerg Wunderlich

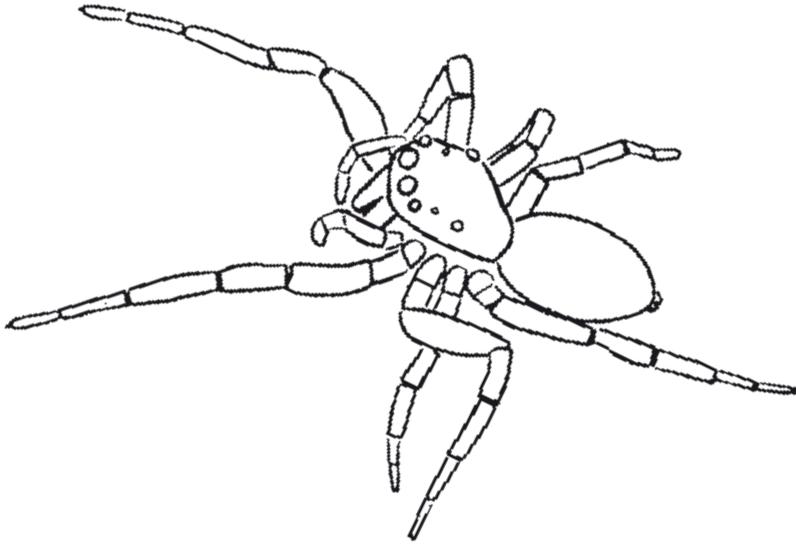
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A Jumping spider (Salticidae),  
the most diverse family of spiders.

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I asked successful and thankful several authors for using their drawings in exchange with my drawings.

**Abbreviations:**

CJW = collection of J. WUNDERLICH, laboratory of arachnology.  
SMF = Senckenberg-Museum Frankfurt a. M.

**INTRODUCTION**

In the present volume 15 papers on extant and fossil spiders – including Eocene Baltic amber and Cretaceous Burmese (Myanmar) amber spiders – are published. Most papers are written by the editor (JW), a single one by P. JÄGER, one by PETER JÄGER in cooperation with the editor, and one by S. TOFT in cooperation with the editor. The papers on the determination of the genera of the families Corinnidae, Philodromidae and Zodariidae may complete the book on the determination of European spider families by the present author, Beitr. Araneol., 8 (2012) (in prep.).

## IDENTIFICATION KEY TO THE EUROPEAN GENERA OF THE SPIDER FAMILY ZODARIIDAE (ARANEAE)

JOERG WUNDERLICH, 69493 Hirschberg, Germany.

**Abstract:** A key is given to the 6 European genera of the spider family Zodariidae (Araneae): *Amphiledorus* JOCQUE & BOSMANS 2001, *Lachesana* STRAND 1932, *Palaestina* O. PICKARD-CAMBRIDGE 1872, *Pax* LEVY 1990, *Selamia* SIMON 1873, and *Zodarion* WALCKENAER 1826. Notes are given regarding the diversity, distribution and evolution of these genera and few species.

**Acknowledgements:** With many thanks the figs. 1–2 are taken from JOCQUE (1991), the remaining figs. from LEVY (1990).

Zodariidae is a diverse family of spiders which is mainly distributed in the tropics. Family diagnosis: See the paper on the European spider families in this volume and JOCQUE (1991). The European Zodariidae are ground dwellers and may hide inside sandy tubes. This may be a basic character of the family. Most spiders prey on ants and several are ant-mimicking.

In Europe genera of three SUBFAMILIES occur:

(1) Lachesaninae: *Lachesana* STRAND 1932: 2 species in Greece;

(2) Storeninae:

(a) *Amphiledorus* JOCQUE & BOSMANS 2001: 3 species on the Iberian Peninsula;

(b) *Pax* LEVY 1990 (= *Storamia* JOCQUE 1991): *P. islamita* (SIMON 1873) in Turkey;

- (c) *Selamia* SIMON 1873: Only *S. reticulata* (SIMON 1870) (= *Storena r.*) in S-France, the Iberian Peninsula, Sardinia and Sicily;
- (3) Zodariinae:
- (a) *Palaestina* O. PICKARD-CAMBRIDGE 1872: Only *P. expolita* O. PICKARD-CAMBRIDGE 1872 in Greece and Turkey;
- (b) *Zodarion* WALCKENAER 1826: About 100 species in Southern and 3 in Central Europe.

The DISTRIBUTION and the DIVERSITY of the European genera are remarkable:

(1) Distribution: 5 of the 6 European genera occur in Southern Europe (some also in the Near East, see LEVY (1990, 1992)) but not in Central or Northern Europe. These genera possess a restricted distribution in Europe in contrast to *Zodarion*, see the tab. below. More than 97% of the species of this mainly tropical family are restricted to Southern Europe. – The genus *Zodarion* is an exception: This mainly MEDITERRANEAN taxon (\*) is widely spread but only 3 species reached Central Europe: *germanicum*, *italicum* and *rubidum*. *Z. italicum* and *rubidum* invaded Central Europe only in the second half of the 20th century, probably in connection with the increasing temperature in Central Europe during the last decades. (\*\*), (\*\*\*)

-----

(\*) similar to *Dysdera* (Dysderidae). – Few species of *Zodarion* have been introduced to several parts of the world.

(\*\*) *Z. italicum* is now a quite frequent species in my garden in S-Germany near Heidelberg. The same is true for *Macaroeris nidicolens* (Salticidae) which invaded Germany a few years ago and is now the most frequent Jumping Spider in my garden besides *Heliophanus cupreus*.

(\*\*\*) First proof of *Zodarion andalusiicum* JOQUE 1991 for Portugal: Algarve, ca 20 km East of Faro, in dunes of a small island S Fuzeta, 1♂ JW leg. in VI 2011. The species was known only from S-Spain (Andalusia) up to now, which is not far from the Algarve.

(2) Diversity: The diversity of a single genus – *Zodarion* – is quite remarkable: In contrast to few (8) species of the remaining (5) European zodariid genera about 100 *Zodarion*-species in the mediterranean area exist which are documented mainly by papers by BOSMANS, e. g. in 2011.

To my knowledge the genus is absent from the Eocene (Baltic amber), see WUNDERLICH (2004: 1578–1611). The absence of Eocene European species of *Zodarion* may indicate a late origin of this genus. It appears enigmatic that in the Mediterranean area so extremely numerous species evolved, more than in other European spider genera. Is its adaptive radiation connected with the European radiation of its prey, the ants? – Furthermore it is remarkable that (a) the genus *Zodarion* is not a tropical but a subtropical genus, and (b) members of this genus are distinctly smaller in average than members of the remaining European zodariid genera – an adaptation to the prey?

**Key to the European genera of the family Zodariidae:**

Note: Their distribution may be helpful for determining the genera.

1 Body length usually 1.5–4 mm, rarely more than 5 or 6 mm. Anterior median eyes distinctly largest in the most frequent members of *Zodarion* (fig. 1), small in the rare genus *Palaestina* (fig. 2). Few indistinct bristles on the slender legs, 0–2 dorsally on the femora. Southern & Central Europe. Zodariinae. About 100 species . . . . . 2

- Larger spiders, body length usually 6.5–10 mm, in *Amphiledorus* 4–8 mm. Anterior median eyes not distinctly largest. Numerous strong bristles on the legs which are mostly stout. Southern Europe. 7 species. . . . . See the tab. 1 below

2(1) Anterior median eyes distinctly largest, posterior eye row strongly recurved (fig. 1). Few leg bristles, 0–2 on the femora I–III, usually none on IV. ♂-opisthosoma usually smooth, rarely with a dorsal scutum (\*). Southern and Central (\*\*) Europe. About 100 species . . . . . Zodarion

- Anterior median eyes small, posterior eye row almost straight (fig. 2). Leg bristles absent. ♂-opisthosoma with a dorsal scutum similar to fig. 5. Greece and Turkey. Only *P. expolita*. See JOCQUE (1991: 137–139). . . . . Palaestina

(\*) *E. g. cypricum, geticum, granulatum* and *scutatum*, see LEVY (1992: 94).  
 (\*\*) *Z. germanicum, italicum* and *rubidum*.

Character	<i>Amphiledorus</i>	<i>Lachesana</i>	<i>Pax</i>	<i>Selamia</i>
colour of the prosoma	yellow-orange	mainly yellow-orange	dark brown	red-brown
teeth of the cheliceral promargin	1	2	2	2
scutum of the ♂-opisthosoma	–	–	+ (fig. 5)	–
special characters	embolus origin in middle of the tegulum (fig. 3)	♂-chelicerae strongly curved (fig. 4)	see fig. 5 (scutum)	long posterior spinnerets (fig. 6)
distribution	Iberian Peninsula	Greece	Turkey	Iberian Penins., Sardinia, Sicily
species	3 (*)	2	<i>islamita</i>	<i>reticulata</i> (*)
references	JOCQUE & BOSMANS 2001, PEKAR, ... (2003)	JOCQUE (1991)	LEVY (1990)	PEKAR et al. (2003)

(\*) Copulatory organs: *Amphiledorus* (♂) fig. 3, *Selamia* figs. 7–8. The body length of *S. reticulata* is 7.7 (♂) – 10.1 mm, the body length of *Amphiledorus* is 4–8 (♀) mm.

Tab. 1. Comparison of the four European not zodariine genera

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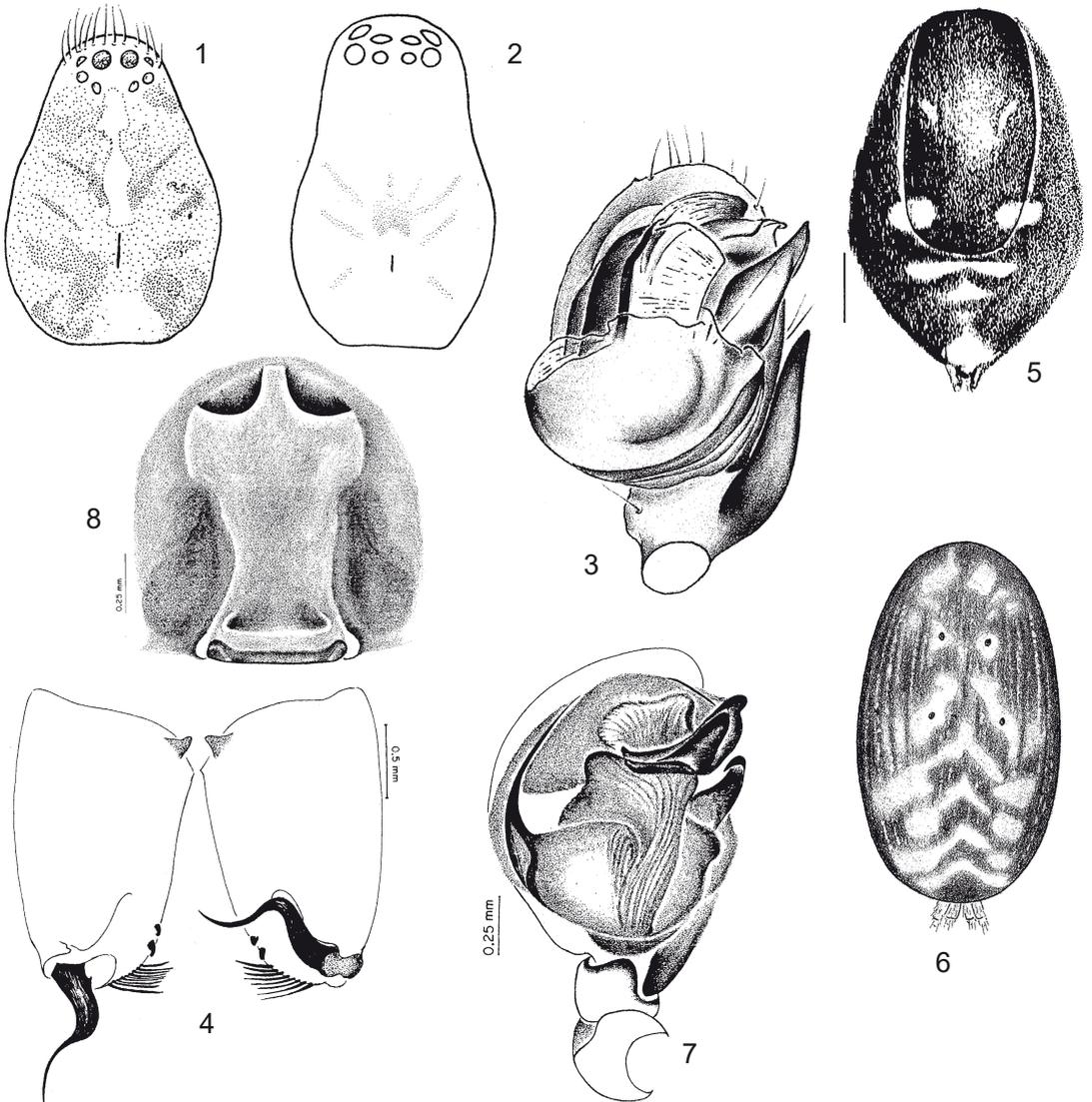


Fig. 1) *Zodarion* sp., dorsal aspect of the prosoma;

fig. 2) *Palaestina expolita* O. PICKARD-CAMBRIDGE 1872, dorsal aspect of the prosoma;

fig. 3) *Amphiledorus histrionicus* (SIMON 1884), ventral aspect of the left ♂-pedipalpus;

fig. 4) *Lachesana rufiventris* (SIMON 1873), posterior aspect of the ♂-chelicerae;

fig. 5) *Pax libani* (SIMON 1873), dorsal aspect of the ♂-opisthosoma;

fig. 6-8: *Selamia reticulata* (SIMON 1870); 6) dorsal aspect of the ♀-opisthosoma; 7) ♂, ventral aspect of the left pedipalpus; 8) ♀, epigyne.

## IDENTIFICATION KEY TO THE EUROPEAN GENERA OF THE SPIDER FAMILY CORINNIDAE (ARANEAE)

JOERG WUNDERLICH, 69493 Hirschberg, Germany.

**Abstract:** A key is given to the 11 European genera of the spider family Corinnidae (Araneae). The relationships of the family and of some genera are discussed.

Material studied is kept in the Museum Senckenberg Frankfurt a. M. and in the collection of the author.

Acknowledgement: I thank JAN BOSSELAERS for the loan of a female of *Arabelia pheidoleicomes* and a fruitful discussion.

Corinnidae (German name “Ameisen-Sackspinnen” but not “Rinden-Sackspinnen”) is a family of spiders which is diverse in the tropics. For a long time it has been included within the Clubionidae or partly within the Liocranidae (the Phrurolithinae). Diagnosis and relationships to the related Clubionidae and Liocranidae: See the paper on the European spider families in Beitr. Araneol. 8.

Useful hint for the determination: Besides the fine structure of the prosomal cuticula – which is difficult to study with a help of a light microscope in numerous taxa – it is more easy to distinguish taxa of the Corinnidae and the Liocranidae by a comparison with the subfamilies of the Corinnidae (see the key to the subfamilies below): After the exclusion of the four corinnid subfamilies a questionable taxon may most probably be

a member of the family Liocranidae. Furthermore the tendency for a reduction of leg bristles (especially on legs III–IV) exists in several taxa of the Corinnidae in contrast to the Liocranidae, and the Clubionidae as well.

Diversity: Corinnidae is a fairly diverse family, see the paper on the European spider families in Beitr. Araneol. 8, in which a family diagnosis is included. In Europe – included are here the Macaronesian Islands with *Creugas* of the subfamily Corinninae from the Canary Islands – 11 genera of 4 or 5 subfamilies occur. Most genera are represented by only one or two species in Europe, only *Phrurolithus* – 7 species – is fairly diverse. – REMARK: The genera *Metatrachelas* and *Paratrachelas* were split off from the closely related *Trachelas* only during the last three years.

Myrmecomorphy: Corinnidae is one of numerous families in which myrmecomorphy evolved. The myrmecomorphy is quite differently marked in this family, conspicuously in some genera like *Phrurolithus* and the other taxa of this subfamily in Europe – except *Orthobula charitonovi* and *Arabelia pheidoleicomis* which are not ant-shaped –, varying strongly within all subfamilies, and apparently it evolved several times convergently.

Distribution of the genera (see also the tab. 1–2 below): Nine genera of this mainly tropical family are restricted to Southern Europe, only the genera *Cetonana* (the single species *laticeps*) and few species of the distinctly ant-shaped genus *Phrurolithus* occur north of the Alps; *Phrurolithus* even reaches Scandinavia. Most European taxa occur on the Iberian Peninsula, including members of the distinct ant-shaped genera which include the endemic genus *Phrurolinillus*. Great Britain was invaded solely by *Phrurolithus szilyi*, apparently only during the last century. *Creugas* and *Trachelas* reached the Canary Islands (*Creugas* was probably introduced by man), *Liophurillus* is known from Madeira besides Southern Europe, *Metatrachelas* from the Azores besides Southern Europe. The endemic genus *Arabelia* is restricted to Greek islands and the widely distributed genus *Orthobula* is known only from Turkey within the region treated.

### **List of the European taxa of the family Corinnidae**

in the alphabetic order of their genera; including *Creugas* from the Canary Islands and of *Arabelia*.

*Arabelia* BOSSELAERS 2009. Subfamily Phrurolithinae. Only the type species *A. pheidoleicomis* BOSSELAERS from Greek islands (Cyprus, Lesbos, Rhodes). Figs. 42–48.

RELATIONSHIPS: This myrmecophilic (not myrmecomorphic) species has originally – with hesitation – been described as a taxon of the family Liocranidae, based on the

female sex only, but BOSMANS (2011) transferred it to the Corinnidae with the first description of a male of this species, without giving a reason for the transfer. – I studied a female of *Arabelia* and I found the structure of the prosomal cuticula finely scaly – a typical character of the Corinnidae in contrast to the Liocranidae. I cannot confirm the existence of a gnathocoxal depression. The oval posterior median eyes, the only 2 retromarginal denticles on the fang furrow, and the very few bristles on legs III–IV (only 1–2 on tibia IV besides a single femoral bristle), lead me to the subfamily Phrurolithinae, although an anterior bristle of the chelicerae and a ventral hump of the femur of the male pedipalpus – both exist in most (but not all) members of the Phrurolithinae – are absent in *Arabelia*, which I regard as an unusual member of the Phrurolithinae.

*Castianeira* KEYSERLING 1879. Subfamily Castianeirinae. Only *C. badia* (SIMON 1877), Iberian Peninsula: Spain. Figs. 19–20.

*Cetonana* STRAND 1929 (= *Ceto* SIMON 1874, praeocc.). Subfamily Trachelinae. Only *C. laticeps* (CANESTRINI 1868), Europe. Figs. 49–51.

*Creugas* THORELL 1878. Subfamily Corinnidae. Only *C. gulosus* THORELL 1878 (= *Corinna senegalensis*). Canary Islands (cosmopolitan). Figs. 21–22.

*Liophrurillus* WUNDERLICH 1992. Subfamily Phrurolithinae. Only *L. flavitarsis* (LUCAS 1846) from S-Europe and Madeira. Figs. 26–32.

*Metatrachelas* BOSSELAERS & BOSMANS 2010. Subfamily Trachelinae. *M. macrochelis* (WUNDERLICH 1992) (= *Trachelas m.*): Spain, Canary Islands, Azores; *M. rayi* (SIMON 1878) (= *Trachelas r.*): Spain, S-France, Italy. Figs. 5–10.

*Orthobula* SIMON 1897. Subfamily Phrurolithinae. Only *O. charitonovi* (MIKHAILOV 1986) (= *Trachelas c.*): Turkey (widely distributed in Asia). Figs. 38–41.

*Paratrachelas* KOVBLYUK & NADOLNY 2009. Subfamily Trachelinae. *P. ibericus* (BOSSELAERS 2009) (= *Trachelas i.*), *maculatus* (THORELL 1875) (= *Trachelas m.*), and *validus* (SIMON 1884) (= *Trachelas v.*). Iberian Peninsula, S-France. Figs. 3, 17–18.

*Phrurolinillus* WUNDERLICH 1995. Subfamily Phrurolithinae. *P. lisboensis* WUNDERLICH 1995 and *tibialis* (SIMON 1878) (= *Micariosoma t.*, *Phrurolithus t.*) (♀ unknown). Iberian Peninsula. Figs. 33–37.

*Phrurolithus* C. L. KOCH 1839. Subfamily Phrurolithinae. 7 species in Europe. Figs. 23–25.

*Trachelas* L. KOCH 1872. Subfamily Trachelinae. *T. minor* O. PICKARD-CAMBRIDGE 1872 (mediterranean) as well as 2 species from the Canary Islands: *canariensis* WUNDERLICH 1987 (and Iberian Peninsula as well) and *uniaculeatus* SCHMIDT 1956. Figs. 11–16.

**Key to the corinnid genera of Europe:**

Note: The distribution may help to determinate some of the genera.

1 Leg BRISTLES ABSENT (\*) but at least the male tibia and metatarsus I–II may bear ventral-lateral rows of cusps (very short spines, similar to figs. 3–4) or thickened hairs (fig. 5), fig. 6 (♀). The prosoma is most often distinctly convex (figs. 1, 8), its cuticula is frequently distinctly wrinkled (figs. 7–8), the chelicerae are usually powerful (fig. 8). Body length usually less than 5 mm, only in *Cetonana* (figs. 49–51) 5–7mm. Southern Europe. Subfamily Trachelinae . . . . . Tab. 1

- Leg bristles existing (e. g. long paired ventral tibial and metatarsal bristles on the anterior leg as in fig. 27), cusps absent. Prosoma usually low, powerful chelicerae exist in *Creugas* (no. 3). Body length variable. . . . . 2

2(1) Body length 5–8.6 mm. Metatarsus I–II bear 2 pairs of ventral bristles. Iberian Peninsula and Canary Islands, very rare. . . . . 3

- Body length less than 5 (about 2 up to 5) mm. Metatarsus I–II bear at least 3 pairs of ventral bristles. Mediterranean and Central Europe, not rare. Subfamily Phrurolithinae . . . . . 4

3(2) Tibia I bears 5 pairs of ventral bristles. Legs III–IV bear numerous bristles in contrast to other European Corinnidae in which none or very few bristles exist on these legs. Body stouter, prosoma 1.23–1.34 times longer than wide. ♂-pedipalpus (fig. 21): Tibia with 3 apophyses, embolus large. Epigyne (fig. 22) with two depressions. Only *C. gulosus*. Canary Islands. Subfamily Corinninae . . . . . Creugas

- Tibia I bears 2 pairs of ventral bristles. Body more slender, prosoma 1.34-1.48 times longer than wide. ♂-pedipalpus (fig. 19): Tibia without apophysis (only with a hook), bulbus pear-shaped. Epigyne/vulva fig. 20. Only *C. badia*. Iberian Peninsula (Spain). Subfamily Castianeirinae. . . . . Castianeira

4(2) Distinctly ant-mimicking spiders; the dark opisthosoma bears white spots, see e. g. SAUER & WUNDERLICH (1997: Photo p. 67). The chelicerae bear an anterior bristle in the basal half (fig. 4) in the European taxa. Femur of the ♂-pedipalpus with a ventral hump (arrow in fig. 23, fig. 28). – Whole Europe (*Phrurolithus*) or Southwest Europe (3 genera) . . . . . Tab. 2

- Not ant-shaped spiders. A cheliceral bristle exists in *Orthobula* but is absent in *Arabeilia*. Hump of the femur of the ♂-pedipalpus absent. Eastern Mediterranean. . . . . 5

5(4) Body length 2–4 mm. Chelicerae without an anterior bristle in the basal half. Prosoma and opisthosoma unicoloured, prosoma reddish, fading to orange in alcohol. Opisthosoma long oval (fig. 42). Lenses of the posterior median eyes oval (fig. 42). ♂-pedipalpus fig. 47–48, bulbus without apophyses; epigyne fig. 46. Only *A. pheidole-icomis*. Greek islands . . . . . Arabella

- Body length less than 2 mm. Chelicerae with an anterior bristle in the basal half similar to fig. 26. Prosoma and opisthosoma bicoloured in the single European species, light and darker grey. Opisthosoma short, ovoid (fig. 38). Lenses of the posterior median eyes circular. ♂-pedipalpus figs. 39–40, conductor existing; epigyne fig. 41. Only *O. charitonovi*. Turkey . . . . . Orthobula

(\*) A single dorsal bristle may exist on femur IV in *Trachelas uniaculeatus*.

Character	<i>Cetonana</i>	<i>Metatrachelas</i>	<i>Paratrachelas</i>	<i>Trachelas</i>
body length	5–7 mm	less than 5 mm		
prosomal cuticula	weakly wrinkled	mostly weakly wrinkled	wrinkled	wrinkled
♂: tibial/meta-tarsal cusps	existing comp. fig. 3	absent (fig. 5)	existing (fig. 3)	existing (fig. 4)
d. scutum of the ♂-opisthosoma	absent but leathery	absent	existing (fig. 3)	existing (as fig. 3)
patellar apophysis of the ♂-pedipalpus	absent	absent	absent	existing (figs. 11, 15)
anterior epigynal hood or rim	small (fig. 51)	existing (fig. 10)	existing (fig. 18)	absent (fig. 13)
ecology	under bark	ground spiders		
species	<i>laticeps</i> (= <i>Ceto l.</i> )	<i>macrochelis, rayi</i>	<i>ibericus, maculatus, validus</i>	<i>canariensis, minor, uniaculeatus</i>
distribution	Southern- and Central Europe	Western mediterr., Italy, Azores	Iberian Penins. S-France	Mediterranean, Canary Islands

**Tab. 1.** Characters of the European corinnid genera of the subfamily **Trachelinae**

Character	<i>Liophrurillus</i>	<i>Phrurolinillus</i>	<i>Phrurolithus</i>
dorsal-basal femoral bristles	usually 1 on all femora		absent at least on III–IV
pro-/retromarginal teeth of the cheliceral fang furrow	2(-4)/2	3/2	0/1
tibial apophyses of the ♂-pedipalpus	2; one short (fig. 28)	1 long and slender (fig.33)	1 very large (fig. 23)
bulbus/embolus	large embolus		large tegulum
epigyne/vulva	lateral depressions (figs. 30, 32)	(figs. 36, 37)	strongly sclerotized (fig. 25)
species	<i>flavitarsis</i>	<i>lisboensis, tibialis</i>	7 species
distribution	Southern Europe, Madeira	Iberian Peninsula	Europe

**Tab. 2.** Characters of the distinctly ant-shaped European corinnid genera of the subfamily **Phrurolithinae**. – See also the genus *Orthobula* (key no. 5) which is not distinctly ant-shaped, and has a short (ovoid) shape of the opisthosoma.

## SUPPLEMENT

### Key to the corinnid subfamilies of the world:

1 Colulus well developed. Most often strongly ant-shaped spiders. ♂-pedipalpus: Retrolateral tibial apophysis usually absent, cymbium very long, usually enclosing the long embolus almost up to the tip of the cymbium (fig. 19), conductor and tegular apophysis absent . . . . . Castianeirinae

- Colulus absent or quite indistinct. Ant-shaped or not ant-shaped spiders. ♂-pedipalpus: Retrolateral tibial apophysis existing, cymbium shorter (e. g. figs. 15, 29), conductor or tegular apophysis frequently existing (figs. 17, 21, 24) . . . . . 2

2(1) Legs bristle-less, ventral cusps (fig. 4) may exist on legs I–II; a single femoral bristle on the posterior leg exists very rarely. Cephalic part wide anteriorly and distinctly convex (figs. 7–8) . . . . . Trachelinae

- Leg bristles existing at least on legs I–II. Cephalic part rarely wide and distinctly convex, the thoracic part may even be highest (similar to fig. 2 but see fig. 43) . . . . . 3

3(2) Retromargin of the fang furrow with 4–8 teeth or denticles, chelicerae powerful, anteriorly distinctly bulging, without an anterior bristle. Posterior median eyes circular. Femur of the ♂-pedipalpus without a hump. . . . . Corinninae

- Retromargin of the fang furrow in almost all species with 2 denticles, chelicerae anteriorly not distinctly bulging, most often with 1–2 anterior bristles in the basal half (fig. 26). Posterior median eyes frequently (!) oval (fig. 42). Femur of the ♂-pedipalpus usually with a ventral hump usually in the distal half (figs. 23, 28) . . . . . Phrurolithinae

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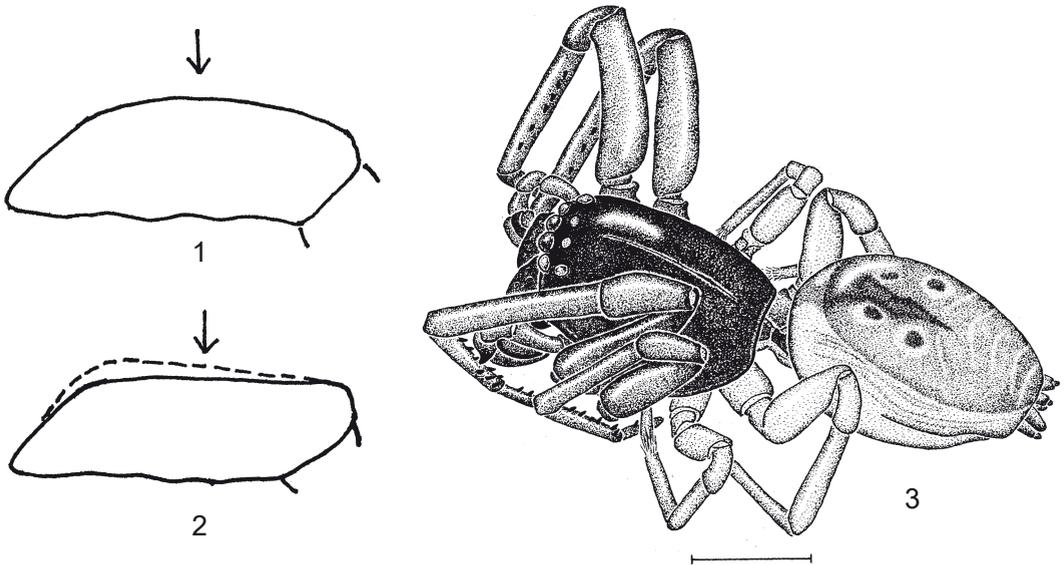


Fig. 1) Corinnidae: Trachelinae sp., outline of the prosoma. Eyes are not drawn. Note the distinctly convex dorsal profile (arrow). In other Corinnidae like Phrurolithinae the prosoma is low. See also fig. 43 (*Arabelia*);

fig. 2) Zoridae/Liocranidae sp.: *Liocranum* sp. and *Zora* sp. (dotted line), outline of the prosoma. Eyes are not drawn. Note the straight dorsal profile (arrow) which is even highest in the thoracal part of *Zora*;

fig. 3) *Paratrachelas atlantis* BOSSELAERS & BOSMANS 2010, oblique dorsal aspect of the male. Note the wrinkled prosoma, the ventral cusps (short spines) of the legs I–II, and the large opisthosomal scutum. Scale bar 1 mm. Taken from BOSSELAERS & BOSMANS (2010);

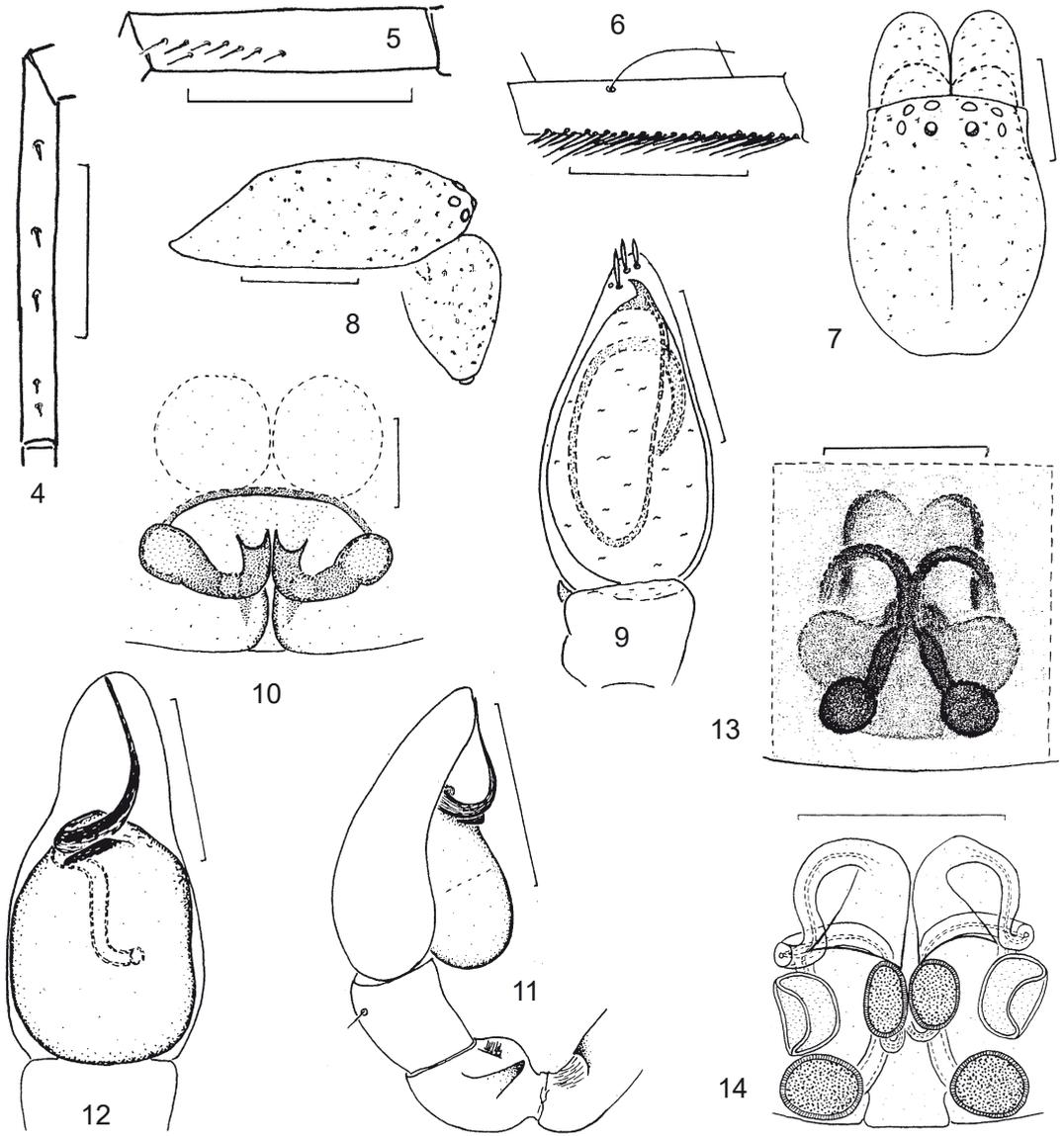
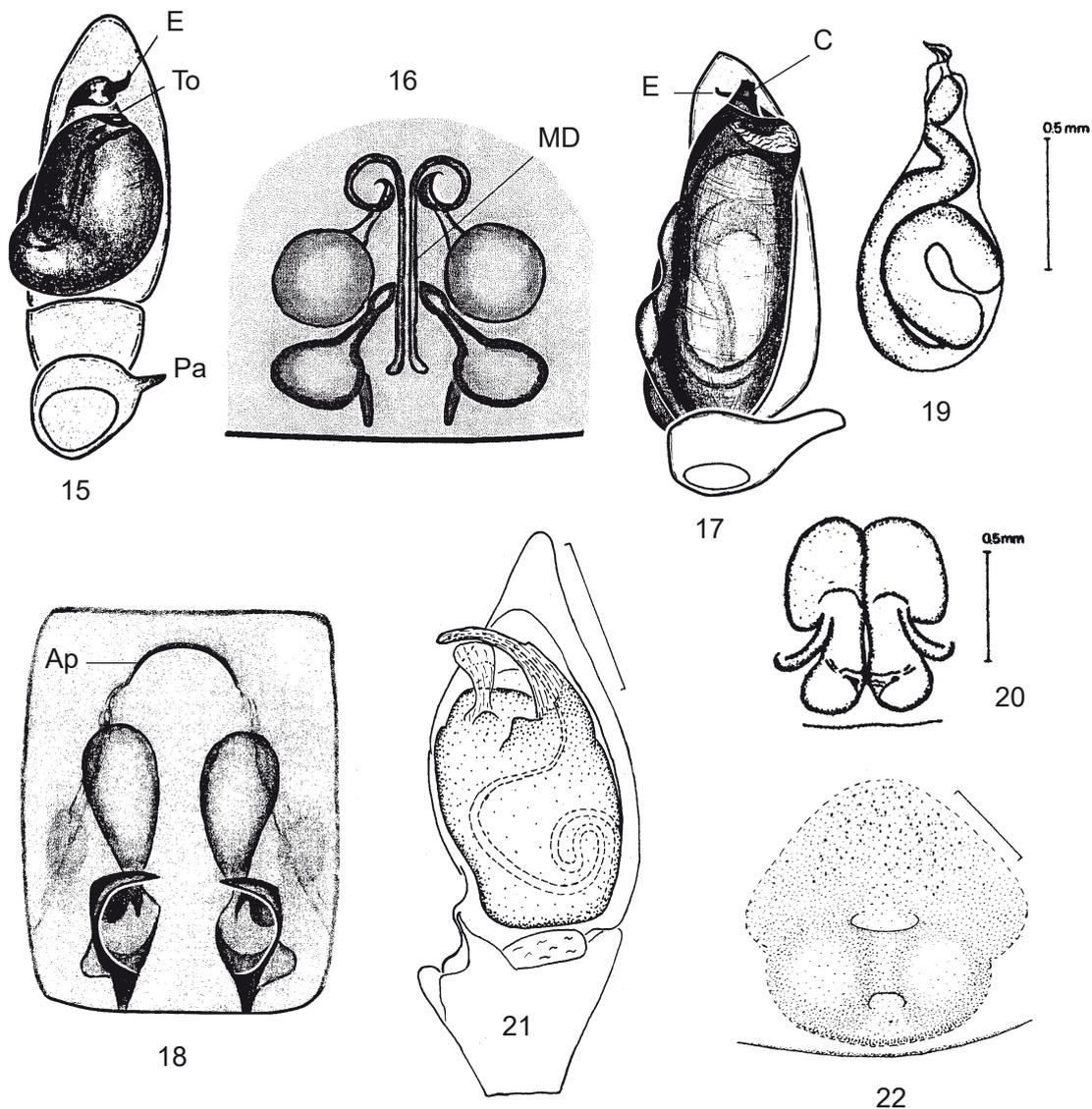


fig. 4) *Trachelinae* sp., ♂, proventral aspect of the right metatarsus I with short spines. Scale bar 0.5;

figs. 5-10: *Metatrachelas macrochelis* (WUNDERLICH 1992); 5) ♂, proteral aspect of the right tibia I. Note the slightly thickened hairs. Normal hairs are not drawn; 6) ♀, retrolateral aspect of the left tibia I; 7-8) dorsal and lateral aspect of the ♂-prosoma; 9) ♂, ventral aspect of the right pedipalpus; 10) dorsal aspect of the vulva. Scale bars 0.5 in figs. 5 and 7-8, 0.1 in fig. 1, 0.2 in the remaining figs.;

figs. 11-14: *Trachelas canariensis* WUNDERLICH 1987; 11-12) ♂, retroteral and ventral aspect of the right pedipalpus; 13-14: epigyne and dorsal aspect of the vulva. Scale bars 0.2;

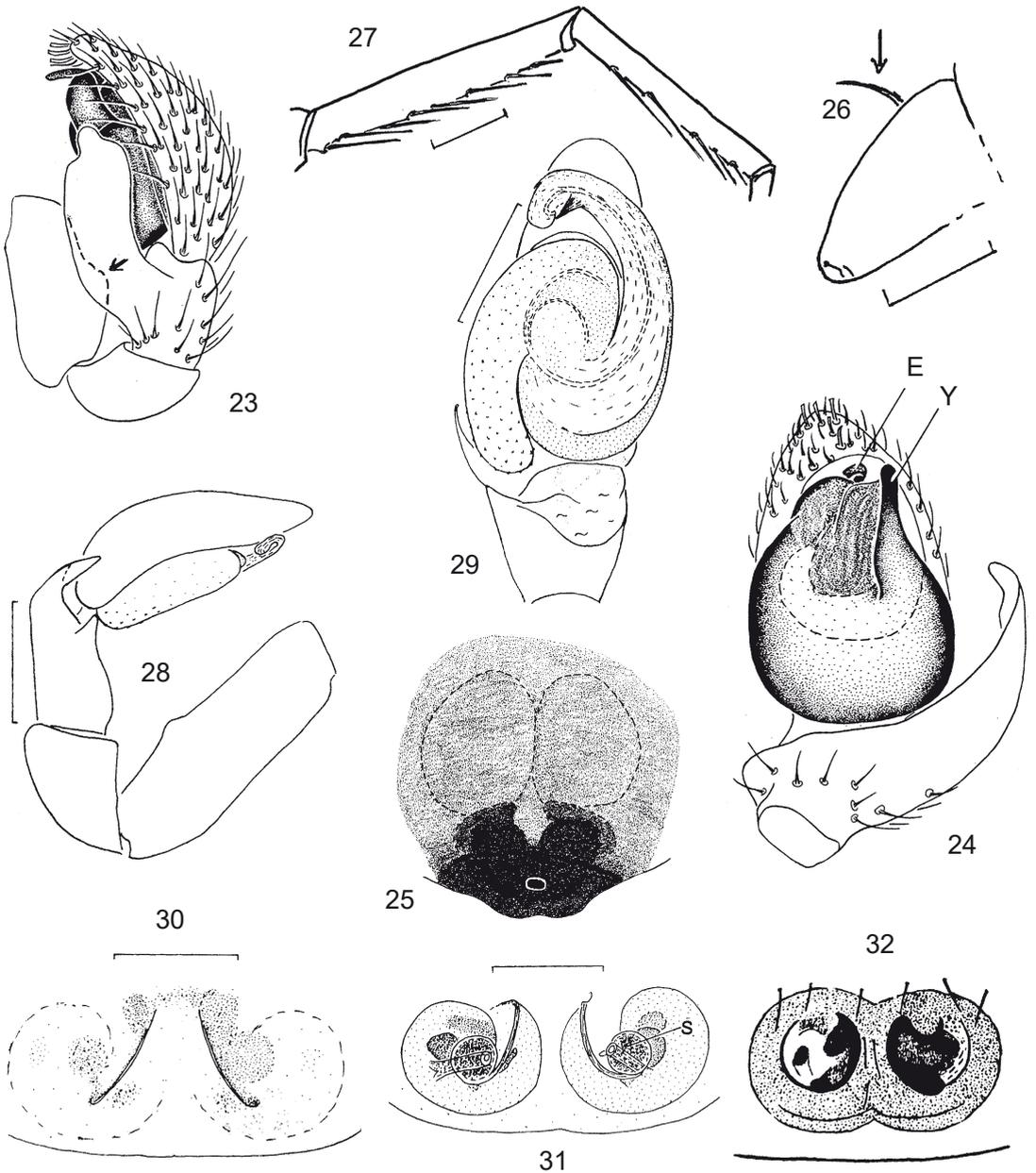


figs. 15-16: *Trachelas minor* O. PICKARD-CAMBRIDGE 1872; 15) ♂, ventral aspect of the left pedipalpus; 16) ventral aspect of the vulva. Taken from KOVBLIYUK & NADOLNY (2009);

figs. 17-18: *Paratrachelas maculatus* THORELL 1872; 17) ♂, ventral aspect of the left pedipalpus; 18) epigyne. Taken from KOVBLIYUK & NADOLNY (2009);

figs. 19-20: *Castianeira badia* (SIMON 1877); 19) ♂, ventral aspect of the right bulbus; 20) dorsal aspect of the vulva. Taken from CAMARGO & FERRANDEZ (1984);

figs. 21-22: *Creugas gulosus* THORELL 1878; 21) ♂, ventral aspect of the right pedipalpus; 22) epigyne. Scale bars 0.5 and 0.2;



figs. 23-25: *Phrurolithus festivus* (C. L. KOCH 1835); 23-24) ♂, retrolateral and ventral aspect of the left pedipalpus. The arrow in fig. 23) points to the femoral hum which is hidden in this position; 25) epigyne. Taken from GRIMM (1986), slightly modified;

figs. 26-32: *Liophrurillus flavitarsis* (LUCAS 1846); 26) ♂♀, retrolateral aspect of the left chelicera. Note the anterior bristle (arrow); 27) ♂♀, retrolateral aspect of the right leg I; 28-29) ♂, retrolateral and ventral aspect of the right pedipalpus; 30-31) epigyne and dorsal aspect of the vulva with sperm in the left receptaculum; 32) epigyne which is partly covered by a plug, taken from DENIS (1964: fig. 23) (under *Phrurolithus grandis*). Scale bars 0.5 in fig. 27, 0.3 in fig. 28, 0.2 in the remaining figs.;

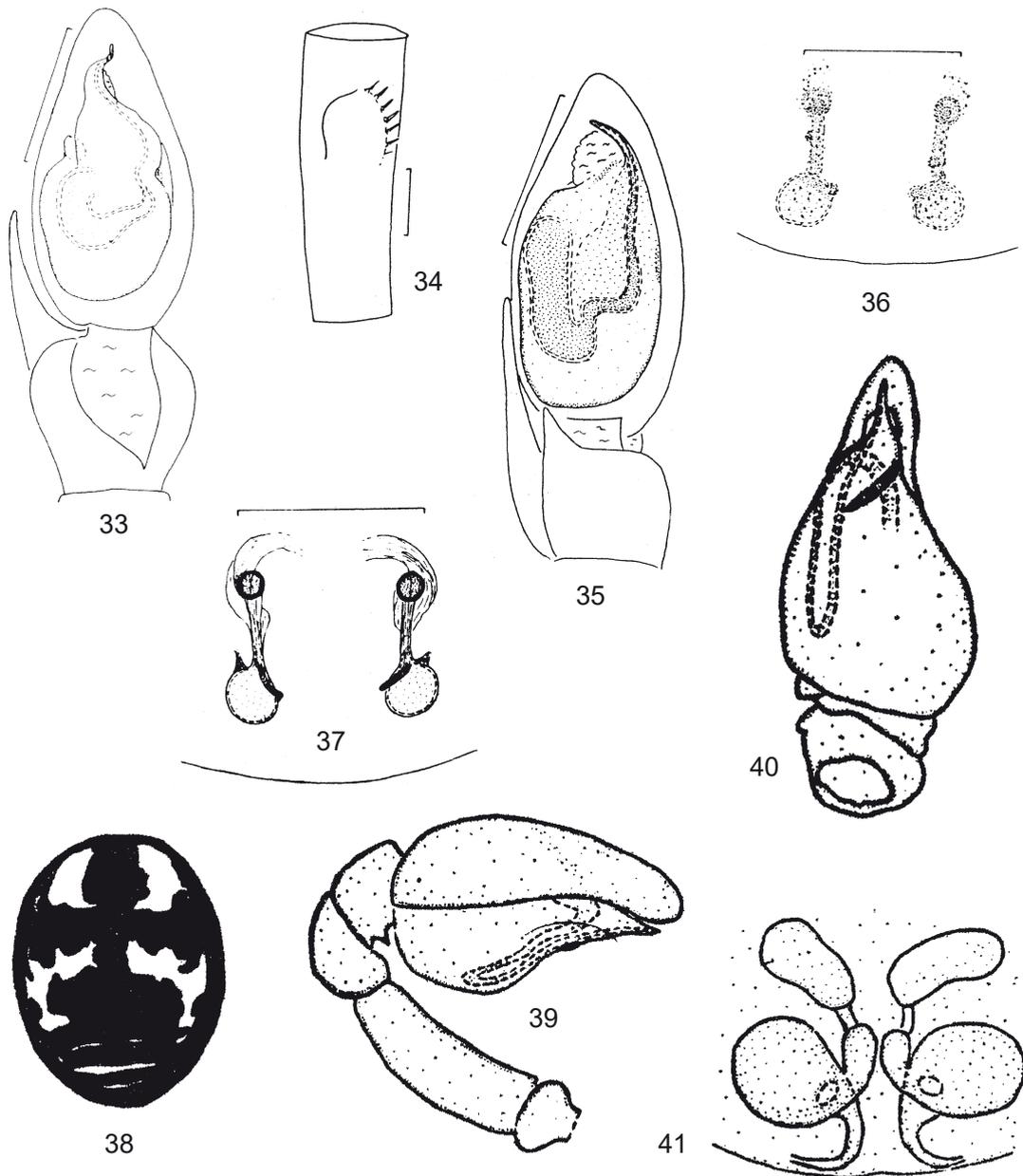
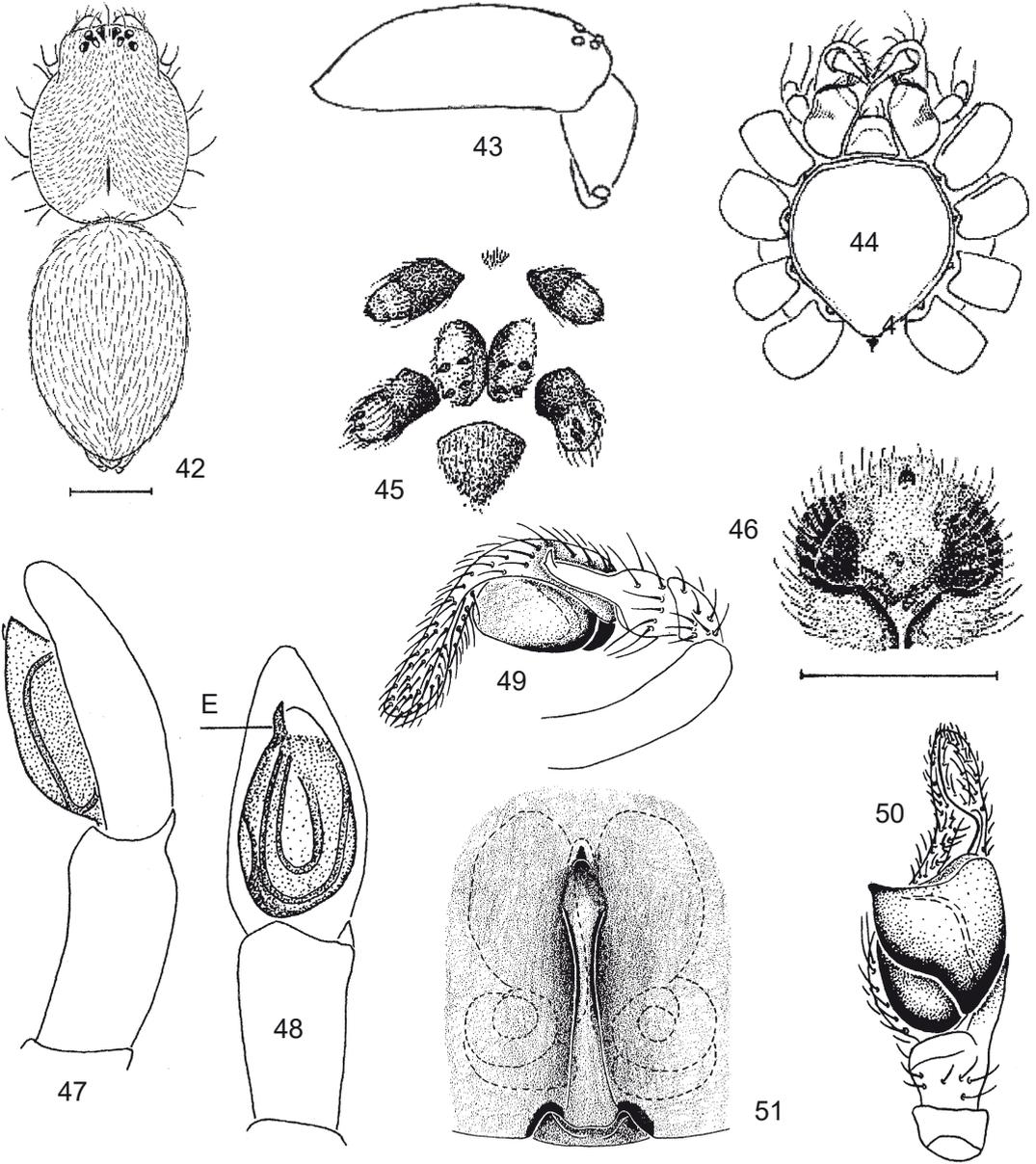


fig. 33) *Phrurolinillus tibialis* SIMON 1878), ♂, ventral aspect of the right pedipalpus. Scale bar 0.2;

figs. 34-37: *Phrurolinillus lisboensis* WUNDERLICH 1995; 34) ♂, ventral aspect of the femur of the right pedipalpus; 35) ♂, ventral aspect of the right pedipalpus; 36-37) epigyne and dorsal aspect of the vulva. Scale bars 0.2;

figs. 38-41: *Orthobula charitonovi* (MIKHAILOV 1986); 38) dorsal aspect of the opisthosoma; 39-40) ♂, lateral and ventral aspect of the pedipalpus; 41) vulva;



figs. 42-48: *Arabelia pheidoleicomis* BOSSELAERS 2009; 42-46) ♀; 42) dorsal aspect of the body; 43) lateral aspect of the prosoma; 44) ventral aspect of the prosoma. In contrast to this drawing I did not find a gnathocoxal depression in a female from Rhodos; 45) spinnerets; 46) epigyne. Taken from BOSSELAERS (2009) (under Liocraniidae); 47-48) ♂, retrolateral and ventral aspect of the left pedipalpus (E = embolus). Taken from BOSMANS (2011);

figs. 49-51: *Cetonana laticeps* (CANESTRINI 1868); 49-50) ♂, retrolateral and ventral aspect of the left pedipalpus; 51) epigyne. Taken from GRIMM (1986) (under *Ceto l.*, Clubionidae: Corinninae).

## CONTRIBUTION TO TAXONOMY AND EVOLUTION OF THE EUROPEAN GENERA OF THE SPIDER FAMILY PHILODROMIDAE (ARANEAE)

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**Key words:** Araneae, camouflage, determination, ecophylogeny, ecotaxonomy, Europe, Holarctic, new and re-elevated genera, Palaearctic, Philodromidae, spiders.

**Abstract:** A provisional identification key to the 11 European genera of the spider family Philodromidae (Araneae) is provided. Numerous **new combinations** are proposed. The taxa *Emargidromus n. gen.*, *Philodromimus n. gen.*, and *Pulchellodromus n. gen.* (all from *Philodromus*) are erected. The taxonomical level of certain taxa is discussed; *Paratibellus* SIMON 1932 is regarded as a genus of its own but not as a part of *Thanatus* C. L. KOCH 1837. The taxa *Artanes* THORELL 1870 (= *Horodromoides* GERTSCH 1933), *Rhysodromus* SCHICK 1965, *Tibellomimus* GERTSCH 1933 and the American taxon *Philodromoides* SCHEFFER 1905 (all from *Philodromus*) are **revived** or **re-elevated** to genus rank. Notes are given on some American genera; *Philodromoides*, *Ebo* KEYSERLING and *Titanebo* GERTSCH are restricted to the New World. The value of the camouflage and the habitat preference in higher philodromid taxa for the taxonomy and for phylogenetic conclusions (ecophylogenetics) are pointed out. The absence of a proof of Eocene philodromid fossils is shortly discussed.

Acknowledgement:

The following drawings are taken from various authors with many thanks:

1: DAHL; 2: LOCKET & MILLIDGE; 3-5: LEVY; 9-14, 19-21, 23-24, 30b, 38b, 46-48, 52-54: ALMQUIST; 15-17, 56-58: MUSTER; 22, 43: ROBERTS, 25: BRAUN; 33: SIMON; 34: MAURER & WALTER; 51: DONDALE & REDNER.

Material studied of all genera is stored in the SMF and in the private collection of the author (CJW).

Contents: The main paragraphs of this paper are arranged in the following order: Selected characters, intrageneric variability and convergences, ecophylogenetics, ecotaxonomy, fossils, informations on the European philodromid genera including their diagnoses, identification key to the European philodromid genera.

Abbreviation: "S & W" indicates photos of the Philodromidae in the book by SAUER & WUNDERLICH (1997: 91-95): Die schönsten Spinnen Europas nach Farbfotos erkannt (The most beautiful spiders of Europe, identified by coloured photos).

The aims of this paper are to provide a relatively simple and usable identification key to the European philodromid taxa which are regarded as genera by me, and to answer the following questions: How many genera of the family Philodromidae exist in Europe and in the Holarctic Region? Which taxa should be re-elevated to genus rank? What is the ecophylogenetical value of the habitat preference in supraspecific philodromid taxa?

Family characters: Philodromidae ("Running Crab Spiders") are fast running spiders which possess a distinctly depressed body, a laterigrade leg position, and a camouflage coloration of the body (figs. 1–3; S & W: 91–97).– Further important diagnostic characters (number of cheliceral teeth (see also below, figs. A, B), "rings" around the lateral eyes (see also directly below and figs. A, B), position of the tarsal trichobothria), and relationships of this family: See the paper on the European spider families in Beitr. Araneol. 8. under "diagnoses, ...".

Remarks on selected characters within the family Philodromidae and examples of peculiar intergeneric variability and convergences mainly regarding European taxa:

CAMOUFLAGE COLORATION and camouflage behaviour are common within the Philodromidae, see figs. 2–3 and the the photos in S & W: 91–97. Ground-living fast running spiders on sand are usually sand-coloured; dark longitudinal bands (*Tibellus*, fig. 2) and a dark heart mark (e. g. *Thanatus*, fig. 3; see directly below) may help to make the outline of the body/opisthosoma more indistinct. The body of *Artanes* in a "sit-and-wait-position" may resemble lichens. Behaviour: A typical resting position with the legs stretched forward and backward along the stems of low plants exists in *Tibellus*, see S & W: 99.

A distinct dark HEART MARK exists in several genera, especially in females, most distinct in *Thanatus*, fig. 3; see below (“ecophylogenetics”, and the key to the genera).

SEXUAL DIMORPHISMS besides the length of body and legs is strongly variable in certain species: The males are darker coloured (strongly e. g. in *Philodromus aureolus*, see S & W: 91), and usually the leg scopula is distinctly stronger developed in the females (see above).

TARSAL BRISTLES are usually absent – like in most other members of the RTA-clade – but exist in most members of *Artanes* (fig. 6).

A SCOPULA under tarsus and metatarsus (distally) I–II is usually well developed at least in the females, but it is only weakly developed in the males of certain taxa like *Philodromimus dispar* and in most *Tibellomimus*.

An ELONGATION OF LEG II and an ENLARGEMENT OF THE ANTERIOR MEDIAN EYES – mainly in *Halodromus* and the American genera *Ebo* and *Titanebo* – evolved, apparently independently, within the family Philodromidae, see MUSTER (2009: 48).

The LENSES OF THE LATERAL EYES are most often surrounded by distinct humps of guanine “rings” (fig. 4), but such humps/rings are quite indistinct developed in the genera *Paratibellus*, *Thanatus* and *Tibellus* (fig. 5) which all are members of clade I (fig. A).

TEETH OF THE ANTERIOR MARGIN OF THE CHELICERAL FANG FURROW: In *Thanatus* usually a single tooth, but two teeth may exist in certain species like *pictus*.

APOPHYSES of articles of the MALE PEDIPALPUS: Tibial apophyses of the ♂-pedipalpus exist usually in a number of 1–3, but in *Tibellus maritimus* such an apophysis is completely absent and in *T. oblongus* (fig. 52) as well as in certain species of *Rhysodromus* (like *histrion*, fig. 50) only a single small apophysis exists. In *Artanes* (fig. 7) a DORSAL tibial apophysis exists, in *Pulchellodromus* (fig. 56) a VENTRAL tibial apophysis. Only in *Halodromus* (fig. 15) – as well as in a small species of the American subgenus *Locupletus* of *Rhysodromus* – an apophysis of the patella exists.

Ecology, ecophylogenetics, ecotaxonomy, and Eocene fossils: MUSTER (2009) based his philodromid phylogeny mainly on (genital)morphological characters and molecular data, but – with the exceptions of *Artanes* and *Halodromus* – not on ecological characters like dwelling on the ground or in higher strata of the vegetation. Data on the distribution and the localities of collecting are given by several authors, but only very few on the habitat. In my opinion the habitat preference is an important taxonomical character in several taxa and may be helpful in solving phylogenetic questions, and helpful in taxonomy, too.

Most philodromid species are either ground dwellers (mainly in sandy areas/within scarce vegetation) or dwellers of higher strata of the vegetation. Members of *Tibellus* have a somewhat intermediate position, living on lower plants mainly in sandy areas. Species of *Artanes* and the *Pulchellodromus punctigerus* species-group (mainly) – which are not related to each other – are dwellers of tree bark. *Ebo*: See below.

It is remarkable **(1)** that most taxa of clade I in the sense of MUSTER (2009: 142) are ground dwelling spiders (usually in sandy habitats); only few are dwellers of lower plants (*Tibellus*) or mainly dwellers of tree bark: Species of the *punctigerus* species-group of *Pulchellodromus*. Contrarily the species of clade II in the sense of MUSTER all are dwellers of HIGHER strata of the vegetation (figs. A) (1) and B). **(2)** that a number of two teeth of the anterior margin of the cheliceral fang furrow exists only in two genera of clade I (in *Tibellus* and certain *Thanatus*); in the remaining genera only a single tooth exists in this position (rarely no tooth), see figs. A and B. The absence of elevated lateral eye lenses – a plesiomorphic character? – also exists only within clade I (in the genera *Paratibellus*, *Thanatus* and *Tibellus*). – (Furthermore the taxa of clade I are partly restricted to Southern Europe in contrast to the genera of clade II whose distribution extends north of the Alps without an exception).

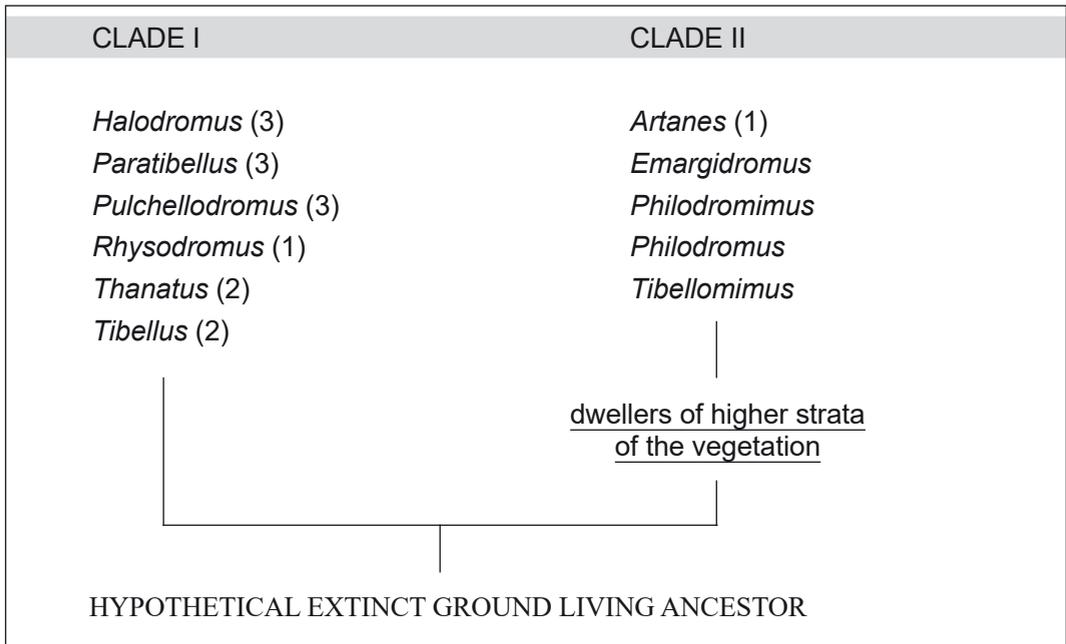


Fig. A. Possible origin and evolution of the preference of higher strata in the European genera of the family Philodromidae. (Clades I and II in the sense of MUSTER (2009)).

Remarks:

- (1) Members of *Artanes* and the *Pulchellodromus punctigerus* species-group (mainly) are dwellers of the bark of trees, apparently a convergently evolved pattern.
- (2) Genera in which the anterior margin of the cheliceral furrow bears two teeth (only partly so in *Thanatus*) – a plesiomorphic character?
- (3) Genera in which all (*Halodromus*) or almost all species are restricted to Southern Europe.

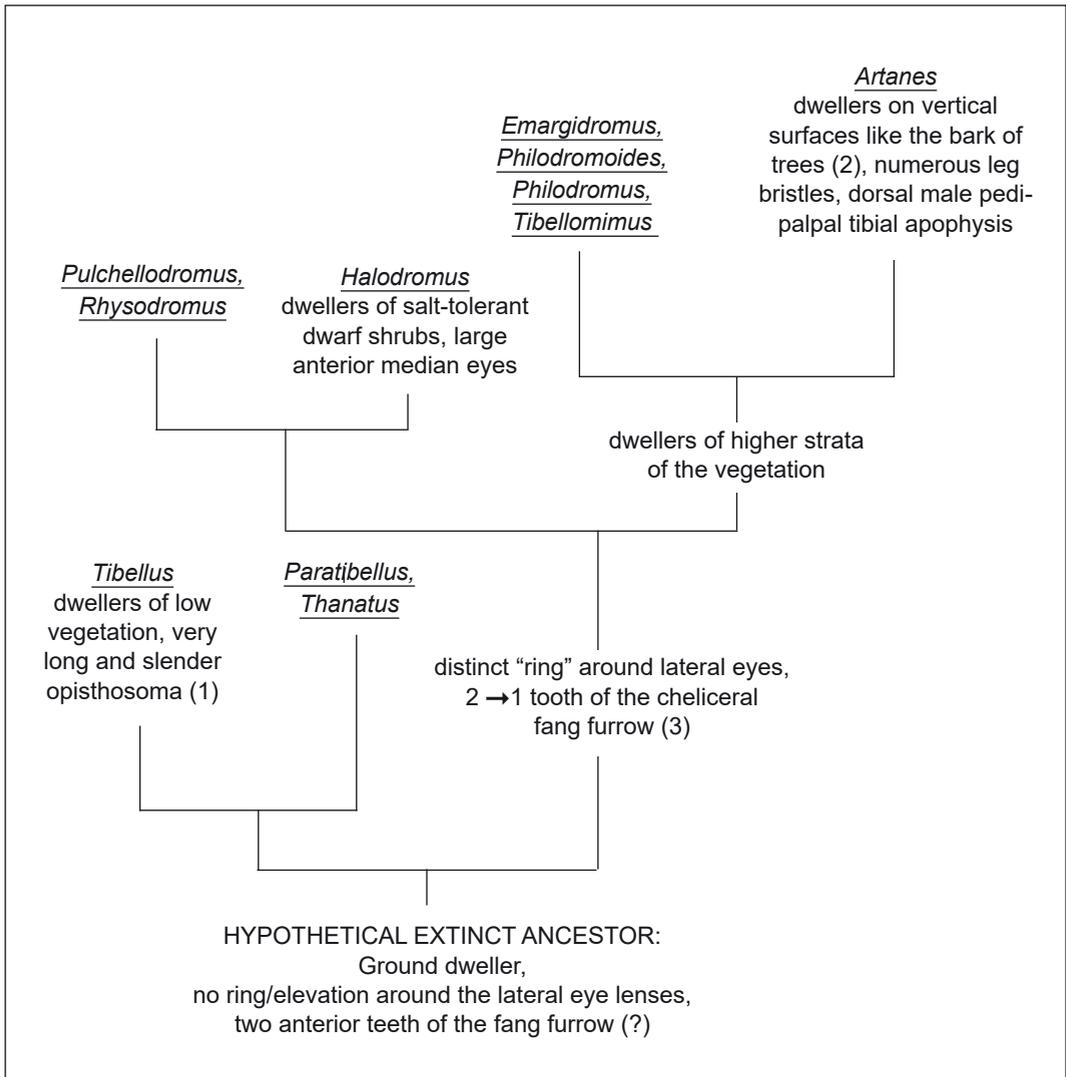


Fig. B. Simplified possible "ECOCLADOGRAM" of the European genera of the family Philodromidae. Few morphological characters are added.

Remarks:

- (1) A character similar to *Paratibellus*.
- (2) Members of the *Pulchellodromus punctigerus* species-group are – mainly – dwellers of the bark of trees, too.
- (3) A reduction of the number of teeth of the fang furrow exists also in *Paratibellus* and several *Thanatus*.

**POSSIBLE CONCLUSIONS AND DISCUSSION:** Putting together (COMBINE) most important morphological, genetical and ecological characters of the higher philodromid taxa, as well as the knowledge of their distribution, their coloration and of their fossils (see below) – which apparently ARE PARTLY LINKED TO EACH OTHER and so build a remarkable puzzle – I suppose that ...

(a) because of the existence of usually several teeth in taxa related to the Philodromidae (probable outgroups like Sparassidae) the number of TWO teeth of the anterior margin of the fang furrow may be a basal pattern of the family Philodromidae, and the reduction to only a single tooth or none may be a derived pattern, see fig. B;

(b) the ground-living life style is a basal pattern of the Philodromidae (see fig. B) in contrast to the dwelling in higher strata of the vegetation of genera like *Artanes*, *Emargidromus*, *Philodromimus* and *Philodromus*; which are surely derived taxa, and are mainly taxa of the “Old World”. Most members of the Nearctic genus *Ebo* like *bucklei*, *latithorax* and *pipiensis* are found in grassland litter (C. DONDALE in litt.).

(c) the dark lanceolate heart mark is very frequent within the Philodromidae at least in females (fig. 3), but absent, e. g., in derived bark-dwellers like *Artanes* (in my opinion nothing else than A LOSS because of the different kind of camouflage which evolved in these bark-dwellers, see fig. B), is also a basal pattern of this family, connected with the ground-living in scarce vegetation in which the spiders may be freely observable. It is absent or indistinct in *Ebo*. The dark mark may help to make the outline of the body more indistinct.

(d) The number of genera of the family Philodromidae is only about half as high in the Nearctic Region compared with the Palaearctic, and thus the evolution of the most basal philodromid branch appears more likely in the Palaearctic than in the Nearctic.

Therefore I conclude that the dwelling in higher strata of the vegetation is a derived character, an apomorphic character of the clade II in the sense of MUSTER (2009), and that this ecological pattern CONVERGENTLY EVOLVED at least two more times (see b): In the *punctigerus* species-group of *Pulchellodromus* and probably in few species of *Ebo* like *latithorax* which were collected in houses or on the foliage of pine trees besides (!) grassland litter according to DONDALE (person commun. in VIII 2011).

If ground-dwelling and the number of two cheliceral teeth (see fig. B) are regarded as plesiomorphic characters – and the dwelling of higher strata of the vegetation as well as a reduced number of cheliceral teeth as derived – the branch *Paratibellus* + *Thanatus* + *Tibellus* may be regarded as the most basal philodromid branch (which exists mainly in the Palaearctic), and probably also *Ebo*. MUSTER (2009) regards the American genus *Ebo* as most basal, being the (plesiomorphic) sister group to all other holarctic philodromid genera, of the clades I and II in his sense. I am not sure about the basal position of the genus *Ebo*. – REMARK: Besides their long leg II the “*Ebo*-like running crab spiders” of the Old World in the sense of MUSTER (2009) – the genus *Halodromus* – has not much in common with the Nearctic genus *Ebo* whose members possess no distinct dark heart mark and no pedipalpal patellar apophysis. See also above (d).

FOSSILS: A proof of Eocene (Baltic amber) philodromid fossils is lacking although this family is diverse in Europe today. I suppose that the most basal (holarctic) genera of this family – members of clade I sensu MUSTER (2009); see figs. A and B – are ground-liv-

ing spiders on sandy areas but not of higher strata of the vegetation (and forests) like the genera *Artanes* and *Philodromus* of clade II in the sense of MUSTER (2009). The reason for the absence of Eocene fossils of the Baltic amber forest may simply be the absence of FOREST-dwelling Philodromidae in the Eocene and/or the evolution of such species only later, in the Oligocene or in the Miocene. Eocene ground-living Philodromidae of sandy areas may have existed outside the Eocene forests, and were not collected by the resin producing trees. Probably a – juvenile? – aeronautic member of the Philodromidae has been captured by the fossil resin and will be discovered in the future.

The evolution/diversification of philodromid taxa was – similar to the evolution of the families Lycosidae (and Zodariidae?) – probably connected with the relatively late evolution of grassland (open biotopes) after the Eocene. See the paper on Cretaceous spiders.

Historical taxonomy and selected problems in the taxonomy of the Philodromidae and certain other spider families: The high number of ecological and morphological patterns having evolved convergently, as well as the intrageneric variability – e. g. of the size and the position of the eyes, of the number/reductions of leg bristles, of the development of leg scopulae, and of structures of the male pedipalpus like the number of the tibial apophyses (e. g. in *Philodromus* s. str. and in *Thanatus*) – caused confusions and an only slow progress in the recognition of true relationships of philodromid taxa and subtaxa. American philodromid genera have been investigated mainly by SCHICK (1965) and in several papers by DONDALE & REDNER (e. g. 1976). Phylogenetic studies of the European genera of the family Philodromidae have been neglected for a long time, and investigations are still in progress, see the important works by MUSTER (e. g. 2007, 2009), who included molecular data in his studies and who provided a plausible cladogram (2009), recognizing *Ebo/Titanebo* as the (basal) sister group to all remaining holarctic philodromid genera, and *Artanes* as the most derived taxon (of his clade II). In several parts the present paper is based on the important work by MUSTER although I am in doubt about the basal position of the Nearctic genus *Ebo*, see above “Possible conclusions”.

Only three or four European philodromid genera were generally accepted up to the end of the 20th century when I started my studies on this family but I am quite sure that the very diverse genus *Philodromus* (s. l.) in the traditional sense has to be split into several genera, partly in the sense of SCHICK (1965) and MUSTER (2009, 2010); see e. g. the genera *Artanes* and *Emargidromus* below. Taxa previously created e. g. by SCHICK (1965) – corresponding with neglected papers by ARCHER regarding genera of the Theridiidae or by LOHMANDER regarding genera of the family Clubionidae – were not accepted by most authors. Apparently certain referees blocked the “revival” or re-elevation of genera like *Artanes* (= *Horodromoides*) which was re-elevated to genus rank e. g. by LOGUNOV & KUNT (2010), see also MUSTER (2010). *Artanes* was described not less than one and a half century ago by the famous arachnologist THORELL. In his World Spider Catalog PLATNICK (2011) did not accept this genus because “... this unjustified elevation of an automorphic species group would render *Philodromus* paraphyletic...”. But an accepted genus *Artanes* as a top taxon (of *Philodromus* s. l.) would not concern other groups of the diverse and not monophyletic genus *Philodromus* s. l. in the former sense. *Philodromus* s. l. in the sense of MUSTER (2009) is split here, and no paraphyletic taxon remains. See the remark below at *Artanes*.

A situation similar to the Philodromidae exists in the families Hahniidae and Clubionidae, see Beitr. Araneol., 3 (2004: 1413–1428) and 5 (2008: 140–469). Like in the

families Clubionidae and Theridiidae the relationships of Nearctic and Palaearctic philodromid genera have not been well compared for a long time. The genus *Ebo* is one of the exceptions: Old World species – which were previously regarded as members of the New World genus *Ebo* – are recently recognized as members of a clearly distinct new genus, described as *Halodromus* MUSTER 2009.

According to MUSTER (2009: 55) “*Rhysodromus* clearly deserves re-elevation to genus rank...”, but it was not re-elevated by this author. The same is true for *Titanibo*.

DONDALE & REDNER (1976: 128–129) provided a KEY to the American “species-groups” of the genus *Philodromus* s. l. which cover most of the European philodromid taxa, and which are regarded as genera in this paper:

*aureolus*-group = *Philodromus* s. str.,

*infuscatus*-group: *Philodromoides* (fig. 55) (America),

*dispar*-group: *Philodromimus*,

*histrion*-group: *Rhysodromus*,

*fuscumarginatus*-group: *Artanes* (*validus* in America),

*imbecillus*- (America); *rufus*-group: *Tibellomimus* s. str..

Remarks on Nearctic taxa as well as certain taxa of the Palaearctic (see also directly above): The species of the *Philodromus aureolus*-group are regarded by me as members of *Philodromus* s. str.. Species of the *histrion*-group including *fallax* are regarded as members of *Rhysodromus*. *Tibellomimus* s. l. is quite diverse and has to split, see below: *Pulchellodromus* and *Tibellomimus*. The American (nearctic and neotropical) *Philodromus infuscatus*-group – see DONDALE & REDNER (1969), MUSTER (2009) (fig. 55) – does, according to the structures of its bulbus, not fit in any group outside America, and is coextensive with *Philodromoides* SCHEFFER 1904 sensu SCHICK 1965 which may not be a part of *Tibellomimus*. The Nearctic genera *Apollophanes* O. PICKARD-CAMBRIDGE (also North Asia), *Horodromus* CHAMBERLIN and *Titanebo* GERTSCH are not treated in this paper. – The Palaearctic genera *Halodromus*, *Emargidromus* and *Philodromimus* are absent in the Nearctic (the only member of *Philodromimus* – *dispar* – has been introduced to the Nearctic).

## The European genera of the Philodromidae

The following genera are treated in this paper (their type species are listed, too):

*Artanes* THORELL 1870; *margaritatus* (CLERCK 1757);

*Emargidromus* n. gen.; *emarginatus* (SCHRANK 1803) (monotypical);

*Halodromus* MUSTER 2009; *pallidens* (LEVY 1977);

*Paratibellus* SIMON 1932; *oblongiusculus* (LUCAS 1846) (monotypic),  
*Philodromimus* n. gen.; *dispar* (WALCKENAER 1826) (monotypic);  
*Philodromus* WALCKENAER 1826; *aureolus* (CLERCK 1757);  
*Pulchellodromus* n. gen.; *pulchellus* (LUCAS 1846);  
*Rhysodromus* SCHICK 1965; *histrion* (LATREILLE 1819);  
*Thanatus* C. L. KOCH 1837; *formicinus* (CLERCK 1757);  
*Tibellomimus* GERTSCH 1933; *lineatus* GERTSCH 1933;  
*Tibellus* SIMON 1875; *oblongus* (WALCKENAER 1802).

Distribution of the genera in Europe: Most genera occur in Europe from the South to the North (not repeated below), only three genera are restricted – or almost restricted – to Southern Europe: (1) The monotypic genus *Paratibellus* occurs northward up to Switzerland, (2) *Pulchellodromus* (most species of the *punctigerus* species-group exists in the Western Mediterranean, *ruficapillus* reaches Austria), and (3) *Halodromus* occurs in the Southwest (Iberian Peninsula and Canary Islands (few species exist also in Northern Africa and on the Cape Verde Islands)). – See also the Nearctic genera above.

Diversity and species richness: The genera *Artanes*, *Philodromus*, *Thanatus*, and the diverse genus *Pulchellodromus* are most rich in species in Europe. In *Halodromus* only one species is known from Spain, and a second species from the Canary Islands. Only two European species are known from *Rhysodromus*. *Emargidromus*, *Paratibellus* and *Philodromimus* are represented by a single species only (at least in Europe).

**Artanes** THORELL 1870 (figs. 6–10; S & W: 93, 95 (*emarginatus*: See *Emargidromus*))

Synonyms: *Artamus* C. L. KOCH 1837, praeocc., and *Horodromoides* GERTSCH 1933;  
type species: *Horodromoides validus* GERTSCH 1933. (= *Philodromus fuscomarginatus*-group). See DONDALE & REDNER (1975).

Type species: *Araneus margaritatus* CLERCK 1757.

LOGUNOV & KUNT (2010) re-elevated *Artanes* to generic rank (including 17 species), MUSTER (2009) considered “the forgotten genus *Artanes* ... a subgenus of *Philodromus*” as “clearly a distinct lineage characterized by numerous synapomorphies.” But apparently in that paper he was not allowed by reviewers to re-elevate this taxon to genus rank. See the remark above.

**Diagnosis**: Femur III not shorter than I or IV or even longer. Numerous leg bristles: Tibia I with 3–5 pairs of ventral bristles and short apicals; metatarsi I–II with 3–4 pairs of

ventral bristles (including short apicals). At least tarsi I–III bear usually a pair of lateral bristles (fig. 6) with the exception of *fuscomarginatus* and *margaritatus*. ♂-pedipalpus (figs. 7–8): Tibia with 3 apophyses, one in a DORSAL position, cymbium and bulbus flat and wide, almost circular, bulbus with a long and distinct suture (S in fig. 8); epigyne/vulva (e. g. figs. 9–10) with a pair of large grooves, receptacula seminis voluminous, receptacula heads and distinct ducts absent.

Further characters: Larger spiders, body length 4–8 mm. Lanceolate dark heart mark absent.

**Relationships**: See *Emargidromus* n. gen. and *Philodromimus* n. gen.

Species in Europe: (a) *marginatus*-group: *marginatus*; (b) *poecilus*-group: *blanckei*, *femurostriatus*, *fuscomarginatus*, *johani*, *laricum*, *parietalis*, *pentheri*, *pinetorum*, *poecilus*, and 4 nomina dubia, see MUSTER (2009). – (A single species – *validus* – in North America).

Ecology: The spiders are dwellers of higher strata of the vegetation: At the bark of trees, probably mainly of needle trees, preferring vertical substrate.

**Emargidromus n. gen.** (figs. 11 – 14; S & W: 93 under *Artanes*)

Type species (by monotypy): *Aranea emarginata* SCHRANK 1803.

The gender of the name is masculine.

**Diagnosis**: Metatarsus I–II with only 2 pairs of long ventral bristles (no apicals). ♂-pedipalpus (figs. 11–12): Tibia besides a pointed retrolateral apophysis with a peculiar long, almost blunt and ridge-like retroventral apophysis, the conductor bears an apical spine (arrow in fig. 11). Epigyne (fig. 13) with an u-shaped sclerotized structure around a pit, vulva (fig. 14) with sclerotized long and S-shaped ducts and globular receptacula seminis.

Further characters: Body length 4.2–6.5 mm. Lanceolate dark heart mark absent. Tarsal and metatarsal scopula well developed in the female, less developed in the male. Tibia of the ♂-pedipalpus (fig. 12) strongly bent, cymbium almost symmetrical, fairly oval, embolus long and thin, originating at the base of the bulbus, encircling the bulbus which is clearly longer than wide.

**Relationships**: *Emarginatus* has been considered as a species of the genus *Philodromus* up to now. MUSTER (2009) regarded *emarginatus* as sister to *Philodromimus dispar* (= *Philodromus d.*) + *Artanes*, and also related to *Philodromus* s. str. (the former *aureolus* species-group). The pedipalpal tibial apophyses, the shape of cymbium and

tegulum, the structures of bulbus, epigyne and vulva are clearly different; see the key to the genera. – No bark dwellers in contrast to *Artanes*.

**Ecology:** Dwellers of higher strata, mainly of needle trees, no bark dwellers.

Species in Europe: The type species.

**Halodromus** MUSTER 2009 (figs. 15–17)

Type species: *Ebo patellidens* LEVY 1977 from Israel. Further species: See below.

**Diagnosis:** Anterior median eyes distinctly largest, leg II longest, strongly elongated (at least 1.4 times longer than I), pedipalpal PATELLA WITH A LARGE APOPHYSIS (fig. 15). Epigyne (e. g. fig. 16) quite variable, with a large septum, lateral grooves, and a pair of anterior AND posterior guiding pockets, vulva (e. g. fig. 17) with the glandular heads sitting directly on the receptacula seminis.

Further character: Body length 2–5 (♀) mm, philodromid tegular apophysis existing. Position of the long ventral distal metatarsal I bristles beyond the middle of the article. Dark lanceolate heart mark distinct.

**Relationships:** In the related European genera leg II is shorter (see the key), a pedipalpal patellar apophysis is absent, the structures of bulbus and epigyne are different. In *Thanatus* leg IV is usually longer than II. See the discussion on the relationships of *Ebo* above (“Possible conclusions”).

Species in Europe: See the distribution.

**Ecology:** The ground-living spiders are dwellers of salt-tolerant dwarf shrubs; MUSTER (2009).

**Distribution:** The Old World only: Iberian Peninsula, Spain (*H. barbarae* MUSTER 2009), North Africa, Cape Verde Islands, and Canary Islands (*H. patellaris* (WUNDERLICH 1987) (under *Ebo*). *E. patellidens*: See above, the type species.

**Paratibellus** SIMON 1932 (figs. 33–34a)

Type species (by monotypy): *Philodromus oblongiusculus* LUCAS 1846 (probably a second species of the genus exists in Asia, see LOGUNOV (1996)).

**Diagnosis:** Opisthosoma long and slender, at least 1.8 times longer than wide. Lateral eyes not on elevations as in fig. 5. ♂-pedipalpus (fig. 33): Tibial apophysis (arrow) in a distinct space from the end of the article and in a more ventral position, embolus thin and strongly bent, in a distal position. Epigyne (fig. 34) small and with a long septum, vulva (fig. 34a) with large and oval receptacula seminis and two pairs of glandular heads.

Further character: Leg scopula only fairly developed. Opisthosoma with a distinct dark lanceolate heart mark in the anterior two thirds (as in fig. 3).

**Relationships:** LOGUNOV (1996) regarded *Paratibellus* as a synonym of *Thanatus* contra MUSTER (2009). In *Thanatus* the low eye lenses and the distinct heart mark are similar to *Paratibellus* but the opisthosoma is less slender (usually less than 1 ½ times longer than wide), the leg scopula is dense, the retrolateral pedipalpal tibial apophysis has a retroapical position, the structures of the larger epigyne and the vulva are different.

**Ecology:** The spiders are ground dwellers in scarce vegetation of dry areas like *Thanatus*.

**Distribution** in Europe: The Southern part and Switzerland.

**Philodromimus n. gen.** (figs. 18–21; S & W: 91 under *Artanes dispar*)

(= *Philodromus dispar* species-group). See DONDALE & REDNER (1969).

Type species: *Philodromus dispar* WALCKENAER 1826 (the only species in Europe).

**Diagnosis:** Tibia I bears 4–6 pairs of ventral bristles (and short apicals). ♂-pedipalpus (figs. 18–19): Tibia with a single ventral tripartite apophysis (probably fused parts of originally three separate apophyses), cymbium retrobasally with a small finger-shaped sclerotized outgrowth, shape of cymbium and bulbus wide, flat, almost circular, and with a distinct suture, embolus long, encircling the bulbus. Epigyne (fig. 20) with a long and almost parallel-sided septum, no groove, vulva (fig. 21) with long, coiled ducts which curve medially.

Further characters: Prosoma black in the male, margin with a narrow white band (see S & W: 91, under *Artanes*) which is less distinct in the female; lanceolate dark heart mark absent. Leg scopula I–II absent in the male, quite weakly developed in the female.

**Relationships:** According to the wide and flat cymbium and bulbus, the distinct fold of the tegulum and the shape of the embolus *Artanes* s. str. is strongly related. In *Artanes* the leg scopulae are stronger developed, the anterior tibia bears either 3 pairs

of ventral bristles (and short apicals) or 4-5 pairs (and apicals). In this case at least the anterior tarsi (!) bear most often a pair of lateral bristles (fig. 6), with the exception of *fuscmarginatus* and *margaritatus*. The copulatory organs are also quite different: The male pedipalpal tibia bears three separate apophyses including a DORSAL one (fig. 7), a retrobasal outgrowth of the cymbium is absent, the epigyne bears a pair of grooves, distinct ducts of the vulva are absent. Members of *Artanes* are bark dwellers.

Species in Europe: Only the type species.

Ecology: The spiders are dwellers of higher strata of the vegetation of bushes and trees (not on the bark).

**Philodromus** WALCKENAER 1826 **s. str.** (figs. 22–25; S & W: 91, 93, 95)

(= *Philodromus aureolus* species-group). See BRAUN (1965).

Type species: *Araneus aureolus* CLERCK 1757.

**Diagnosis:** Copulatory organs rather uniformly: ♂-pedipalpus (figs. 22, 25): Cymbium ASYMMETRICAL (usually distinctly), widened prolaterally in a special way in the distal half (arrow in fig. 22), tibia with 3 apophyses (the intermediate one may be reduced), retrolateral one longest, the ventral apophysis is usually wide (slender in *collinus*). A large flat and stiff sciny CONDUCTOR (C in fig. 22) exists between the distal part of the embolus and the tegulum and supports the embolus. A spine-shaped “intertegular retinaculum” (arrow in fig. 25) exists in all species but is not observable in some species in the ventral aspect. The base of the long embolus is most often thickened (X in fig. 22) (not in *fuscolimbatus*, *lunatus* and *vagulus*). Epigyne/vulva (figs. 23–24) with almost globular receptacula seminis, a large median septum, and a pair of large lateral sclerotized “FOLDS” (F in figs. 24, 25b).

Further characters: Body colour quite variable, its length usually 3–8.75 (♀) mm, usually 4–6 mm, lanceolate dark heart mark more or less distinct or completely absent, e. g. in the male of *P. aureolus*, see S & W: 91.

**Relationships:** In the related genera the shape of cymbium, bulbus, embolus, conductor, epigyne and vulva are different; see the key.

Species in Europe: About 15 species, see MUSTER & THALER (2004).

Ecology: The spiders are dwellers of higher strata of the vegetation, of bushes and trees.

***Pulchellodromus* n. gen.** (figs. 49, 56–58)

Corresponding with the *Philodromus pulchellus* species-group. MUSTER (2009: 143) regarded *glaucinus* and *pulchellus* as members of different subgroups.

The gender of the name is masculine.

**Diagnosis:** Leg II not distinctly longer than I. ♂-pedipalpus (figs. 49, 56, 58) with a flat and transparent ventral tibial apophysis which is usually longer than the retroletaral apophysis, retrobasal cymbial hook well developed, embolus relatively short, originating in a distal position and usually hidden in the ventral aspect of the bulbus, embolar apophysis large. Epigyne (fig. 57) with only fairly long ducts which are not coiled, with globular receptacula seminis and distinct glandular heads.

Further characters: Tibia I in the European species with 2 pairs of ventral bristles and a short apical pair. Dark heart mark existing or absent. Cymbium and bulbus long oval.

**Relationships:** In *Tibellomimus* a retrobasal cymbial hook is absent (fig. 41), the embolus bears also a large apophysis but it is longer, free observable and originating in a basal position. The epigyne (fig. 57) bears long and coiled ducts in contrast to the short ducts in *Pulchellodromus*.

Remarks: MUSTER et al. (2007) treated the *Philodromus pulchellus* species-group of the Mediterranean. The European species of the *rufus*-group (*albidus*, *rufus*) is distinct but may be related according to MUSTER et al. (2007: 49). The *pulchellus* species-group is regarded here as the new genus *Pulchellodromus*. The phyletic relationships within this taxon are discussed by MUSTER et al. (2007: 46), see fig. 4 p. 45, a cladogram combined by molecular data as well as morphological characters which show two groups which correspond with their life style: Members of the first group are dwellers of higher strata of the vegetation, mainly of the bark of trees, and I call it the *punctigerus* group (*afroglaucinus*, *lamellipalpis*, *punctigerus* and *wunderlichi*). The second group – which I call the *pulchellus* group: *bistigma*, *glaucinus*, *medius*, *pardalis*, *pulchellus* and *simoni* – are to my knowledge mainly dwellers on the ground although *ruficapillus* has been reported from lower grassy vegetation by DUMA (2008). – The *histrion*-group (= *Rhysodromus* SCHICK 1965) may also be related; according to MUSTER (2009: 55) *Rhysodromus* clearly reserves re-elevation to generic rank; see below.

Species in Europe (n. comb, from *Philodromus*): *Bistigma*, *glaucinus* (fig. 49), *medius*, *pulchellus* (figs. 56–57), *punctigerus* (= *glaucinoides*) (Canary Islands), *ruficapillatus*, *simoni*, *wunderlichi* (fig. 58), and 2 insufficiently known species, see MUSTER et al. (2007).

**Ecology:** Either mainly ground-dwellers (the *pulchellus*-group) or mainly bark-dwellers, the *punctigerus*-group, see above (“Remarks”).

**Distribution in Europe:** The Southern part, northward up to the Pannonian plain in Austria (*ruficapillus*).

***Rhysodromus*** SCHICK 1965 (**gen. re-elev.**) (figs. 46–48, 50–51)

(= *Philodromus histrio* species-group).

Type species: *Thomisus histrio* LATREILLE 1819.

See SZITA & LOGUNOV (2008), DONDALE & REDNER (1975, 1976), and MUSTER (2007, 2009).

**Diagnosis:** Metatarsus I bears usually 2 pairs of ventral bristles of which the second pair is situated in the middle of the article or more basally. ♂-pedipalpus (figs 46, 50): Embolus stout, frequently straight, terminating to the tip of the tegulum.

Further characters: Dark lanceolate heart mark distinct. Leg scopulae dense, especially in the female. Cymbium and bulbus long-oval.

Subgenera according to SCHICK (1965): (1) *Rhysodromus* SCHICK 1965: Patella of the ♂-pedipalpus (figs. 46, 50) without a retroapical apophysis, ventral pedipalpal tibial apophysis existing or absent, the sclerite supporting the conductor is movable.

(2) *Locupletes* SCHICK 1965: Patella of the ♂-pedipalpus with a small retroapical apophysis, tibia with a rounded apophysis, the sclerite supporting the embolus is a fixed apophysis. Type species is the holarctic *Philodromus alascaensis* KEYSERLING 1884. – *R. fallax* may be the member of a further subgenus.

**Relationships:** The combination of characters do not exist in another philodromid genus; see the key to the genera. In *Pulchellodromus* and *Tibellomimus* the second pair of ventral metatarsal bristles is situated beyond the middle of the article, the female tarsal scopula is scarce, the embolus is not stout and straight in *Tibellomimus*.

Species (n. comb., from *Philodromus*) (the European species are marked with an asterix): *Ablegminus*, *alascaensis*, *angulibulbis*, \**fallax* (figs. 46–48), \**histrio* (figs. 50–51), *lachowensis*, \**lepidus* (?), *mysticus*, *timidus*, *triangulatus*, *tuvinensis*, *xerophilus* and *xinjiangensis*.

Ecology: The European spiders live on the ground, usually in sandy areas.

**Distribution:** Holarctic (both subgenera).

***Thanatus*** C. L. KOCH 1837 (figs. 3, 26–40; S & W: 95, 97)

Type species. *Araneus formicinus* CLERCK 1757.

Synonymy: According to LOGUNOV & HUSENOV (2008: 127) *Paratibellus* SIMON 1932 – with the European type species *Philodromus oblongiusculus* LUCAS 1846) –

is a synonym of *Thanatus*, contra MUSTER (2009). In my opinion *Paratibellus* (see above) should be regarded as a genus of its own. – I do not want to exclude that *Vatchellia* CAPORACCIO 1935 – according to the original description and drawings – may be a member of the genus *Thanatus*.

**Diagnosis:** Lateral eyes (fig. 5) small and not on (distinct) humps, femur/leg IV usually longer than II, embolus long, strongly bent in the distal half, in an about transverse position and like a half-circle in some species (figs. 27–28, 32, 36, 40–41). Epigyne: The variability is shown in the figs. 26, 29–31, 37–38), vulva with gland heads anteriorly of the receptacula seminis (figs. 30b, 38b).

Further characters: Posterior eye row strongly recurved (fig. 5), opisthosoma fairly to distinctly longer than wide, lanceolate dark heart mark distinct in the anterior two thirds of the opisthosoma (fig. 3). The leg scopula is well developed. The tibia and metatarsus I–II bear 2 pairs of ventral bristles, short apical bristles exist rarely.

**Relationships:** See *Paratibellus*. In *Tibellus* the eyes and the leg bristles are similar but the opisthosoma bears a dark median band in its WHOLE length (fig. 2), the embolus is stout and (almost) straight (fig. 52), and glandular heads of the vulva (fig. 54) are absent in a position like in *Thanatus*.

Species in Europe: 20.

Ecology: Ground spiders, frequent within scarce vegetation or on sandy areas.

**Distribution:** Holarctic.

**Tibellomimus** GERTSCH 1933 **s. str. (gen. re-elev.)** (figs. 41–45; S & W: 93)

(= *Philodromus rufus* species-groups)

See DONDALE & REDNER (1968), MUSTER (2009), MUSTER et al. (2007).

Type species: *Tibellomimus lineatus* GERTSCH 1933 (= *floridanus* BANKS 1904).

**Diagnosis:** Embolus (fig. 42) very long and originating basally on the tegulum; epigyne (fig. 43) with long and coiled ducts.

Further characters: Light colour of body and legs, dark heart mark existing, see S & W: 93. Lateral eyes on distinct humps (guanine rings) similar to fig. 4. Femur/leg IV shorter than II, the second pair of metatarsal I bristles is situated beyond the middle of the article.

**Relationships:** In *Pulchellodromus* the embolus is shorter, originating more distally, the epigyne has shorter ducts which are not coiled. In *Rhysodromus* the second pair of the metatarsal I bristles is situated in the middle of the article or more basally, the structures of the genital organs are different, see above.

Ecology: Dweller of higher strata of the vegetation (not on bark).

Species in Europe: *Albidus* and *rufus* (**n. comb.**) (from *Philodromus*).

Note on the determination of the European species: In *rufus* (figs. 44–45) the origin of the embolus is more basally (arrow), it describes a wider curve (X) than in *albidus* (figs. 41–42), and the parembolar apophysis (P) is larger. The tibial apophysis as well as epigyne/vulva are quite variable in both species.

**Distribution:** Holarctic.

*Tibellus* SIMON 1875 (figs. 52–54; S & W: 97, 99)

Type species: *Aranea oblonga* WALCKENAER 1802.

**Diagnosis:** Anterior margin of the cheliceral fang furrow with 2 teeth. Opisthosoma slender, at least twice as long as wide (fig. 2), prosoma and opisthosoma IN THEIR WHOLE LENGTH with a distinct dark brown median band (fig. 2), see S & W: 97. Lateral eyes not on distinct humps. ♂-pedipalpus (e. g. fig. 52) with a stout and almost straight embolus in a distal position, epigyne e. g. as in fig. 53, vulva (fig. 54) with large receptacula seminis.

Further characters: Larger spiders, body length 7–11 mm. No or only a single small (fig. 52) tibial apophysis of the ♂-pedipalpus.

**Relationships:** See *Thanatus* and *Paratibellus*.

Species in Europe: Probably 4.

Ecology: The spiders are usually dwellers of lower plants and are more frequent in sandy areas.

Behaviour: Typical resting position with the legs stretched forward and backward along the stems of low plants, see S & W: 99. Camouflage: See above.

**Distribution:** Holarctic.

## Key to the European genera of the Philodromidae

### Remarks:

- (1) The lateral eyes are usually situated on distinct humps ("rings") around their lenses) (fig. 4) but such "rings" are absent in *Paratibellus*, *Thanatus* and *Tibellus* (figs. 2–3).
- (2) The determination of females of certain genera is difficult, even after the investigation of the vulva.
- (3) The body length varies in some species by more than 100%.
- (4) Almost 90 % of the species are found in the genera after the no. 5. – The males of three of the most diverse genera are easy to recognize according to their relatively constant configuration of the structures of their pedipalpi: In *Artanes* (as well as in *Philodromimus dispar*) the shape of the bulbus is almost circular and disc-shaped (nos. 4 and 6, figs. 8, 19), in *Philodromus* s. str. (no. 7, figs. 22, 25) the cymbium is asymmetrical, widened prolaterally in the distal half, in *Thanatus* (no. 8, figs. 27, 31–32, 36) the distal half of the long embolus is strongly bent, usually has a transverse position, and may even build a half-circle.
- (5) The ecology, see figs. A and B, and the distribution may be helpful to determine the genera: *Halodromus* is restricted to Southern Europe, almost all species of *Pulchellodromus* (except *ruficapillus*) as well as *Paratibellus oblongiusculus* do not occur north of the Alps, see above. Members of the remaining genera occur north of the Alps.

1 Opisthosoma slender, at least twice as long as wide, prosoma and opisthosoma IN THEIR WHOLE LENGTH with a distinct dark brown median band (fig. 2) (besides lateral bands), see S & W: 97. The anterior margin of the cheliceral fang furrow bears **2** teeth. ♂-pedipalpus (e. g. as in fig. 52) with a stout and almost straight embolus in a distal position, epigyne/vulva e. g. as in fig. 53–54. Large spiders, body length 7–10 mm. Usually on lower plants in sandy areas. 4 species, 2 in Central Europe. . . . . *Tibellus*

- Shape of the opisthosoma variable, if quite long – e. g. in *Paratibellus* (no. 2) and certain *Tibellomimus* (no. 10) – the body is less than 6 mm long, and the dark heart mark is ABSENT IN THE DISTAL THIRD (similar to fig. 3) or completely absent. Anterior margin of the fang furrow usually with a single tooth, rarely without tooth, two teeth exist only in very few *Thanatus* (no. 8). Spiders of the soil or of higher strata . . . . . 2

2(1) Opisthosoma long and slender, at least 1.8 times as long as wide. ♂-pedipalpus (fig. 33): Position of the retrolateral tibial apophysis in a certain distance from the tibial end. Epigyne/vulva: Figs. 34–34a. Dark heart mark distinct, similar to fig. 3. Only *oblongiusculus*. Ground spiders. Southern Europe and Switzerland . . . . . *Paratibellus*

- Opisthosoma usually about as long as wide or fairly longer, very long and slender e. g. in certain *Tibellomimus*, no. 10. Genital organs different . . . . . 3
  
- 3(2) Leg II distinctly elongated, its femur at least 1.4 times longer than I. Anterior median eyes distinctly largest. Patella of the ♂-pedipalpus (e. g. as in fig. 15) with a large apophysis, epigyne (e. g. fig. 16) with anterior and posterior pockets, vulva as in fig. 17. Ground spiders in salt-tolerant dwarf shrubs. Southern Spain and Canary Islands (Lanzarote) a single rare species each. . . . . Halodromus
  
- Length of leg II variable, its femur less than 1.4 times longer than I. Anterior median eyes not distinctly largest. Pedipalpal patellar apophysis absent, epigyne different (e. g. figs. 23, 29): no or only a single copulatory pocket. Dwellers of higher strata of the vegetation or ground spiders. . . . . 4
  
- 4(3) Tibia I–II with 4–6 pairs of LONG ventral bristles, leg scopula absent. Prosoma black in the male, in the middle part light in the female, margin with a striking narrow white band, see S & W: 91. ♂-pedipalpus (figs. 18–19): Cymbium and bulbus wide, disc-shaped, similar to *Artanes* (no. 6), cymbium retrobasally with a small finger-shaped sclerotized outgrowth. Epigyne (fig. 20) with a large almost parallel-sided septum, vulva (fig. 21) with long and thick coiled ducts. On bushes and trees. Only *P. dispar*. . . . . Philodromimus
  
- Tibia I usually with 2–3 pairs of long ventral bristles, a pair of additional short apical ventral bristles may exist. If there are 4–5 pairs of ventral tibial bristles the tarsi I–II most often bear a pair of lateral bristles (fig. 6: the *Artanes poecilus* species-group). Leg scopula usually well developed at least in the female. Retrobasal cymbial outgrowth existing in *Pulchellodromus* (no. 10, fig. 56), epigyne/vulva quite different. Prosomal colour different or fairly similar. In higher strata of the vegetation or on the ground. . . 5
  
- 5(4) ♂-pedipalpus (figs. 11–12): Tibia long and distinctly bent, bearing a pointed retrolateral apophysis and a long, wide, blunt and gutter-shaped retroventral apophysis, bulbus with a long and mainly hidden embolus, tegulum with a retrolateral spine (arrow in fig. 11). Epigyne (fig. 13) with a u-shaped sclerotized structure around a pit which may be indistinct, vulva (fig. 14) with long, thick and S-shaped ducts. Metatarsus I–II bear 2 pairs of long ventral bristles (no apicals). Body length 4.2–6.5 mm. Only *E. emarginatus*. Mainly on needle trees (no bark dweller). . . . . Emargidromus
  
- Copulatory organs quite different, pedipalpal tibia not or only slightly bent, apophyses different, body length variable . . . . . 6
  
- 6(5) Numerous leg bristles: Metatarsus I–II bear 3–4 pairs of long ventral bristles (incl. apicals). At least tarsi I–II usually bear a pair of lateral bristles (fig. 6), with the exception of *fuscomarginaus* and *margaritatus*. Femur III not shorter than I or IV or even longer. ♂-pedipalpus (e. g. figs. 7–8): Tibia – besides a ventral and a retrolateral apophysis – with an additional DORSAL apophysis. Shape of cymbium and bulbus rather uniform, disc-shaped, about circular (fig. 8), similar to *Philodromimus*, no. 4, but a cymbial tooth is absent and epigyne/vulva are quite different. Epigyne variable, e. g. as in fig. 9, receptacula seminis very large, “heads” absent (fig. 10). Larger spiders, body length 4–8 mm. On the bark of trees (see no. 10). Ten species . . . . . Artanes

- Fewer leg bristles: Metatarsus I-II bear only 2 pairs of ventral bristles. Tarsi without bristles. Femur III usually shorter than I or IV. Tibia of the ♂-pedipalpus with 1 or 2 apophyses, dorsal apophysis absent, cymbium and bulbus longer than wide (e. g. figs. 22, 27). Larger spiders or spiders smaller than 4 mm. . . . . 7

7(6) Copulatory organs rather uniform: ♂-pedipalpus (figs. 22, 25): Distal part of the cymbium in the European species asymmetrical (usually distinctly) widened prolaterally in a special way in the DISTAL half (arrow in fig. 22), embolus long, well observable, and most often thickened basally (X in fig. 22), a large sciny conductor (C in fig. 22) exists between the distal part of the embolus and the tegulum. Epigyne/vulva (figs. 23–24, 25a–b) with almost globular receptacula seminis, a large medium septum and large, strongly sclerotized lateral “FOLDS” (F in figs. 23, 25b). On bushes and trees (if not fallen down). Frequent, 15 species in Europe . . . . . Philodromus s. str.

- Distal part of the cymbium symmetrical or only slightly asymmetrical near the middle (figs. 27, 32, 49–50), conductor, embolus, epigyne and vulva different (e. g. figs. 38, 43, 51). Ground spiders or spiders of higher strata. . . . . 8

8(7) Femur/leg IV usually longer than II, occasionally both equal in length. Lateral eyes small, not on humps (fig. 5). Embolus long, strongly bent in the distal half, in an almost transverse position and like a half-circle in some species (figs. 27, 36). Epigyne quite variable (figs. 26f). Dark lanceolate opisthosomal mark usually quite distinct. (fig. 3), see S & W: 95. Ground spiders within scarce vegetation. 20 species. . . . . Thanatus

- Femur/leg IV shorter than II. Lateral eyes on distinct humps (guanine rings) similar to fig. 4. Opisthosomal heart mark indistinct or distinct (in most *Rhysodromus*). Copulatory organs e. g. as in figs. 41–51. Ground living spiders (*Rhysodromus*) or spiders of higher strata of the vegetation (*Tibellomimus*) . . . . . 9

9(8) Metatarsus I with 2 pairs of ventral bristles of which the second pair is situated in the middle of the article or more basally. Dense tarsal scopula, especially in the female. ♂-pedipalpus (figs. 46, 49, 50): Embolus stout, frequently straight, and terminating to the tip of the tegulum. Epigyne e.g. figs. 47, 51. Ground spiders. E. g. *fallax* and *histrion* . . . . . Rhysodromus

- Metatarsus I with 2 pairs of long ventral bristles, the second pair beyond the middle of the article. Tarsal scopula more sparse. Embolus (figs. 42, 56, 58) not stout, stronger bent, bearing a long “parembolic apophysis” (fig. 45). Epigyne e. g. as in figs. 43, 57. Ground living spiders or dwellers of higher strata of the vegetation . . . . . 10

10(9) Colour of body and legs yellowish. Retrobasal cymbial hook absent (fig. 41). Embolus (fig. 42) very long, originating basally on the tegulum and free observable. Epigyne (fig. 43) with long and coiled ducts. Dwellers of higher strata of the vegetation. *Albidus* and *rufus*. Europe . . . . . Tibellomimus

- Colour more grey. Retrobasal cymbial hook (CyP in fig. 56) well developed. Embolus (figs. 56,58) shorter, originating more distally, and hidden in the ventral position. Epigyne/vulva (fig. 57) with shorter ducts which are not coiled. Ground living spiders (the *pulchellus*-group) or dwellers of higher strata, mainly on bark (the *punctigerus* group). Southern Europe and Southeastern Austria (*ruficapillus*) . . . . . Pulchellodromus

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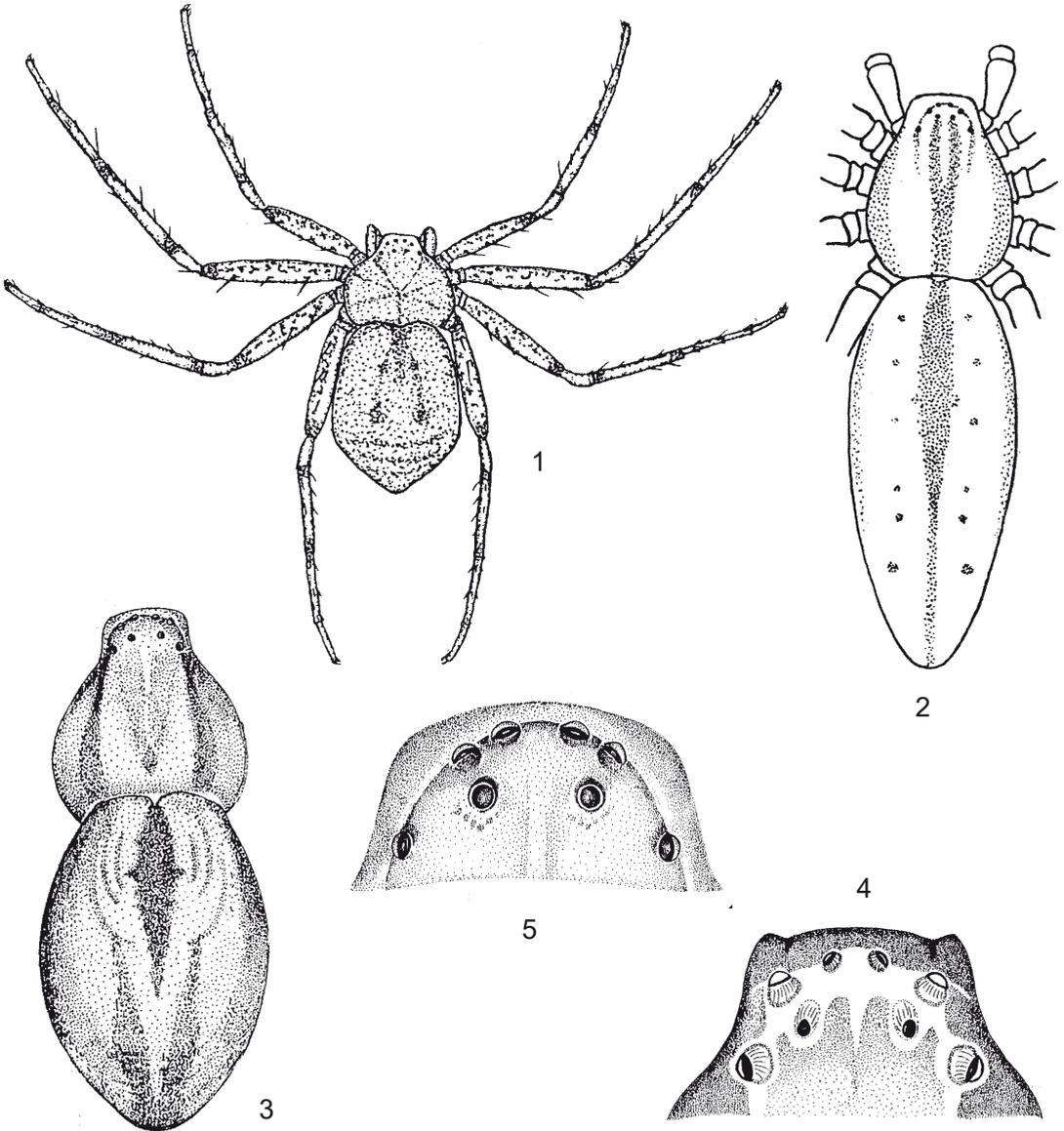


Fig. 1) Philodromidae sp., dorsal aspect of a typical member of a Running Crab Spider like *Philodromus*, *Thanatus* or *Tibellomimus*. (The quite different resting position in another genus: See S & W: 99 (*Tibellus*));

fig. 2) *Tibellus maritimus* (MENGE 1875), dorsal aspect of the body;

fig. 3) *Thanatus vulgaris* SIMON 1870, dorsal aspect of the body;

fig. 4) *Pulchellodromus glaucinus* (SIMON 1870), ♀, dorsal aspect of the eyes;

fig. 5) *Thanatus vulgaris* SIMON 1870, ♀, dorsal aspect of the eyes;

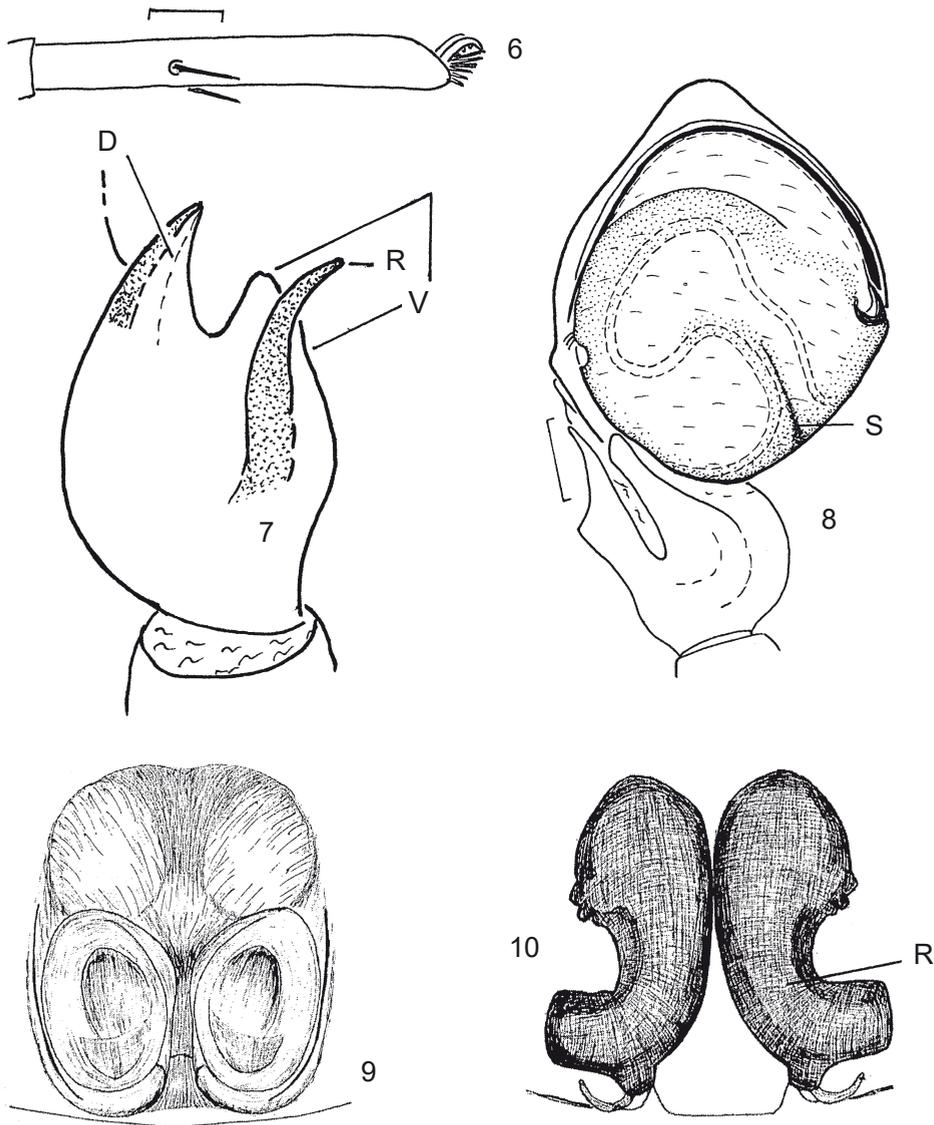
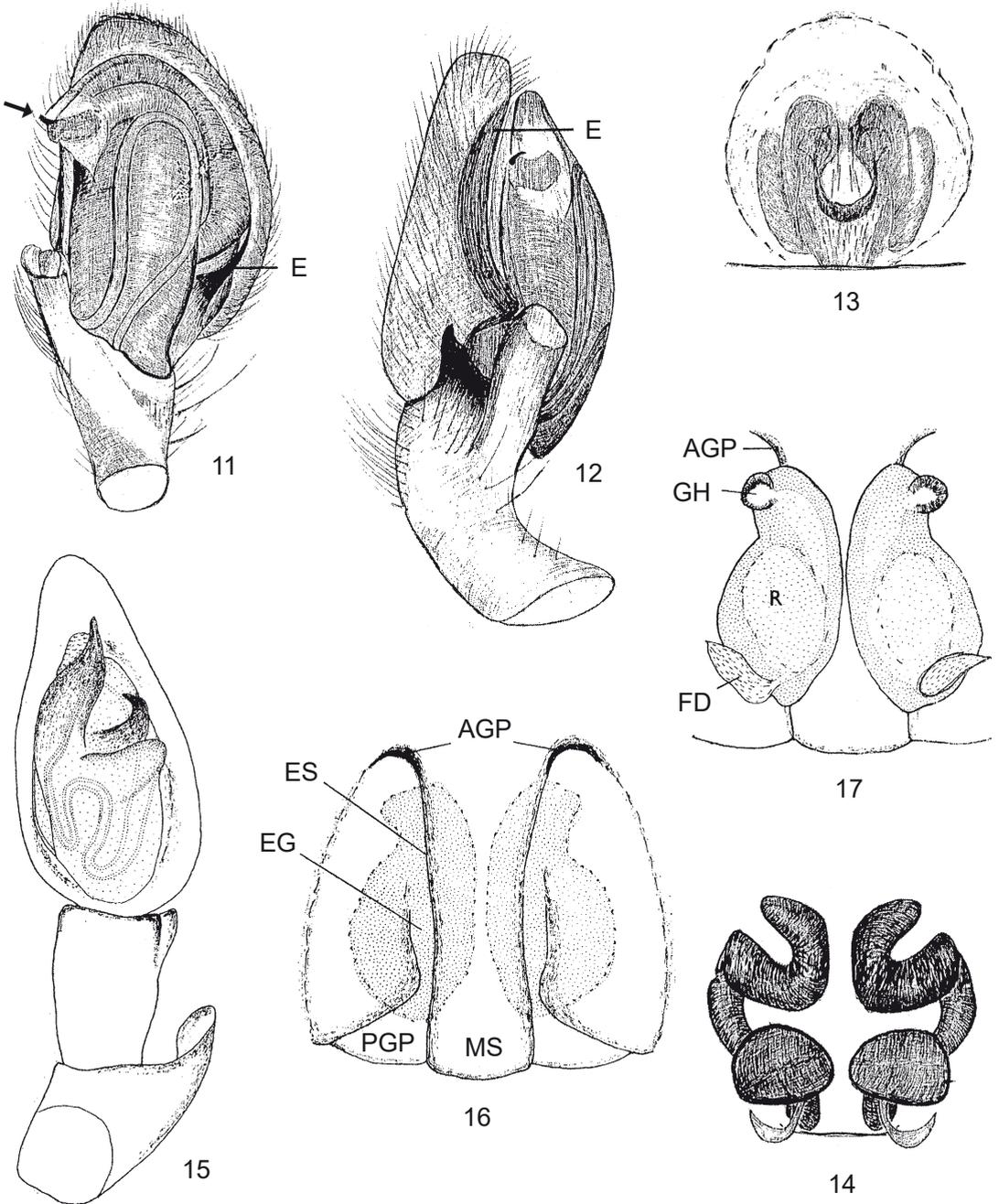


fig. 6) *Artanes poecilus* (TORELL 1872), ♀, prolateral aspect of the left tarsus I. Note the pair of lateral bristles. Hairs are not drawn; scale bar 0.2 mm;

fig. 7) *Artanes fuscomarginatus* (DE GEER 1878), ♂, retrolateral aspect of the right pedipalpal tibia. D = dorsal apophysis, R = retrolateral apophysis, V = ventral apophysis;

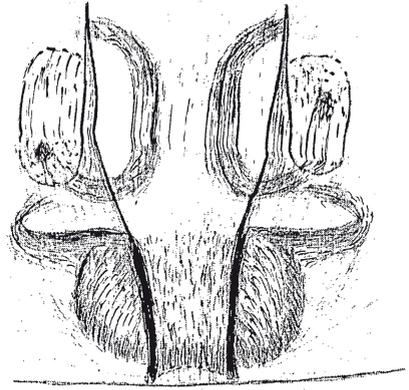
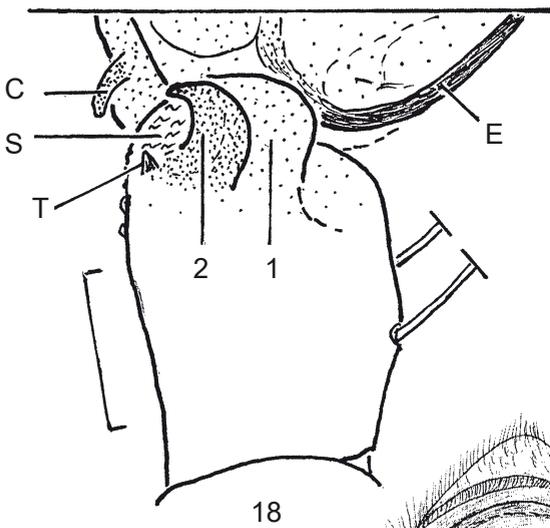
fig. 8) *Artanes* sp., ♂, ventral aspect of the right pedipalpus; S = suture (fold); scale bar 0.2;

figs. 9-10) *Artanes margaritatus* (CLERCK 1757), epigyne and vulva; R = receptaculum seminis;

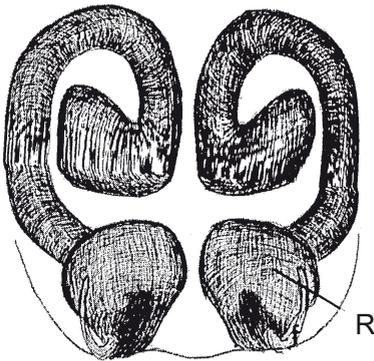


figs. 11-14: *Emargidromus emarginatus* (SCHRANK 1803); 11-12) ♂, ventral and retro-lateral aspect of the right pedipalpus; the arrow points to the tegular spine; E = embolus; 13-14) epigyne and vulva;

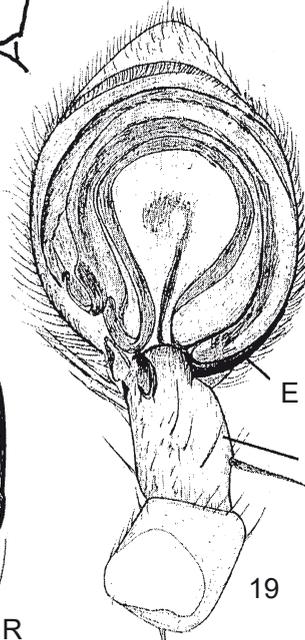
figs. 15-17: *Halodromus barbarae* MUSTER 2009; 15) ♂, ventral aspect of the left pedipalpus; 16-17) epigyne and dorsal aspect of the vulva;



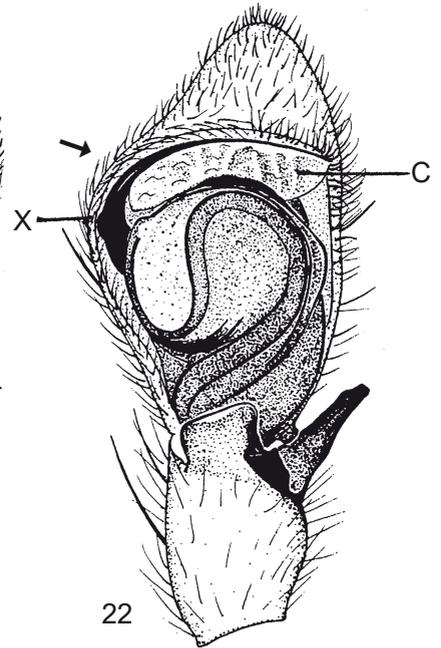
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22

figs. 18-21: *Philodromimus dispar* (WALCKENAER 1826); 18) ♂, ventral aspect of the tibia of the right pedipalpus; C = small retrobasal outgrowth of the cymbium, E = basal part of the embolus, 1 = weakly sclerotized part of the ventral apophysis, 2 = strongly sclerotized part of the ventral apophysis with its scinny part (S) and its tiny basal tooth (T); scale bar 0.2; 19) ♂, ventral aspect of the right pedipalpus; E = embolus; 20-21) epigyne and vulva; R = receptaculum;

figs. 22-24: *Philodromus aureolus* (CLERCK 1757); 22) ♂, ventral aspect of the left pedipalpus; C = conductor, X = thickened part near the base of the embolus; the arrow points to the widened retrolateral part of the cymbium; 23-24) epigyne and vulva with receptaculum seminis (R), and fold (F);

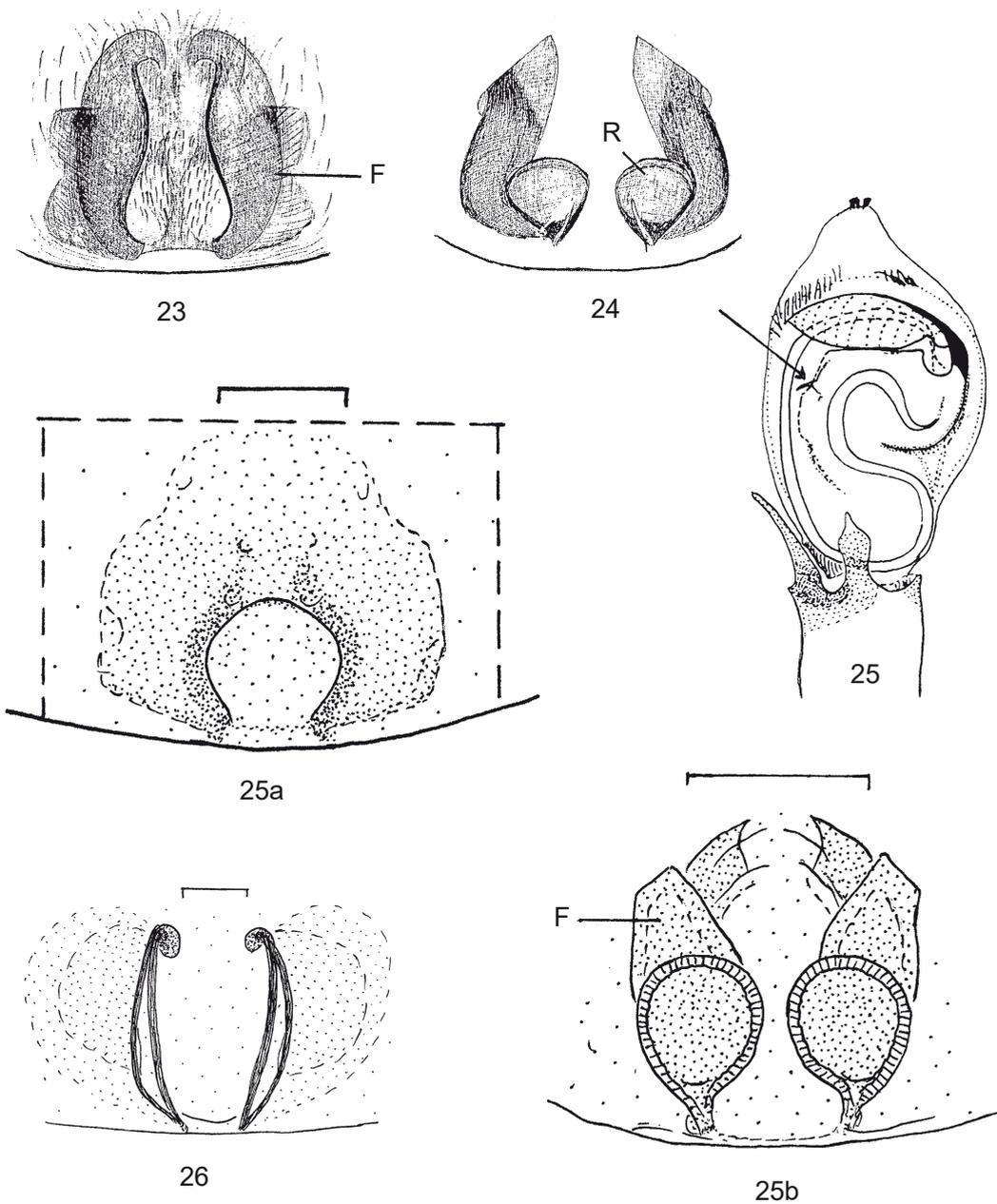
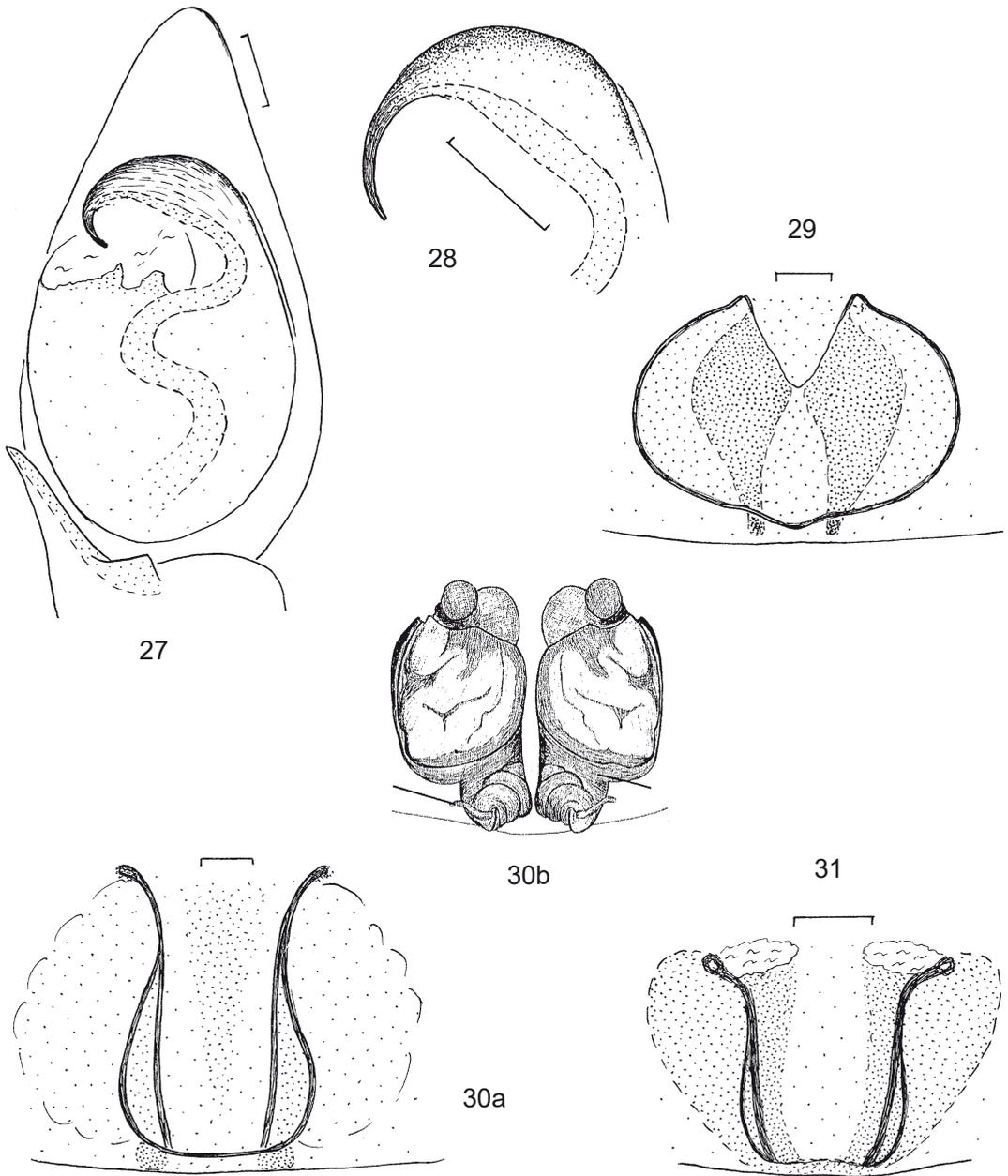


fig. 25) *Philodromus collinus* C. L. KOCH 1835, ♂, ventral aspect of the right pedipalpus; the arrow points to the “intertegular retinaculum”;

figs. 25a-b) *Philodromus* sp. indet. from South Portugal (near Tavira) (CJW), ♀, epigyne and dorsal aspect of the vulva, scale bars 0.2;

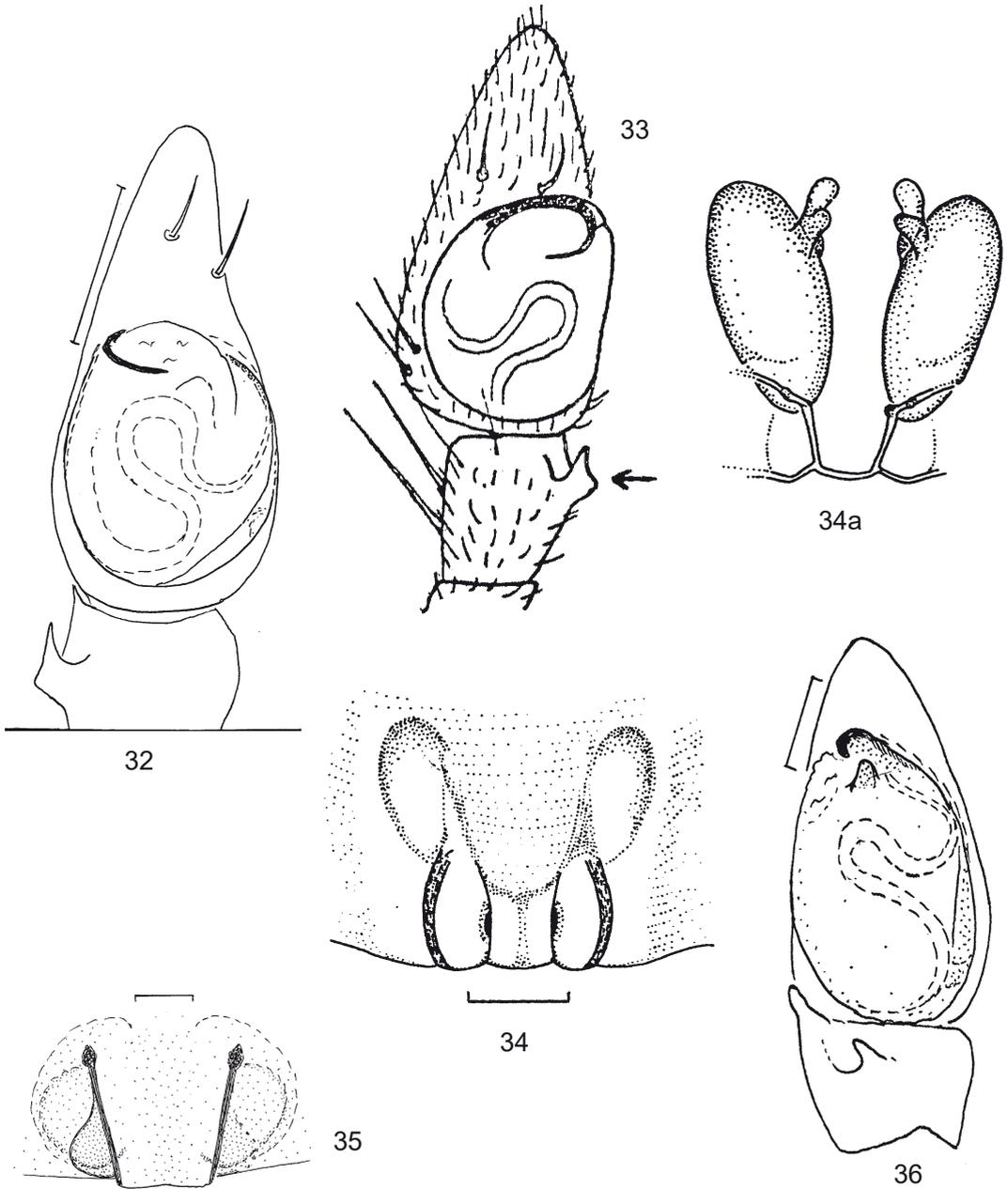
fig. 26) *Thanatus arenarius* L. KOCH 1872, epigyne; scale bar 0.1;



figs. 27-29: *Thanatus atratus* SIMON 1875; 27-28) ♂, ventral aspect of the right pedipalpus and enlarged embolus in a slightly apical aspect; see figs. 39-40; 29) epigyne (quite similar: *T. vulgaris*); scale bar 0.1;

figs. 30a-30b) *Thanatus formicinus* (CLERCK 1757), epigyne and vulva; scale bar 0.1;

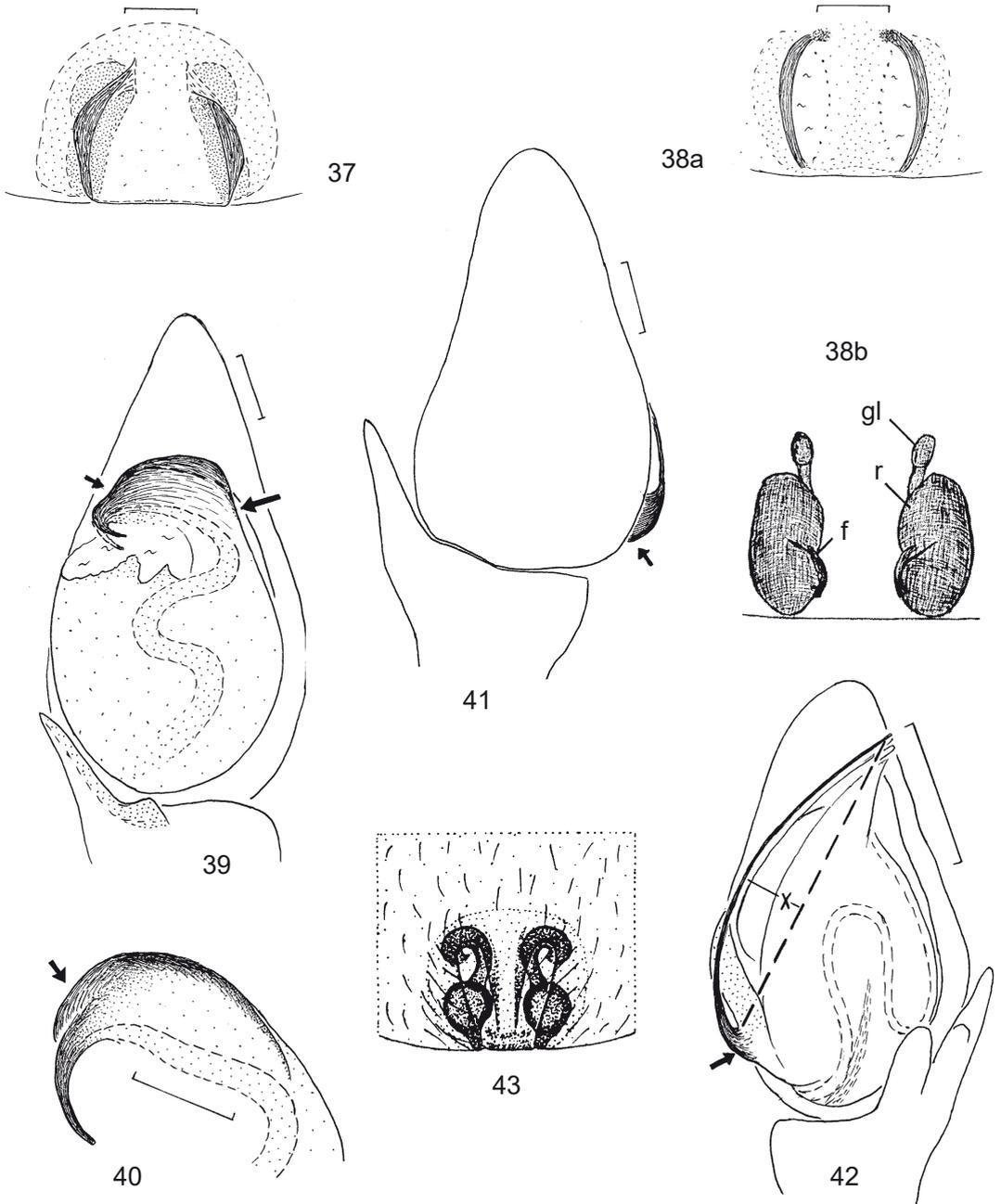
fig. 31) *Thanatus pictus* L. KOCH 1881, epigyne; scale bar 0.1;



figs. 32-34a: *Paratibeltus oblongiusculus* (LUCAS 1846); 32-33) ♂, ventral aspect of the right and left pedipalpus, variability; 34) epigyne; 34a) vulva;

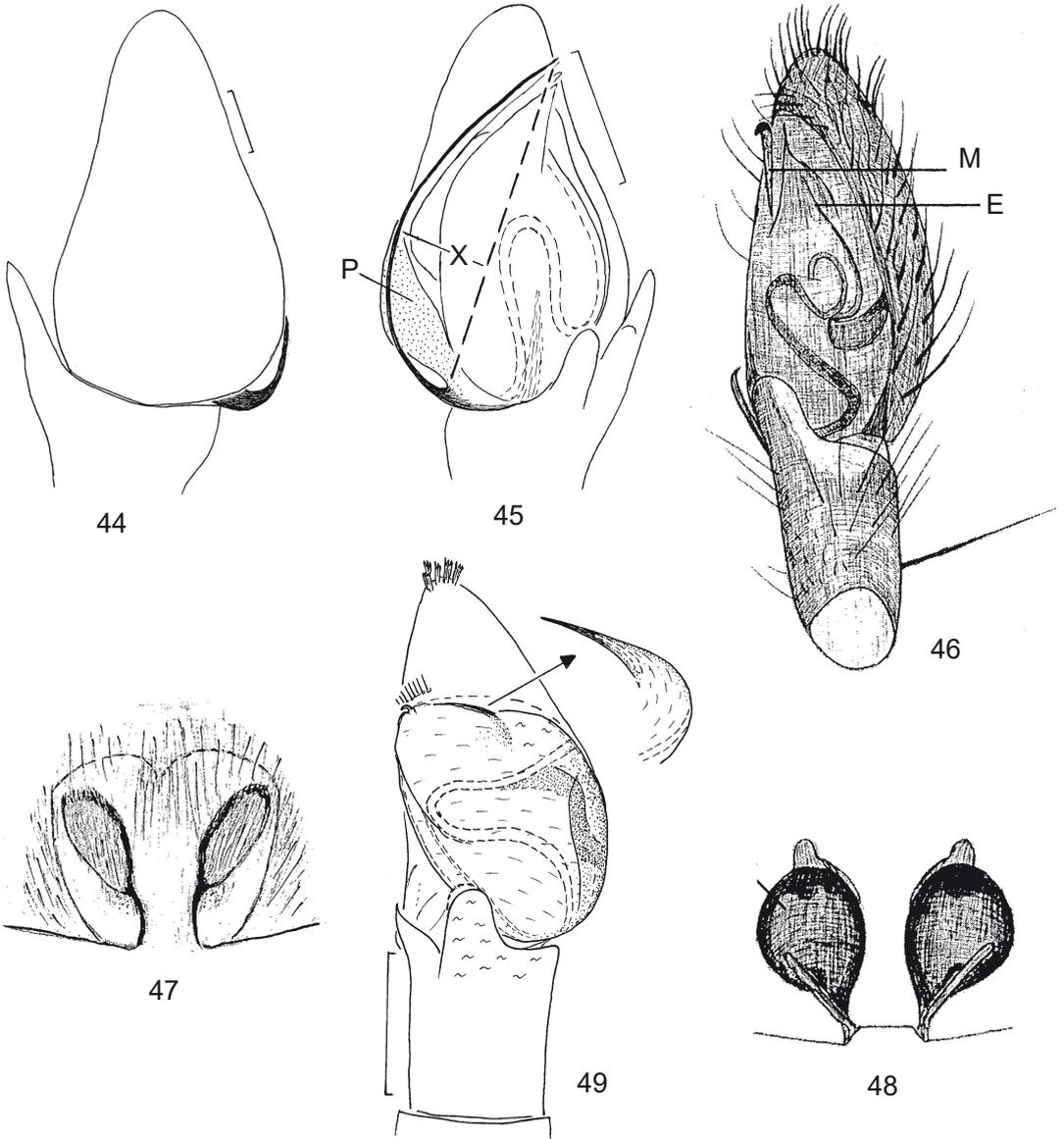
fig. 35) *Thanatus sabulosus* (MENGE 1875), epigyne; scale bar 0.1;

figs 36-38b): *Thanatus striatus* C. L. KOCH 1845; 36) ♂, ventral aspect of the right pedipalpus; 37-38a) ♀, epigyne (variability), scale bar 0.1; 38b) vulva;



figs. 39-40: *Thanatus vulgaris* SIMON 1870; ♂, ventral aspect of the right pedipalpus and the enlarged embolus in a more apical position; the arrows point to the differences to *T. atratus*, see figs. 27-28; scale bar 0.1;

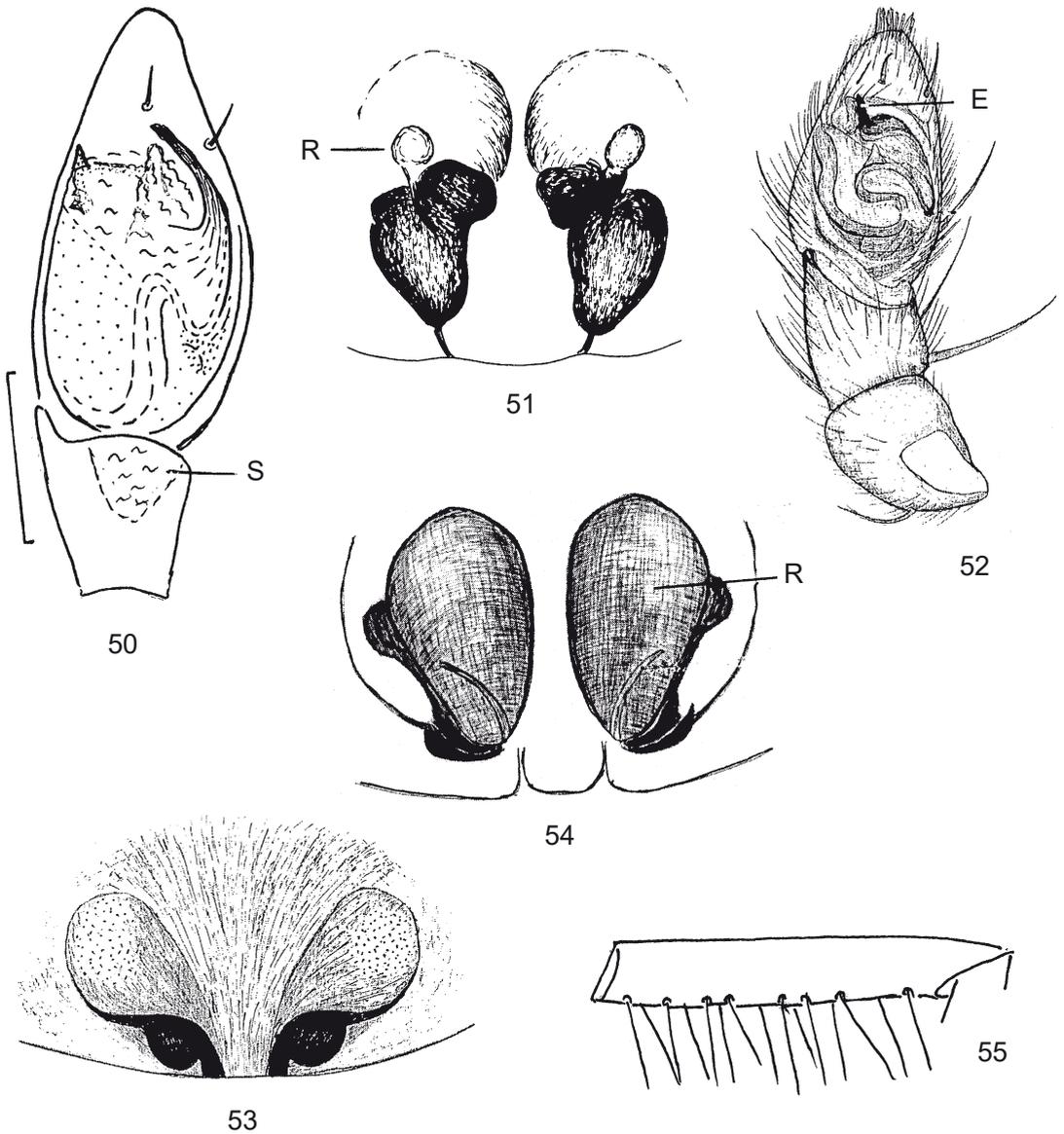
figs. 41-43: *Tibellomimus albidus* (KULCZYNSKI 1911); 41-42) ♂, dorsal and ventral aspect of the left pedipalpus; scale bar 0.1 and 0.2; 43) epigyne;



figs. 44-45: *Tibellomimus rufus* (WALCKENAER 1826), ♂, dorsal and ventral aspect of the left pedipalpus; P = parembolar apophysis; scale bar 0.1 and 0.2;

figs. 46-48: *Rhysodromus fallax* (SUNDEVALL 1833); 46) ♂, ventral aspect of the right pedipalpus; E = embolus, M = "median" apophysis; 47-48) epigyne and vulva; R = receptaculum seminis;

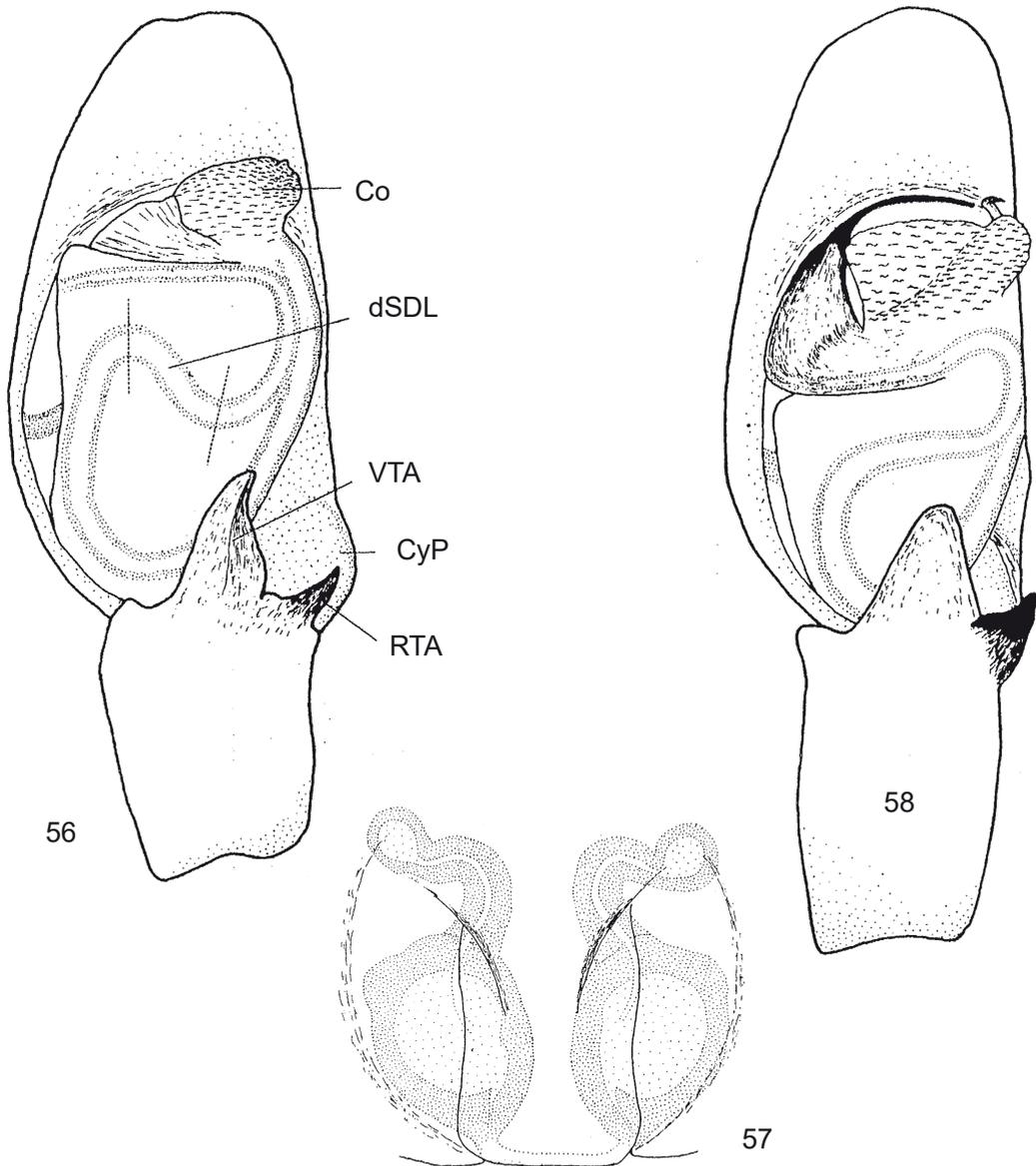
fig. 49) *Pulchellodromus glaucinus* (SIMON 1870), ♂, ventral aspect of the right pedipalpus; the dotted line shows the variable size of the ventral tibial apophysis. The arrow points to the embolus shown in an apical position; scale bar 0.2;



figs. 50-51: *Rhysodromus histrio* (LATREILLE 1819), ventral aspect of the right ♂-pedipalpus and the vulva; R = receptacular organ ("head"); S = sciny field; scale bar in fig. 50) 0.1;

figs. 52-54: *Tibellus oblongus* (WALCKENAER 1802); 52) ♂, ventral aspect of the right pedipalpus; E = embolus; 53-54) epigyne and vulva; R = receptaculum;

fig. 55) *Philodromoides infuscatus* (KEYSERLING 1880) (USA), ♀, retrolateral aspect of the right femur III-IV. Note the long ventral hairs which I found much shorter in the male as well as on femora I-II in the female;



figs. 56-57: *Pulchellodromus pulchellus* (LUCAS 1846); 56) ventral aspect of the left ♂-pedipalpus; 57) epigyne;

fig. 58) *Pulchellodromus wunderlichi* (MUSTER & THALER 2007), ventral aspect of the left ♂-pedipalpus.

**NOTES ON THE GENUS *ARIADNA* AUDOUIN (ARANEAE: SEGESTRIIDAE) AND DESCRIPTION OF A NEW SPECIES FROM FRANCE**

JOERG WUNDERLICH, 69493 Hirschberg.

**Abstract:** *Ariadna gallica* n. sp. (Araneae: Segestriidae) is described from France. Some notes are added to the revision by WUNDERLICH (2011) of the fairly diverse Westpalaeartic genus *Ariadna*. A second male of *Ariadna inops* WUNDERLICH 2011 from Portugal is described.

Only a single species of the genus *Ariadna* AUDOUIN 1826 – *insidiatrix* – has been reported from Europe until 2010. Remarkably this species is actually absent from this continent (!), see WUNDERLICH (2011). Including the new described species I now know 11 species from Europe and the Western Palaeartic; 10 species were treated by WUNDERLICH (2011), and more species are expected in “spider’s terrae incognitae” like the Balkan Peninsula and Asia Minor. In 2011 several “hidden” species or species which have erroneously been synonymized with *Ariadna insidiatrix/spinipes* by E. SIMON (1914) and mistaken by other authors were revived.

Luckily I was the first author and only investigator who has the opportunity to study almost all West-Palaeartic species – including numerous males – of the remarkable genus *Ariadna*.

Ecology: I found tubes and specimens of most species in fairly shadowish localities of quite steep slopes along roads within only fairly hard earth and stones which were

scarcely covered with moss and lichens (no grass), not together with members of *Segestria* which may be competitors. In very few of such localities in France, Italy and Portugal I found *Ariadna*. Only two times I found – in Portugal – a population of several specimens closely together within few square meters. Most of other congeneric spiders were accidentally collected by me and other authors, usually single specimens out of their tubes. – In contrast to the kind of habitat described above I found the two males of *A. inops* within their tubes in an open locality on a sandy ground quite near a beach at the underside a sponge-like piece of plastic.

Taxonomy: In the genus *Ariadna* exists enormous taxonomical problems. Most species are more easy to identify by their distribution (\*) – and the short-living rare males (\*\*) by the modifications of their anterior metatarsi – than by the structures of their frequently quite similar padipalpi. An investigation of the vulvae of most species is still wanting; their careful preparation is difficult.

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(\* ) See the map given by me (2011: 179) (“sp.” is *gallica* n. sp.). – An exception are populations of *A. algarvensis* and *inops* in Southern Portugal near Cacela Velha, which exist separated by only very few kilometers. The ecology of these species is quite different, see above, so they will not exist syntopically.

(\*\*) A male of *A. inops* lived only few weeks as an adult spider in captivity in my laboratory, see below. At least 11 (!) species exist in the Western Palaearctic; specimens of *Ariadna* – and most probably populations, too – are actually not rare but their tubes may easily be overlooked or mistaken with members of the related genus *Segestria* or other genera.

In this paper I describe a new species from France, *A. gallica*. The only known two males of this species have erroneously been included in the description of *A. euro-paensis* WUNDERLICH 2011. Furthermore I describe – after its last moult – the second adult male of *A. inops* WUNDERLICH 2011 – this male has originally been treated as a juvenile paratype –, and a female of an undetermined species (?= *ionica* (O. PICKARD-CAMBRIDGE 1873)). Some corrections and additional notes regarding a previous paper by WUNDERLICH (2011) are given below.

Corrections and additional notes regarding my revision of the genus *Ariadna* (2011):

P. 179, map: *Ariadna* sp. has turned out as an undescribed species, *A. gallica* n. sp.

P. 182, key no. 5(4) - -: Read “*gallica* WUNDERLICH 2012” instead of “sp. indet.”, and add “figs. 22–26” (under *A. euro-paensis* in that paper). See also below (*A. gallica*).

P. 185: (a) after "*Ariadna europaensis* n. sp.": Only "(figs. 17–21)" <figs. 22–26 = *A. gallica* n. sp., see below>; (b) (references 1951 and 1967): These papers (partly 1951) refer to *Ariadna gallica*, see below.

P. 186: (a) In the text the figs. 22–26 have to remove from *A. europaensis* because they refer to *A. gallica* n. sp., see above; (b), Distribution: Remove "France" (in France occurs *A. gallica*, see below).

### ***Ariadna algarvensis* WUNDERLICH 2011**

**Material:** SW-Portugal, E Faro, Cacela Velha, the same locality (2) of the paratypes of the species, see WUNDERLICH (2011: 189); 1 subad. ♂ (paratype) JW leg. 23. V. 2010, moulting in V/VI 2011, fed with *Drosophila* sp.; it died in XI 2011 (it has been dried out for 1–2 weeks); ♂ paratype R149/AR/CJW, exuvia and remains of prey of this spider R150/AR/CJW.

Measurements (in mm) and proportions: Prosoma: Length 2.5, width 1.3, leg I: Femur 2.6, tibia 2.1, leg II: Femur 2.5, tibia 2.3; tibia I 6.3 times longer than high, pedipalpal femur 3.1 times longer than high.

Colour: Body dark brown, legs light to medium brown, not darkened.

Metatarsus I as in fig. 42, pedipalpus as in fig. 43 given by WUNDERLICH (2011: 197).

Remarks: (1) In the original diagnosis of this species the relation of length and height of the male tibia I has been noted as 6.8 to 7.2 but in the present male it is only 6.3. – (2) The present male lived adult for about six month in my private laboratory.

### ***Ariadna* sp. indet. (*ionica* (O. PICKARD-CAMBRIDGE 1873) ?)**

**Material:** Greece, Preveza city, 1♀ JÖRGEN LISSNER leg. 6. VII 2011, det. *Ariadna ionica*, coll. J. L. 7939.

Measurements (in mm): Prosoma (apparently it is slightly shrunked): Length 3.2, width 2.1; leg I: Femur 2.3, patella 1.0, tibia 1.75, metatarsus 1.5, tarsus 0.5, tibia II 1.7, tibia III 1.1, tibia IV 1.6.

Colour: Body and legs I–II mainly dark brown, legs III–IV medium brown.

Tibia and metatarsus I bear 5 pairs of strong ventral bristles each. Eyes: Posterior row straight, posterior median eyes almost contiguous.

**Relationships:** Probably *A. ionoca* (O. PICKARD-CAMBRIDGE 1873), a species known from Corfu, but a male from the females locality is needed for a sure determination.

**Distribution:** Greece.

***Ariadna gallica* n. sp.** (figs. 1–3; further previous figs.: See the remarks below)

*Ariadna europaensis* WUNDERLICH 2011 (part.), see below, e. g. p. 185, 195: figs. 22–26 refer to *A. gallica*.

“sp.”, Beitr. Araneol., 6: 179 (map).

“sp. indet.”, Beitr. Araneol., 6: 182 (key 5 --).

**Remarks:** (1) The males from SW-France which were treated under *Ariadna insidiatrix* by DENIS (1934, 1951) (from Port Cros, a small Island near Toulon), and LEDOUX (1967) (from Banyuls) are now regarded as members of *A. gallica* n. sp. Recently I had the opportunity to study the male from Port Cros (fig. 1–3). Both males are apparently conspecific, and erroneously were regarded as members of *A. europaensis* WUNDERLICH 2011, although no inclination of the tarsi were reported from these males. The differences between *europaensis* and *gallica*: See below. – (2) SIMON (1914: 116) treated/synonymized erroneously several species under/with *Ariadna spinipes* (= *insidiatrix*), see the revision of *Ariadna* by WUNDERLICH (2011), and reported specimens from France from “Litoral mediterraneen et Corse.” A male of this species from France – which may have been *A. gallica* – was unknown to SIMON. – (3) WUNDERLICH (2011: 185–186) treated *A. europaensis* WUNDERLICH 2011 (figs. 17–21 only!) as well as *A. gallica* n. sp. (figs. 22–26), under *A. europaensis*. I got material of *A. gallica* (sub *insidiatrix*) – a single male – only during printing of the revision of *Ariadna*, by WUNDERLICH (2011: 182). The diagnosis of *A. europaensis* sensu WUNDERLICH (2011: 186) is still correct except that the figs. 22–26 show *A. gallica* n. sp. According to the actual knowledge *A. europaensis* occurs in Northern Italy but *A. gallica* in Southern France. – (4) Trying to collect members of this species in August 2011 in SW-France I was not successful (and the search was definitely finished by a lumbago after two weeks).

**Material:** SW-France, Dpt. Var, Port Cros (a small island near Toulon), holotype ♂ J. DENIS leg. 29. V. 1933, det. erroneously *Ariadna insidiatrix* (= *spinipes*), MNHN Paris. – The left anterior leg of this male has been separated for this study.

**Diagnosis** (♂; ♀ unknown): Leg I (figs. 1–2): Tibia 5.6 times longer than wide, metatarsus modified, swollen, position of the blunt basal clasping spine in 0.42; pedipalpus (fig. 3): Femur 2.9 times longer than high, tibia slightly bulging ventrally-basally like in *A. europaensis* WUNDERLICH 2011, distal part of the embolus long, bent in a right angle, slightly s-shaped.

**Description** (♂):

Measurements (in mm): Body length 6.5, prosoma: Length 3.1, width 2.3; leg I: Femur 3.45 (height 0.6), patella 0.7, tibia 2.8 (height 0.5), metatarsus 3.4 (height 0.2 – 0.4), tarsus 0.8, tibia II 3.1, tibia III 2.0, tibia IV 2.4.

Colour (bleached out) pale, prosoma orange brown, legs yellow brown, tibia I darkened, opisthosoma yellow grey, lateral white stripe not observable.

Prosoma 11.35 times longer than wide, low, hairs short, fovea indistinct, median eyes largest and almost touching, basal cheliceral articles slender, especially retrolaterally bearing long hairs, posterior fang furrow with a single denticle, fangs stout, labium free, 1.5 times longer than wide. – Legs (figs. 1–2; see WUNDERLICH (2011: 195, figs. 22, 24–25): Order II/III/IV (I slightly the longest), femur IV fairly thickened, hairs short, measurements see above, tibia I 5.6 times longer than high, metatarsus I swollen in 0.42 % of the length, and bearing here a blunt clasping spine, a second blunt clasping spine exists proapically. Bristles frequently variable on both sides: Femur I 6/7, tibia I 18/20, tibia IV bristle-less; LEDOUX (1967: 70) reports a single proapical bristle on tibia IV, metatarsus IV 1 ventral-basal and a pair ventral-apical. A scopula is absent, the paired tarsal claws bear usually 8 long teeth, the unpaired claw a single tiny tooth. – Pedipalpus (fig. 3); see the diagnosis and figs. 23 and 26 in WUNDERLICH (2011: 195): Tibia 1.34 times longer than high, bulbous almost globular, the long embolus bears distally a slender seam (arrow).

**Relationships:** In *A. europaensis* WUNDERLICH 2011 from Italy exists a dorsal inclination of the male tarsus, see WUNDERLICH (2011: 195, fig. 20), the position of the metatarsal clasping spine is slightly distally of the middle and not situated on a hump, see WUNDERLICH (2011: 195, fig. 19), and the distal (thin) part of the embolus is slightly shorter, see WUNDERLICH (2011: 195, fig. 21). In *A. brignolii* WUNDERLICH 2011 from Italy tibia I is much longer, the distal (thin) part of the embolus is less bent, see WUNDERLICH (2011: 194, fig. 16). In *A. cyprusensis* WUNDERLICH 2011 from Cyprus the position of the metatarsal clasping spine is in a more distal position than in *gallica* from France. In the male of *A. algarvensis* WUNDERLICH 2011 from Portugal tibia I is 6.3–7.2 times longer than wide, and the tibia of the pedipalpus is STRONGLY bulging ventrally-basally; see WUNDERLICH (2011: 182).

**Distribution:** SW-France (Banyuls and near Toulon).

***Ariadna inops* WUNDERLICH 2011**

2011 *Ariadna inops* WUNDERLICH, Beitr. Araneol., 6: 188–189, figs. 32–37.

The juvenile paratype of this species has been captured by me alive together with the male holotype of this species in V 2010. The last moult happened in IV 2011 and showed that the juvenile was a subadult male. It died at 28. VI. 2011. So the adult male

lived only few weeks. The spider has been fed with numerous Diptera, mainly with *Drosophila* sp. The prey and the spider's moult are kept dry in a small box of plastic, R135/AR/CJW A, the paratype is preserved in a small tube no. R135/AR/CJW.

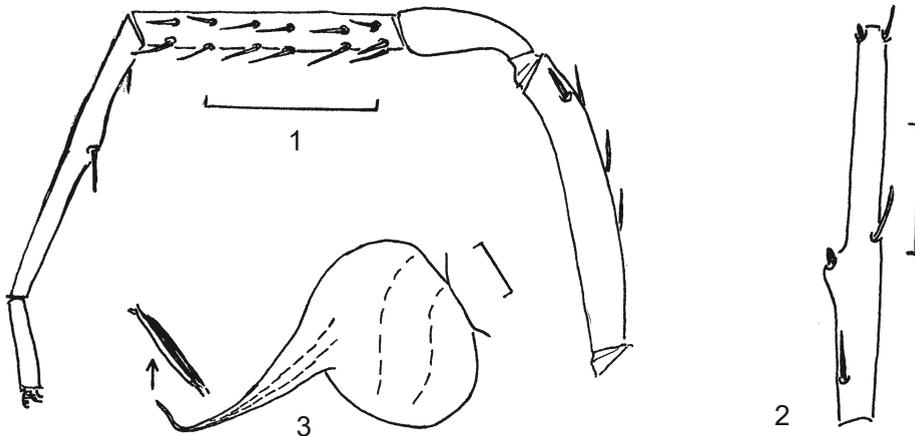
Short description of the paratype: Body length 4.2 mm, prosomal length 2.2 mm, tibia I 1.7 mm, metatarsus I 1.8 mm. The colour is similar to the holotype but the prosoma is dark brown and leg I is fairly darkened, less leg II. Leg I is unmodified. Tibia I is 5.75 times longer than wide, metatarsus I is ten times longer than wide. Tibia I bears 1–2 bristles less than the holotype, the tibiae IV bear 2/3 ventral bristles in a row like the holotype. The pedipalpus is as in the holotype.

**Ecology:** In contrast to other congeneric species (see above) I found the two members of this species within their tubes in an open locality on a sandy ground quite near a beach at the underside of a sponge-like piece of plastic. – Remarkably the localities of *inops* and *algarvensis* (one of two localities of this species) are separated only about 3 kms away from each other.

**Distribution:** SW-Portugal.

REFERENCE; further references see WUNDERLICH (2011: 334–338)

WUNDERLICH, J. (2011): On extant West-Palaeartic (mainly Southern European) spiders (Araneae) of various families, with new descriptions. – *Beitr. Araneol.*, 6: 158–338.



Figs. 1-3: *Ariadna gallica* n. sp., ♂ from Port Cros; 1) retrolateral aspect of the left leg I; 2) ventral aspect of the left metatarsus I; 3) retrolateral aspect of the left bulbus. The arrow points to the enlarged distal part of the embolus. Scale bars 2.0, 1.0 and 0.2 mm.

## NEW AND RARE SPIDERS (ARANEAE) OF THE CANARY ISLANDS

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**Abstract:** The following spiders (Araneae) are described from the Canary Islands (Spain): *Troglohyphantes labrada* n. sp. (Linyphiidae: Linyphiinae), *Walckenaeria microspinosa* n. sp. (Linyphiidae: Erigoninae), and *Zelotes paraegregius* n. sp. (Gnaphosidae). The gnaphosid female of *Nomisia gomerensis* WUNDERLICH 2011 is described for the first time. Shortly described are *Zelotes* sp. indet. and *Heliophanus ?agricoloides* WUNDERLICH 1987 (Salticidae). *Devade indistincta* (O. PICKARD-CAMBRIDGE 1870) is reported for the first time from the Canarian and Macaronesian Islands. Remarks are given on *Lasaeola convexa* (BLACKWALL 1870), and species of the genus *Steatoda* SUNDEVALL 1833 (both Theridiidae) as well as *Leptodrassex hylaestomachi* (BERLAND 1934) (Gnaphosidae). *Teutana grossa* var. *obliterata* FRANGANILLO 1918 (Theridiidae) is regarded as a nomen dubium.

**Key words:** Araneae, Canary Islands, new species, Spain, subspecies.

I thank PEDRO OROMI (University of La Laguna, Tenerife (ULT), Canary Islands, Spain) who sent me larger collections of spiders from the Macaronesian Islands, (mainly from Tenerife, and by the research group GIET) for investigations.

Within this material I identified three undescribed species of the families Linyphiidae and Gnaphosidae from the Canary Islands which are described in the present paper. Some of these species were captured in caves, *Troglohyphantes labrada* is a strongly adapted cave spider; see WUNDERLICH (1993). One species of the family Dictynidae is new to the Canarian and Macaronesian Islands.

Family **THERIDIIDAE**

***Lasaeola convexa*** (BLACKWALL 1870) (under *L. c.* (THORELL 1870), see WUNDERLICH (2011: 256)) from the Canary Islands.

Recently I had the opportunity to compare Canarian spiders with a male from Southern France (Banyuls) (MNHNParis AR 3399) and found the spiders being conspecific. The darkened ♂-tibia I in spiders from the Canary Islands are bleached out now.

Remark: BLACKWALL (1870: 426) characterized the ♀-prosoma as follows: “it has a shallow, oblong indentation in the median line ...”. In all spiders studied by me I did not find a prosomal indentation.

***Steatoda***: Subgenus *Steatoda* SUNDEVALL 1833

Subgenera of *Steatoda*: See WUNDERLICH (2008: 202f).

Four or five species of this subgenus – *grossa*, *latifasciata*, *nobilis*, *?nobilis*, and *triangulosa* – occur on the Canary Islands. Two questionable females of *S. nobilis* from El Hierro and Tenerife each inspired me to write the following part of this paper which includes an identification key to the Canarian species of this subgenus:

1 Prosoma distinctly wrinkled in the male (fig. 1) in contrast to the – sexual dimorphic – smooth prosoma of the female in which the epigyne bears a wide transverse slit-shaped opening (figs. 2–3). Position of the metatarsal I–II trichobothrium in 0.25–0.3. Prosomal length 1.6–2 mm . . . . . *triangulosa*

- ♂♀-prosoma smooth. Position of the metatarsal I–II trichobothrium usually in 0.45–0.83. Prosomal length usually more than 2 mm except in some specimens of *latifasciata*. . . . . 2

2(1) Position of the metatarsal I–II trichobothrium in 0.45–0.55. Opisthosoma with distinct large white markings which may be similar to fig. 1. ♂♀-genital structures: See WUNDERLICH (1992: 585, figs. 604a–b), epigynal septum absent . . . . . *latifasciata*

- Position of the metatarsal I–II trichobothrium in 0.55–0.83. Opisthosoma without distinct large white markings. Median epigynal septum well developed (figs. 4–6). . . . . 3

3(2) Sequence of the thin tibial bristles 2/2/1/2. Prosomal length 2.5–4.6 mm . . . . . 4

- All tibiae bear a single hair-shaped bristle only. Prosomal length 2.0–2.5 mm. Epigynal septum stout (fig. 6) like in *nobilis* (fig. 5) but its base (arrow) possesses a depression in contrast to “usual” *nobilis* . . . . . ?*nobilis*

4(3) Prosomal length usually 3.1–4.6 mm. Epigyne (fig. 5) with a stout septum, anterior margin of the groove usually interrupted in the middle like in questionable *nobilis* (no. 3) in which the septum possesses a basal depression . . . . . *nobilis*

- Prosomal length usually 2.5–3 mm. Epigyne (fig. 4) with a slender septum, anterior margin of the groove (in front of the septum) not interrupted . . . . . *grossa*

***Steatoda (Steatoda) ?nobilis*** (THORELL 1875) (figs. 6–8)

**Material:** (1) El Hierro, Don Justo cave, 1♀ O. MEDINA leg. 17. XI. 1985 (H-DJ-81), ULT no. 68/2010. – (2) Tenerife, small village Romantica W Puerto de la Cruz, 1♀ P. JÄGER leg. 3. VIII. 1993 (A. V. GROMOV det. *Steatoda grossa*), SMF 40907.

**Remark:** The female (1) has been collected in a cave; it is fairly less pigmented than female (2) but does not show adaptations to cave-dwelling like reduced eye lenses or long legs.

Short **description** of the females (1)/(2):

Measurements (in mm): Body length 5.0/5.4, prosoma: Length 2.0/2.5, width 1.7/2.0, tibia I 2.7/3.3, tibia IV 2.2/2.6.

Colour: Prosoma light yellow to orange brown (2), legs not darkened, opisthosoma medium to dark brown (2), anteriorly with a transverse and bent white band, dorsally bearing 4 light spots (1) or 3 (2), laterally 4 light spots (1) or only 3 (2).

All tibiae bear a single hair-shaped dorsal bristle in the basal half (it may be absent but more likely it is rubbed off on some tibiae). The position of the metatarsal I–II trichobothrium is 0.68–0.77 (1) and about 0.8 (2) (\*). – The epigyne (figs. 6–7) has a stout median septum which has an anterior depression (arrow in fig. 6) and an interrupted anterior margin. Vulva: Fig. 8.

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(\* ) I found a remarkable variability in the position of the trichobothrium on the metatarsi I–II in *grossa* and *nobilis* (no difference between these species), e. g. 0.55–0.6 in 2♀ from Tenerife, ULT no. 3403), 0.77–0.83 in ♀ from El Hierro, ULT no. 3313.

**Relationships** (see also the key above): Strongly related are *S. grossa* (C. L. KOCH 1838) (in which the epigynal septum is much more slender, and the anterior margin of the epigynal groove is not interrupted, fig. 4), and – according to the stout epigynal septum and the interrupted anterior margin, fig. 5; see fig. 6) – mainly *S. nobilis* (THORELL 1875). In both species (*grossa* and *nobilis*) – as well as in other congeneric species – the sequence of the thin tibial bristles is 2/2/1/2, but only 1/1/1/1 in the questionable

?*nobilis*. *S. grossa* and *nobilis* are clearly larger, see the key. I found no differences in the vulvae of *nobilis* and ?*nobilis* (fig. 8) besides the size. – Are the reduced number and size of the two questionable females (and the weak difference in the epigyne, too?) nothing else than the result of dwarfism? The status of the questionable females of *nobilis* appears unsure; more specimens and especially males – if possible from the localities listed above – are needed for further studies.

**Distribution:** Canary islands El Hierro and Tenerife.

Remark on “*Teutana grossa* C. K. var *obliterata*” FRANGANILLO 1918 which is known from the Iberian Peninsula, Gijon, Spain: The simple “description” of this taxon is “Abdomen maculis obsoletis”. This characteristic is very near to a nomen nudum; it means not much more than that it is a spider. Type material does apparently not exist; the size, the stage and the the sex of the material is not noted. The colour of the opisthosoma in *grossa* and related species is quite variable. I regard this taxon as dubious (a nomen dubium); it may even not be congeneric with *Steatoda* (= *Teutana*).

## Family LINYPHIIDAE:

Linyphiidae is the most diverse spider family on the Canary Islands. Several species are cave dwellers. In certain genera like *Lepthyphantes* and *Walckenaeria* (see below) subspecies may exist.

## Subfamily Linyphiinae:

### ?*Troglohyphantes labrada* n. sp. (figs. 9–11)

The spider is named after the locus typicus.

**Material:** Canary Island Tenerife, Cueva la Labrada (TL15), holotype ♀ I. IZQUIERDO & C. GARCIA leg. 10. III. 1985, ULT no. 24/2010. Remark: The right leg I and the left leg II of the spider are lost beyond the patella by autotomy. For the study I separated the prosoma from the opisthosoma.

**Diagnosis** (♀; ♂ unknown): Colour pale yellow, eye lenses strongly reduced, epigyne (figs. 9-11) with a large plate-shaped basal part of the folded scape which bears a more slender distal part and a pair of wing-shaped structures which are directed sideward.

**Description** (♀):

Measurements (in mm): Body length 1.8, prosoma: Length 0.6, width 0.5; leg I: Femur 1.1, patella 0.2, tibia 1.0, metatarsus 1.0, tarsus 0.7, tibia II 0.9, tibia III 0.7, tibia IV 1.0; diameter of the eye lenses up to 0.02, basal bristle of tibia I 0.3.

Colour pale yellow, weakly pigments exist around the anterior eye lenses.

Prosoma 1.2 times longer than wide, 8 tiny eye lenses, fovea indistinct, anterior margin of the fang furrow with 3 large teeth, posterior margin with 5 tiny teeth, lateral stridulatory files only fairly well developed, the sternum separates the coxae IV by their diameter. – A claw of the pedipalpal tarsus is absent. – Legs long and slender, order I/IV/II/III, most hairs are rubbed off, bristles long, femur I 1 prolaterally in the distal half (apparently no further bristle but other bristles may be rubbed off), patellae 2, tibiae apparently dorsally 2/2/1/2, I additionally a lateral pair in the distal half, III with a retrodistal one, metatarsi I–III bear a dorsal bristle in the distal half. A metatarsal trichobothrium is absent on IV, its position on I is in 0.11, on III in 0.14. – Opisthosoma oval; the apparently few and long hairs are rubbed off. – Epigyne (figs. 9–11) distinctly protruding, see also the diagnosis.

The **relationships** are unsure; according to the structures of the epigyne the species may more likely be a member of the genus *Troglohyphantes* JOSEPH 1881 than of *Lepthyphantes* MENGE 1866 which I do not want to exclude (a male is needed for a sure determination). – In the only further congeneric species of the Canary Islands – *Troglohyphantes oromii* RIBEIRA & BLASCO 1986 from caves of Tenerife – the epigyne is quite different. – In most species of *Troglohyphantes* femur I bears a DORSAL bristle but not in *T. lucifuga* (SIMON), and probably not in *T. labrada*.

**Distribution:** Canary island Tenerife.

**Subfamily Erigoninae:*****Walckenaeria microspinosa* n. sp.** (figs. 12–15)

The spider is named after its tiny tibial bristles.

**Material:** Canary island Tenerife, Cueva Grande de Chio, holotype ♂ I. IZQUIERDO leg. 20. I. 1986, ULT no. 36/2010 (T-GC-154).

Diagnosis (♂; ♀ unknown): Colour pale yellow brown, eyes fairly small, sequence of the tiny tibial bristles apparently 2/2/1/1 (fig. 8), position of the metatarsal I–II trichobothria in 0.5–0.54, IV in 0.61, cephalic hairs not situated on an outgrowth (figs. 12–13); pedipalpus (fig. 15): Distal branch of the tibial apophysis bent and relatively short, bulbus as in *W. grancanariensis* WUNDERLICH 2011.

**Description** (♂):

Measurements (in mm): Body length 2.0, prosoma: Length 0.9, width 0.65; leg I: Femur 0.95, patella 0.25, tibia 0.9, metatarsus 0.85, tarsus 0.6, tibia II 0.85, tibia III 0.7, tibia IV 1.05.

Colour pale, prosoma and legs yellow brown, opisthosoma light grey.

Prosoma (figs. 12–13) 1.4 times longer than wide, cephalic part fairly elevated, with a brush of spatulate hairs in the field of the median eyes. Eyes fairly small, posterior row slightly procurved, posterior median eyes close together, thoracal fissure well developed, cheliceral stridulatory files widely spaced. The anterior and posterior fang furrow bear 4 teeth, fangs long. – Legs slender, order IV/III/III, hairs short, sequence of the tiny tibial bristles (fig. 14) apparently 2/2/1/1, length on tibia IV 2/3 of the tibial diameter. Position of the metatarsal trichobothria: See the diagnosis. – Opisthosoma almost twice as long as wide, covered fairly scarcely with fairly long hairs. – Pedipalpus (fig. 15; see the diagnosis): Patella twice as long as wide, the tibia bears 2 retrolateral teeth and 3 trichobothria.

**Relationships:** Species-swarms of *Walckenaeria* – and probably subspecies – exist on the Canary Islands, most species on Tenerife, some species are cavernicolous. Certain species evolved probably only recently, their tibial bristles, the position of their metatarsal trichobothria, the cephalic part of the male and the tibial apophysis of the male pedipalpus are only slightly different, the structures of their bulbus may be not distinguishable. – In *W. cavernicola* WUNDERLICH 1992 from Tenerife femur I is 1.6 times longer than the prosoma, in *W. subterranea* WUNDERLICH 2011 from Gran Canaria exist longer hairs of the legs and the cephalic hairs are situated on an outgrowth, in *W. grancanariensis* WUNDERLICH 2011 from Gran Canaria a hump and frequently a “peak” exist in the field of the median eyes, and the distal branch of the pedipalpal tibial apophysis is longer, in *alba* WUNDERLICH and *striata* WUNDERLICH from Tenerife the colour of the body is different and the position of the metatarsal I–II trichobothria is in 0.8–0.9.

**Distribution:** Canary island Tenerife.

Family **DICTYNIDAE**: Subfamily Dictyninae

***Devade indistincta*** (O. PICKARD-CAMBRIDGE 1870) (= *hirsutissima*)

**Material:** Canary island Fuerteventura, Playa Tarajalejo, 3♂3♀ 1juv. GIET leg. 5. II. 2005; 2♂2♀ 1juv. ULT no. 101/2010, 1♂1♀ coll. JW.

The mainly mediterranean genus *Devade* SIMON 1884 and the species *indistincta* are new to the Canarian and Macaronesian Islands.

## Family GNAPHOSIDAE

A dozen genera of this family is known from the Canary Islands, see WUNDERLICH (2011: 399–400). In this paper I treat members of two genera.

### *Leptodrassex hylaestomachi* (BERLAND 1934)

(= *Leptodrassus h.*, see WUNDERLICH (2011: 38, figs. 154–157))

The holotype of this small and pale species has remarkably been taken from the stomach of a frog. It is endemic to the Canary Islands and widely distributed from the Eastern to the Western Islands.

Remark: In most specimens a thoracal fissure is absent or quite indistinct but in a male from Lanzarote (ULT) it is fairly distinct.

### *Zelotes* GISTEL 1848

5 Canarian species of this diverse genus were known to me last year, see WUNDERLICH (2011: 404–407), most species are reported from the Eastern Islands. (*Zelotes gomerae* SCHMIDT has been turned out as a member of the genus *Setaphis*). *Zelotes paraegregius* is the first member of *Zelotes* known from the Western Canary Islands.

### *Zelotes paraegregius* n. sp. (figs. 16–17)

The spider is named after its close relationships to *Z. egregius* SIMON 1914.

**Material:** Canary island El Hierro, Lomo Negro, holotype ♂ I. IZQUIERDO leg. 15. XI. 1985, ULT no. 39/2010 (H-161).

**Diagnosis** (♂; ♀ unknown): Smallest member (body length 4 mm) of the *Zelotes subterraneus* species-group; pedipalpus (figs. 16–17): Tibial apophysis bent dorsally, scinny

apical tibial area almost absent (short arrow), embolus in an oblique position like in *Z. egregius*, crossed by the basal embolar apophysis.

**Description** (♂):

Measurements (in mm): Body length 4.0, prosoma: Length 1.7, width 1.25; leg I: Femur 1.25, patella 0.75, tibia 0.9, metatarsus 0.7, tarsus 0.65, tibia II 0.75, tibia III 0.6, tibia IV 1.15.

Colour: Prosoma mainly dark brown, legs medium brown, opisthosoma grey.

Prosoma 1.36 times longer than wide, bearing some long dorsal hairs, thoracal fissure well developed, eyes small, posterior row straight, posterior median eyes oval, spaced by their radius. Basal cheliceral articles long, with a row of long bristles, anterior margin of the fang furrow with 3 teeth, posterior margin smooth, sternum narrow posteriorly. – Legs only fairly long, order IV/II/III, covered with few long hairs, femora stout. Bristles long and thin, femora 2 dorsally, I, II and IV may bear a prolateral one in the distal half, III bears 2. Patellae with 2 dorsally, no laterals, tibia and metatarsus I–II bristle-less, tibia III–IV with numerous bristles. The tarsi I–II bear an indistinct pseudoscopula and quite weak claw tufts, the tarsal claw IV bears 8 long teeth. – Opisthosoma 1.9 times longer than wide, soft, densely covered with fairly long hairs. The spinnerets are expanded. – Pedipalpus (figs. 16–17; see also the diagnosis): Patella and tibia short, tibial apophysis long and bent dorsally, sclerotized tibial area large (long arrow).

**Relationships:** The body length of other species of the *Z. subterraneus* species-group (= *Zelotes* GISTEL 1848 s. str.) is larger than 4.5 mm. In *Z. aeneus* (SIMON 1878), *Z. egregius* SIMON 1914 (described originally from France; both sexes collected by me in Portugal near Faro and Aljezur, CJW), and *Z. egregioides* SENGLLET 2011 from Spain the tibial apophysis of the ♂-pedipalpus is straight and the structures of the bulbus (e. g. the shape of the embolus) are different; in *aeneus* and *egregius* the basal embolar process has a longitudinal position in contrast to *paraegregius* and *egregioides*.

**Distribution:** Canary island El Hierro.

*Zelotes* sp. indet.

**Material:** Canary Islands, the small island Graciosa north of Lanzarote, Las Aguas, 1 subad. ♀ GIET leg. 1. II. 2005, ULT no. 138/2010.

Measurements (in mm): Body length 5.0, prosomal length 1.7, tibia I 1.15.

Prosoma and legs are light brown, all femora bear long and adpressed dorsal bristles. The prae-epigyne is light, the structures of the vulva are apparently not completely developed, fairly similar to *Z. manzae* (STRAND 1908) from Tenerife and Gran Canaria; the female has most probably been just before the last moult. Adult specimens are needed for a sure determination.

**Distribution:** Canary Island Graciosa north of Lanzarote.

*Nomisia gomerensis* WUNDERLICH 2011: 412, 418–419, figs. 43–46 (♂) (fig. 18)

**Material:** La Gomera, 1♂ 5♀ leg. JØRGEN LISSNER in 8300 Odder, Denmark; e. g., Barranco de Masca, 1♂ 1♀ no. 7608; Las Canadas, Los Roques, no. 7585; as well as nos. 7642 and 4644, near Masca and Agulo.

The female of this species is described for the first time here.

**Description** (♀):

Measurements (in mm): Body length 4.6–5.6, prosoma: Length 2.1–2.3, width 1.6–1.8; leg I (larger ♀ from Masca): Femur: 1.7, patella 0.9, tibia 1.3, metatarsus 1.2, tarsus 1.0, tibia II 1.15, tibia III 0.9, tibia IV 1.6.

Colour mainly grey to grey brown.

Tibia and metatarsus I are bristle-less, tibia II bears a thin long bristle in the basal half, metatarsus II bears a pair of ventral bristles in the basal half.

Epigyne (fig. 18) wider than long, laterally with strongly sclerotized structures, anteriorly with a sclerotized margin, shining receptacula seminis large, slightly ovally, and in a posterior position, a smaller shining paired and almost globular structure exists in a more anterior position.

The male from the Barraco de Masca is smaller than the type material: Body length 3.5 mm, prosomal length 1.6 mm, width 1.2 mm, tibia I 1.2 mm. Tibia I as well II are bristle-less.

**Relationships:** The apparently strongly related *N. fortis* DALMAS 1921 from La Gomera is larger, prosomal length 3.0–4.4 mm, the epigyne is similar wide, but the anterior and median structures are different, see WUNDERLICH (2011: 418, figs. 40–42).

**Distribution:** Canary Island La Gomera.

Family **SALTICIDAE**

*Heliophanus ?agricoloides* WUNDERLICH 1987

**Material:** Canary island Tenerife, Malpais de Rasca, 1♂ PEREZ leg. on *Salsola* plants, ULT no. 97/2010.

The spider's opisthosoma is dark brown, it bears an anterior transverse white band and 2 pairs of white dorsal spots. The pedipalpus is quite similar to *H. agricoloides* but the embolus is a bit longer and the tip of its embolus is slightly bent prolaterally – an intraspecific variability? More conspecific spiders are needed for a sure conclusion.

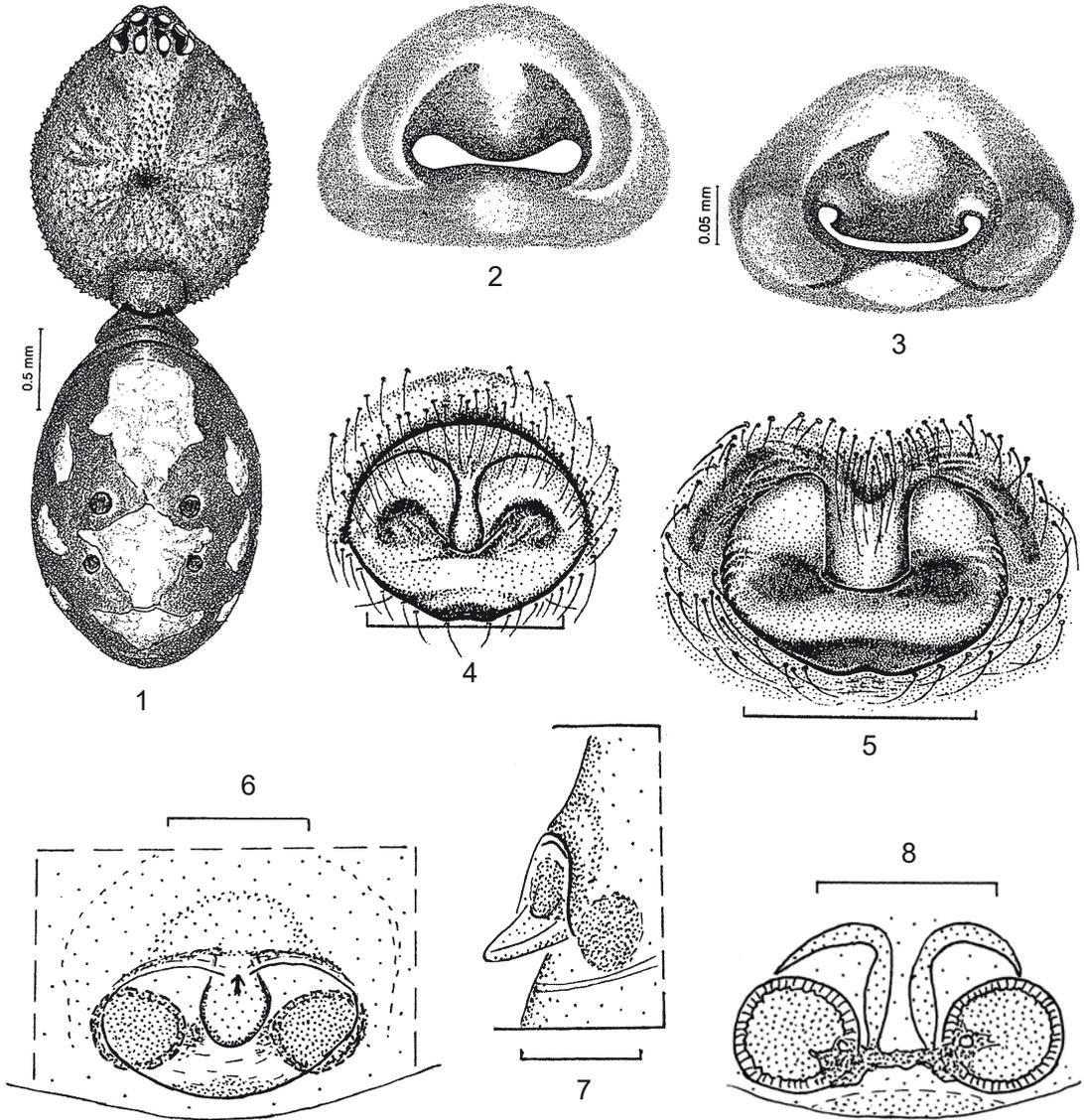
**Distribution:** Gran Canaria and probably Tenerife (the species would be new to this Island).

### Addendum during press:

*Oecobius parapsammophilus* WUNDERLICH 2011 – described from Gran Canaria – has been collected on Tenerife, Puerto de Santiago, 11 IV. 2003, by JØRGEN LISSNER, 8300 Odder, Denmark, 2♂ 2♀, coll. LISSNER 1♂ 1♀ R153/AR/CJW.

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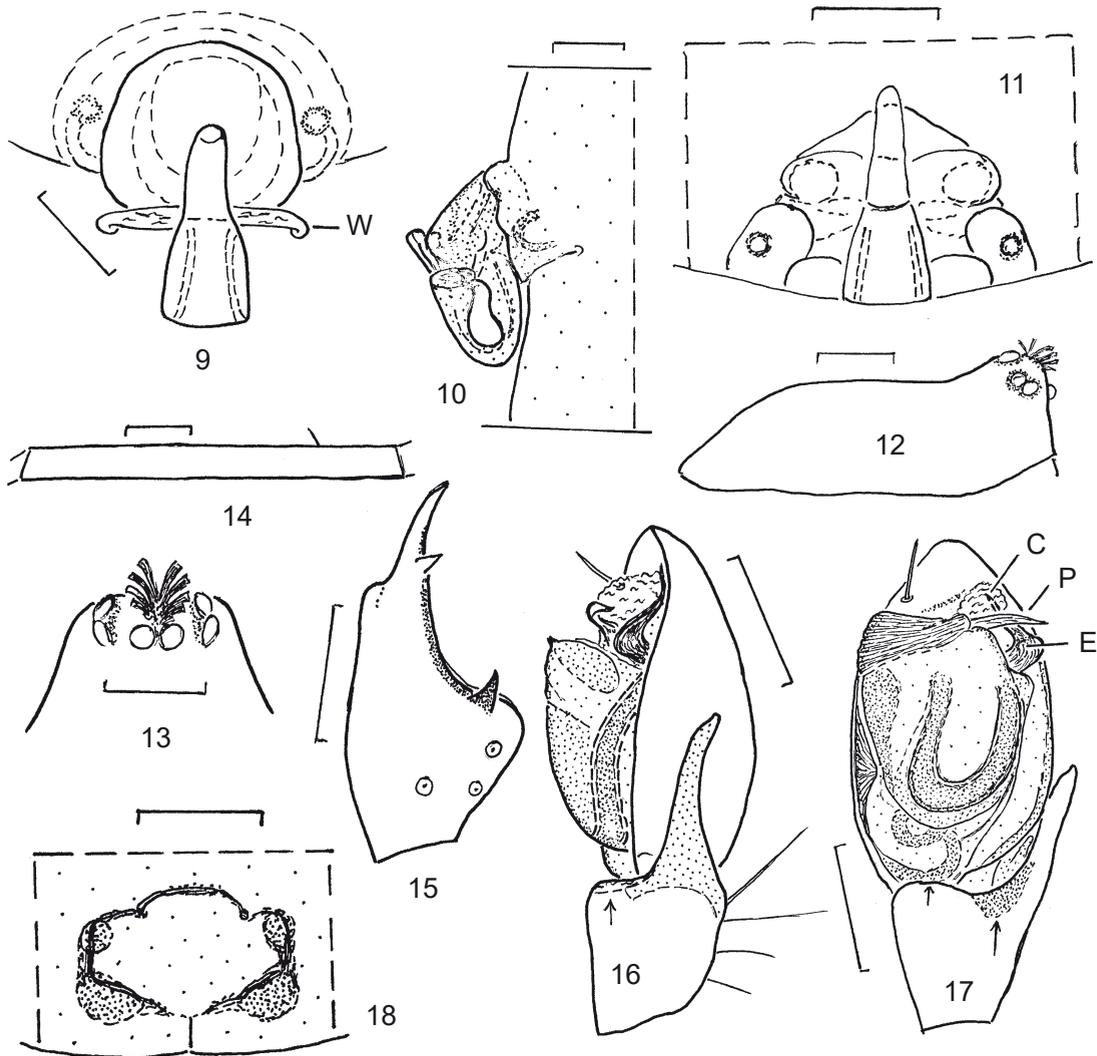


Figs. 1-3: *Steatoda triangulosa* (WALCKENAER 1802); 1) ♂, dorsal aspect of the body; 2-3) ♀, epigyne (variability). The figs. are taken from LEVY (1998);

fig. 4) *Steatoda grossa* (C. L. KOCH 1838), ♀, epigyne. Taken from SNAZELL & JONES (1993);

fig. 5) *Steatoda nobilis* (THORELL 1875), ♀, epigyne. Taken from SNAZELL & JONES (1993);

figs. 6-8: *Steatoda ?nobilis* (THORELL 1875), ♀ from a cave on El Hierro; 6-7) ventral and lateral aspect of the epigyne. Note the stout septum which has a basal depression (arrow in fig. 6); 8) dorsal aspect of the vulva. Scale bars 0.2 mm;



figs. 9-11: *?Troglodyphantes labrada* n. sp., ♀; ventral, lateral and posterior aspect of the epigyne. W = wing-shaped structure. Scale bars 0.1;

figs. 12-15: *Walckenaeria microsetae* n. sp., ♂; 12) lateral aspect of the prosoma; 13) dorsal aspect of the cephalic part. Not all hairs within the eye field are drawn; 14) retrolateral aspect of the left tibia IV. Note the tiny bristle. Hairs are not drawn; 15) dorsal aspect of the right pedipalpal tibia. Scale bars 0.1 in fig. 15, 0.2 in the remaining figs.;

figs. 16-17: *Zelotes paraegregius* n. sp., ♂, retrolateral and ventral aspect of the left pedipalpus. C = conductor, E = embolus, P = basal embolar process. The short arrow points to the area of the sciny apical tibial area which is almost absent in this species. The long arrow points to the strongly sclerotized area at the root of the tibial apophysis. Scale bars 0.2.

fig. 18) *Nomisia gomerensis* WUNDERLICH 2011, ♀, epigyne. Scale bar 0.1.

**NEW SUBRECENT SPECIES OF SPIDERS IN COPAL FROM  
MADAGASCAR, AND ON THE RELATIONSHIPS OF THE COPAL-  
DICTYNINAE WUNDERLICH 2004 (ARANEAE: LINYPHIIDAE,  
THERIDIIDAE, DICTYNIDAE, AND TITANOECIDAE)**

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**Abstract:** The following spider (Araneae) taxa are described from young resin (copal) of North-Madagascar: Linyphiidae: *Madagascarphantes vomerans* **n. gen. n. sp.**; Theridiidae: *Lasaeola (Phycosoma) inclinata* **n. sp.** and *Platnickina duosetae* **n. sp.**; Dictynidae: Flagelldictynini **n. trib.** and *Flagelldictyna copalis* **n. gen. n. sp.**, and *Dictyna rufa* **n. sp.** The endemic monotypic subfamily Copaldictyninae is transferred with hesitation from the Dictynidae to the Titanoecidae (**quest. n. relat.**). A questionable taxon of the family Titanoecidae and true members of the family Dictynidae are described or reported for the first time from Madagascar. 3♂ of *Mysmena* (s. l.) sp. indet. (Mysmenidae) in a single piece of copal are reported which may be members of a kleptoparasitic species.

**Key words:** Araneae, copal, Copaldictyninae, kleptoparasites, Madagascar, spiders, subrecent.

The **material** is kept in the private collection of the author (CJW); it probably will be stored in the future in the Senckenberg Museum Frankfurt a. M. (SMF).

Most (sub)recent spiders in copal from N-Madagascar have been described by WUNDERLICH (2004), (2008), and (2011). This resin functions as a kind of excellent traps. Members of the family Theridiidae are most frequent. The investigation of copal from Madagascar – new reports of taxa even on family level exist – demonstrates that the extant spider fauna of this island is still quite incompletely known. Dictynidae is the fifth spider family which is reported from Madagascar in copal. Previously there has been no proof outside copal. Previous first proofs in copal were Oonopidae, Mysmenidae, Theridiosomatidae, Prodidomidae. It is quite remarkable that among several thousand spiders in copal from Madagaskar I found not a single member of the families Cyatholipidae and Synotaxidae – which are known from more southern parts of Madagascar – or endemic Agelenidae. Here I describe few excellently preserved specimens. – Photos: Part I A, p. 337f.

## Family **MYSMENIDAE**

***Mysmena*** (s. l.) sp. indet. (photo 1)

**Material:** 3♂ in the same piece of copal from Madagascar, F2371/CM/AR/CJW.

**Notes:** The tiny spiders are completely and well preserved; they are similar to *Mysmena copalis* WUNDERLICH 2011, but not closely studied up to now. By splitting *Mysmena* s. l. this species may be the member of a different genus. Members of several mysmenid genera are known as kleptoparasites in the webs of other spiders. The presence of three specimens united in the same piece of copal may be a hint that this species really is a kleptoparasite.

## Family **LINYPHIIDAE**, subfamily Micronetinae (?)

Only half a dozen linyphiid genera and species are known from Madagascar; they probably all are endemic. Here I describe the member of a new genus.

**Madagascarphantes n. gen.**

The name combines the origin of the holotype, Madagascar, and a part of the name of the linyphiid genus *Lepthyphantes*. The gender is masculine.

Type species (by monotypy): *Madagascarphantes vomerans* n. sp.

**Diagnosis** (♂; ♀ unknown): Few leg bristles only: All tibiae bear 1/1 dorsally; femoral; metatarsal and lateral tibial bristles are absent. Pedipalpus (figs. 1–3): Cymbium with a long basal outgrowth which is directed posteriorly, paracymbium strongly bent distally, basally bearing an outgrowth which is directed posteriorly, lamella characteristic and embolus unknown.

Further character: Basal cheliceral article longer than the height of the prosoma.

Close **relationships** are unknown to me. A basal cymbial outgrowth exists in numerous members of the subfamily Micronetinae in which the basal cheliceral articles frequently are smaller and the position of the cymbial outgrowth is not BELOW the pedipalpal tibia. In the African genus *Metalepthyphantes* LOCKET 1968 the chaetoraxy is as in *Madagascarphantes* but a posterior outgrowth of the cymbium is absent. In most members of the Erigoninae exist a single bristle on tibia IV, and the pedipalpal tibia bears an apophysis.

**Distribution**: North Madagascar, subrecent, preserved in copal.

***Madagascarphantes vomerans* n. gen. n. sp.** (figs. 1–3) photo 2

The name of the species points to the bubble of digestive secretion below the mouth parts, from vomere, Latin = vomit.

**Material**: Holotype ♂, in young copal from North Madagascar, 2 separated pieces and remains of grinding, F2358/CM/AR/CJW.

**Preservation and syninclusions**: The spider is very well and completely preserved in a light yellow piece of copal. A droplet of digestive secretion is preserved ventrally in contact to the mouth parts, a bubble exists directly right of the bases of femora I–II, on the right pedipalpal femur and on the right parts of the prosoma. Fissures exist on the surface of the 3 pieces of copal in which a mite, some beetles, Collembola, and Hymenoptera (including 2 ants), 2 Aphidina, a female spider (*Lasaeola*, Theridiidae), and small bubbles are also preserved.

**Diagnosis** (♂; ♀ unknown): See the diagnosis of the genus.

**Description** (♂):

Measurements (in mm): Body length 1.4, prosoma: Length 0.53, width 0.5; opisthosoma: Length 0.75, width 0.5; leg I: Femur 0.6, patella 0.14, tibia 0.63, metatarsus 0.53, tarsus 0.4, tibia II 0.53, tibia III 0.4, tibia IV 0.6.

Colour: Prosoma and legs yellow brown, legs not annulated, opisthosoma dark brown. Prosoma (photo) almost as wide as long, cephalic part not raised, hairs and fovea indistinct, eyes large, posterior row distinctly procurved, posterior median eyes largest, spaced by less than their radius, anterior median eyes smallest, anterior and posterior lateral eyes touching, clypeus shorter than the field of the median eyes, basal cheliceral articles fairly large, not diverging, distinctly longer than the prosomal height, lateral files indistinct or absent, fangs long, the sternum spaces the coxae IV by about their diameter. – Legs (photo) slender and fairly long, bristles long and thin, patellae and tibiae dorsally 1/1, no other bristles; the basal bristle on tibia IV is twice as long as the tibial diameter; metatarsal trichobothria unknown. – Opisthosoma (photo) oval, hairs short and indistinct, genital area distinctly bulging, anterior spinnerets slender, colulus existing. – Pedipalpus (figs. 1–3): Femur slender, patella and tibia short, each bearing an almost hair-shaped bristle, tibial trichobothriae not studied, cymbium, paracymbium and bulbus: See above.

**Relationships and distribution:** See above.

Family **THERIDIIDAE**

Only few members of this family have been described from Madagascar; in copal a diverse fauna is preserved which includes an unknown number of undescribed species of several subfamilies; members of (e. g.) *Argyrodes* s. l., *Episinus*, and *Lasaeola* s. l. are not rare (CJW). Here I describe members of two taxa.

(a) **Subfamily Hadrotarsinae**

Genus **Lasaeola** SIMON 1881 s. l.

The taxonomy of the very diverse genus *Lasaeola* s. l. is still in discussion, see WUNDERLICH (2008: 279ff). Several subgenera have been described, at least some of them may be regarded as genera of their own. Numerous species of *Lasaeola* are preserved in copal of North Madagascar; the opisthosoma of most species is soft. Here I describe a new species in which the opisthosoma bears a large dorsal scutum, a member of the diverse taxon *Phycosoma* O. PICKARD-CAMBRIDGE 1873 (= *Trigonobothrys* SIMON 1889) which is regarded as a genus of its own by several authors.

***Lasaeola (Phycosoma) inclinata* n. sp.** (figs. 4–5), photos 3–4

The name of the species points to the inclined anterior margin of the opisthosoma.

**Material:** Holotype ♂ in subrecent copal from North Madagascar, F2359/CM/AR/CJW, 1 ♂ paratype F2382/CM/CJW.

**Preservation and syninclusions:** The holotype is completely and excellently preserved in a 8 x 1.5 x 1 cm large, light yellow piece of copal. A drop of copal is enclosed in the piece. – Syninclusions: Araneae: *Eriauchenius* sp. (Archaeidae), a ?juv. ♀, remains of two spiders and numerous insects, mainly Diptera and Hymenoptera, furthermore (e. g.) 1 Collembola, 1 Psocoptera; a movable gas bubble in a fluid bubble – The paratype is completely preserved, body length 1.5 mm.

**Diagnosis** (♂; ♀ unknown): Sequence of the long tibial bristles (fig. 4) 2/2/1/2, position of the metatarsal I trichobothrium in 0.78, prosoma (photo) as high as long, opisthosoma bearing a large scutum which is strongly rugose (photo). Pedipalpus: Fig. 5.

**Description** (♂):

Measurements (in mm): Body length 1.7, prosoma: Length 0.65, height 0.65; leg I: Femur 0.75, patella 0.3, tibia 0.5, metatarsus 0.4, tarsus 0.3, tibia II 0.4, basal cheliceral article 0.3.

Colour (photos): Prosoma and opisthosoma dark brown, legs yellow brown, darkened brown are all tarsi, and the distal half of femur IV.

Prosoma (photo) as long as high, highest in the middle, and here dorsally distinctly rugose, dorsally narrowed, behind the highest point with a transverse furrow. 8 eyes, anterior median eyes protruding and distinctly the largest. Clypeus vertical and very long, cheliceral teeth unknown. Prosomal-opisthosomal stridulatory organ most probably absent. – Legs (fig. 4, photo): Order I–IV/III/III, hairs indistinct, all patellae bear 2 dorsal bristles, sequence of the long tibial bristles 2/2/1/2, position of the metatarsal I trichobothrium in 0.78, position of the tarsal I–II organ in 0.17, unpaired tarsal claw small, short hairs of the tarsal IV comb. – Opisthosoma (photo) oval, dorsally completely covered with a strongly rugose scutum, epigaster sclerotized, a large ring around the spinnerets. The dorsal scutum is strongly onclined anteriorly, the spinnerets are short. – Pedipalpus (fig. 5): Patella and tibia fairly short, cymbium with a strong apical hair, structures of the bulbus insufficiently observable, median apophysis apparently absent, embolus apparently indistinct/short.

**Relationships:** Although the absence of a median apophysis is not sure I regard *inclinata* – based on the chaetotaxy and the armoured opisthosoma – as a member of *Phycosoma* which is regarded as a genus of its own by several authors. The shape of prosoma and opisthosoma is different in related species like the species of the Seychelles Islands, e. g., the strongly related *L. (P.) excisa* (SIMON 1888) in which the prosoma possesses dorsal furrows, and the opisthosoma is anteriorly stronger inclined, and furthermore has a pair of humps more posteriorly.

**Distribution:** North Madagascar, subrecent, preserved in copal.

## (b) Subfamily Theridiinae

Genus *Platnickina* KOCAK & KEMAL 2008 (= *Keija*)

*Platnickina duosetae* n. sp. (figs. 6–8) photo 5

The name points to the two dorsal bristles (lat. = setae) on the tibiae I, II and IV.

**Material:** Holotype ♂ in subrecent copal from North Madagascar, 2 separated pieces of copal and remains of grinding, F2360/CM/AR/CJW.

**Preservation and syninclusions:** The spider is very well and completely preserved in a light piece of copal, separated from a small and a large piece. Its opisthosoma is strongly deformed and destroyed, probably eaten out, the prosoma is deformed dorsally; the spider may have been the prey of an unknown arthropod. -- Right and below of the prosoma and below the left legs clumps of white questionable hyphae are preserved. A 3.2 mm long beetle is preserved behind the spider, a juvenile spider and some Diptera exist in the same piece of copal. 3 juv. Araneae (Pholcidae, Theridiidae, indet.), several insects like 5 Collembola and several Diptera are preserved in the pieces which are separated.

**Diagnosis** (♂; ♀ unknown): Sequence of the dorsal tibial bristle 2/2/1/2 (fig. 6), position of the metatarsal I–II trichobothrium in ca. 0.95. Pedipalpus (figs. 7–8): The embolus describes a large loop and has a spiral shape distally.

### **Description** (♂):

Measurements (in mm): Body length 1.35, prosomal length 0.7; leg I: Femur 1.3, patella 0.3, tibia 1.2, metatarsus 0.85, tarsus 0.35, tibia II 0.9, tibia III 0.45, tibia IV 0.6.

Colour: Body medium brown, opisthosoma with white spots, legs light brown, indistinctly annulated.

Prosoma (photo): 8 large eyes, the anterior medians largest, basal cheliceral articles long and fairly slender, teeth of the fang furrow probably absent, fangs long, other mouth parts hidden. – Legs (fig. 6, photo) long and slender, order I/II/IV/III, hairs indistinct, most bristles long and slender, patellae 2 dorsally (the basal one short), sequence of the dorsal tibial bristles 2/2/1/2, position of the metatarsal I–II trichobothrium in ca. 0.95. – Opisthosoma strongly deformed, see above. – Pedipalpus (figs. 7–8): Patella and tibia short, conductor bipartite, embolus long, distally spirally.

**Relationships:** In the strongly related pantropical *P. mneon* (BÖSENBERG & STRAND 1906) – which is not known from Madagascar – the distal loop of the embolus is distinctly smaller/shorter than in *duosetae*, one loop shorter. The chaetotaxy and the trichobothriotaxy of *mneon* have been ignored by previous authors. In the congeneric European species the sequence of the tibial bristles is 1/1/1/1, the sequence in *mneon* is unknown to me. Remarkable is the almost apical position of the metatarsal trichobothrium of *duosetae*. Probably *P. mneon* and *duosetae* are members of a species group or even a genus of its own in which the sequence of the tibial bristles is 2/2/1/2, an almost apical position of the metatarsal trichobothrium and a distal spiral of the embolus exist.

**Distribution:** North Madagascar, subrecent, preserved in copal.

## Family DICTYNIDAE

True members of the family Dictynidae have not been reported from Madagascar; *Copaldictyna*: See below. Here I describe two species of this family.

### Flagelldictynini n. trib.

The name points to the flagelliform embolus and on the family name Dictynidae as well.

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

**Diagnosis** (♂; ♀ unknown): Six large eyes (fig. 9) and probably additional a pair of tiny anterior median eyes, gnathocoxae (photo) not converging, very few leg bristles: A single retrobasal one on tibia III–IV (fig. 10) besides patellar bristles, tarsal trichobothria absent. Pedipalpus (figs. 11–12): No patellar or tibial apophysis, median apophysis ap-

parently absent, embolus thin and extremely long, guided laterally (but not basally) by a long conductor.

Further characters: Tiny spiders, body length only 1 mm, metatarsus IV straight.

The **relationships** are unsure. The cribellum, the absence of tarsal trichobothria, and the plumose cheliceral hairs are as in other Dictynidae; the almost parallel position of the gnathocoxae, the smooth articles of the pedipalpus, and the structures of the bulbus are unusual characters within the Dictynidae. – The anterior median eyes are also reduced in the genus *Lathys* SIMON 1884, but in *Lathys* the chaetotaxy and the structures of the ♂-pedipalpus are quite different; Flagelldictynini is not strongly related to *Lathys* and apparently also not to other Dictyninae.

**Distribution**: North Madagascar, subrecent, preserved in copal.

### *Flagelldictyna* n. gen.

Type species (by monotypy): *Flagelldictyna copalis* n. sp.

**Diagnosis, relationships and distribution**: See the Flagelldictynini.

### *Flagelldictyna copalis* n. gen. n. sp. (figs. 9-12) photo 6

The name of the species points to the young resin (copal) in which the holotype is preserved.

**Material**: Holotype ♂ in young resin (copal), 2 separated pieces of copal, and remains of grinding, F2370/CM/AR/CJW.

**Preservation and syninclusions**: The spider is well but incompletely preserved in a clear light yellow piece of copal. A right leg beyond the patella and most spinnerets are cut off, the opisthosoma is dorsally distinctly depressed. – Two tiny ballets of insects excrement are preserved near the spider. In the separated pieces of copal are a leaf, 2 beetles, some wasps, a termite, a male of *Orchestina madagascariensis* WUNDERLICH 2004 (Araneae: Oonopidae), and several Diptera preserved.

**Diagnosis** (♂; ♀ unknown): See above.

**Description** (♂):

Measurements (in mm): Body length 1.0, prosomal length 0.45; leg I: Femur 0.4, patella 0.18, tibia 0.3, metatarsus 0.25, tarsus 0.2, metatarsus III 0.2, metatarsus IV 0.26.

Colour medium grey, legs not annulated.

Prosoma (fig. 9, photo) about as wide as long, bearing few longer hairs, profile distinctly convex, fovea hidden (absent?), 6 large eyes which are covered with bubbles, and probably additionally a pair of tiny anterior median eyes, posterior row distinctly procurved, clypeus very short, basal cheliceral articles large, slightly diverging distally, condyle well developed, lateral files apparently absent, bearing apically plumose hairs, anterior margin of the fang furrow with 5 long teeth, fangs long, labium wider than long, gnathocoxae distinctly longer than wide, not converging, the wide sternum separates the coxae IV by more than their diameter. – Legs (fig. 10) stout, order IV/I/II/III; hairs short, few thin bristles: Patellae dorsally 1/1, tibia III–IV 1 retrobasally. Trichobothria: Tarsi none, metatarsi a single one in a distal position. Metatarsus IV straight, the calamistal hairs (fig. 10) cover more than  $\frac{3}{4}$  of its length, unpaired tarsal claw small. – Opisthosoma (photo) oval, covered with few shorter hairs, spinnerets incompletely preserved, stout, the anteriors widely spaced, cribellum badly preserved. – Pedipalpus (figs. 11–12, see also the tribe): Femur, patella and tibia stout, without apophyses or bristles, cymbium long.

**Relationships and distribution:** See the new tribe.

**Dictyna** SUNDEVALL 1833 s. l.

The limits of this genus are unsure and probably a matter of opinion. Most members of *Dictyna* s. l. exist on the Northern Hemisphere, African species of *Dictyna* s. str. are quite rare; they are unknown from South Africa.

***Dictyna rufa* n. sp.** (figs. 13–16) photos 7–10

The name of the species points to its redbrown (lat. rufus) colour of the prosoma and legs.

**Material:** 4♂ in subrecent copal from North Madagascar; holotype separated from a larger piece of copal, and remains of grinding, F2372/CM/AR/CJW; paratypes F2373/CM/AR/CJW, F2374/CM/AR/CJW, and coll. ALEX BEIGEL no. MC-121c.

**Preservation and syninclusions:** The spiders are preserved in light yellowish pieces of copal. – The holotype is excellently and completely preserved; a tiny Diptera exists anteriorly below its body. – Further syninclusions: Araneae: Theridiidae indet.: 1 ad. ♂

and 2 juveniles, numerous Diptera and Hymenoptera, 1 Lepidoptera and 2 Auchenorrhyncha. – Paratype F2373 is excellently and almost completely preserved, the right tibia I is amputated near its end, apparently the stump is healed. – Syninclusions: A tiny juvenile Araneae, 1 Lepidoptera, 1 Psocoptera, 1 Coleoptea, 1 Hymenoptera and numerous Diptera. Furthermore preserved are numerous thin needle-shaped particles of unknown origin (they look not natural to me), and probably remains of bark at one end of the piece of copal. – Paratype F2374 is completely and well preserved, dorsal parts of the opisthosoma are cut off within the copal. – Syninclusions: Remains of 5 juvenile Araneae indet., few Hymenoptera and numerous Diptera, an insect indet., and a tiny larva of an insect indet.. -- ♂ from the coll. A. BEIGEL is excellently and completely preserved near the margin of a larger piece of copal. – Syninclusions: A juv. Araneae: Theridiidae indet., an insect larva, and several insects like a Coleoptera, some Diptera and Hymenoptera.

**Diagnosis** (♂; ♀ unknown): Colour of prosoma and legs distinctly redbrown (photos), pedipalpus (figs. 14–16): Tibia bulging retrolaterally but apophyses absent, ctenidia indistinct or absent, conductor widely elongated posteriorly and pointed.

### **Description** (♂):

Measurements (in mm): Body length 1.6–1.7, prosoma: Length 0.78 (holotype), width 0.58; leg I: Femur 0.7, patella 0.17, tibia 0.6, metatarsus 0.45, tarsus 0.3, tibia II 0.45, tibia III 0.35, tibia IV 0.45.

Colour (photos) redbrown, legs not annulated.

Prosoma (fig. 13, photos) 1.34 times longer than wide, cephalic part narrow, fovea indistinct, hairs (most are rubbed off) short, 8 small eyes in a wide field, posterior row slightly recurved, posterior median eyes spaced by almost 1 ½ diameters, basal cheliceral articles large, strongly diverging in the middle part, fang furrow bearing several teeth, fangs long and quite thin, labium distinctly longer than wide and free, gnathocoxae long and converging, the sternum spaces the coxae IV by their diameter. – Legs (photo) fairly slender, order I/II/IV/III, bristle-less, metatarsus IV straight, short hairs of the calamistrum almost along the whole length, metatarsal trichobothria unknown, tarsal trichobothria apparently absent. – Opisthosoma (photo) oval, 1.8 times longer than wide, covered with short hairs, spinnerets short, cribellum hidden. – Pedipalpus (figs. 14–16) (see the diagnosis) with slender articles, no patellar or tibial apophyses, cymbium slender, elongated.

Close **relationships** are unknown to me. In *Archaeodictyna ulova* GRISWOLD & MEIKLE-GRISWOLD 1987, e. g. from Southern Africa, exist apophyses of the articles of the ♂-pedipalpus. In the European *Archaeodictyna ammophila* (MENGE 1871) a pedipalpal tibial apophysis is absent, too, but the structures of the bulbus (e. g. of the conductor) are quite different.

**Distribution:** North Madagascar, subrecent, preserved in copal. – The species may be restricted to the forests of North Madagascar where it apparently was/is not rare.

## Family TITANOECIDAE?

The monotypic subrecent Copaldictyninae WUNDERLICH 2004 has been described in copal from Madagascar as a subfamily of the Dictynidae s. l. The subfamily is transferred here with hesitation to the family Titanoecidae (**quest. n. relat.**), but it may be the member of a family of its own. See the photos 11–12.

The family Titanoecidae is diagnosed by its retrolateral cheliceral stridulatory SPINES (in most taxa) or its retrolateral cheliceral stridulatory FILES (in the Copaldictyninae), as well as by the structures of its male pedipalpus: An ear-shaped lobe of a tibial apophysis, and a retromarginal furrow of the cymbium, both existing in the Copaldictyninae, but absent in the Dictynidae (s. str. and s. l.), see the tab. below.

A long calamistrum on a straight metatarsus IV and “reduced” tarsal trichobothria are characteristic patterns in both families. I do not want to exclude that these two families (and certain others like the Phyxelidae and probably the Nicodamidae) may be members of a branch of its own within or – according to CODDINGTON et al. (2004) – next to the RTA-clade. The RTA-clade in the wide sense is probably not a monophyletic taxon; it may be paraphyletic.

This would be the first report of the cosmopolitical family Titanoecidae from Madagascar.

Character	?Titanoecidae: Copaldictyninae	Titanoecidae: Remaining taxa	Dictynidae
Fovea	distinct	weak	weak
retrolateral cheliceral structures	files	spines	– (+) (*)
gnathocoxal position	slightly converging	almost parallel	usually converging
modified/diverging ♂-chelicerae	–	–	+/-
ventral tibial & metatarsal I spines	+	+	–
ear-shaped lobe of the retrolat. ♂-pedipalpal tibial apophysis	+	+	–
male pedipalpal paratibia	+	–	–
retrolateral cymbial furrow	+	+	–
posteriorly strongly elongated conductor	–	–	usually existing

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 (\*) Rare exceptions: Retrolateral spines – and probably stridulatory files, too – exist in the enigmatic extinct (Baltic amber) genus *Chelicirrum* WUNDERLICH 2004, retrolateral spines exist in the extant species *Lathys dentichelis* (SIMON 1883).

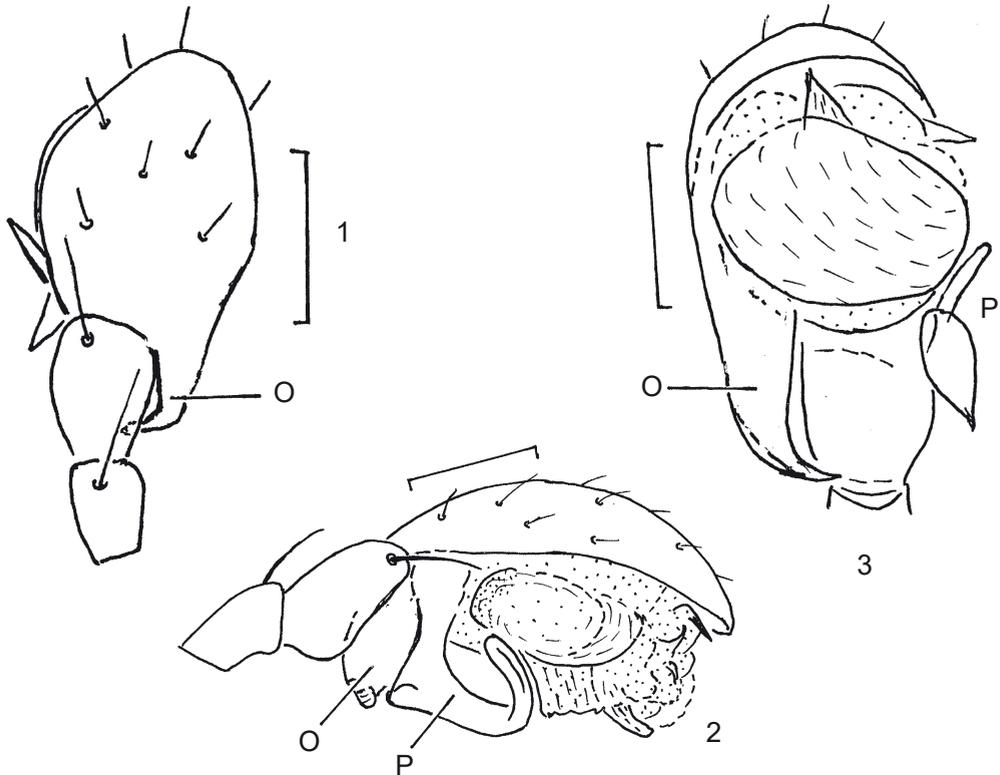
Tab. Selected characters of the families Titanoecidae and Dictynidae

**REFERENCES**, cited

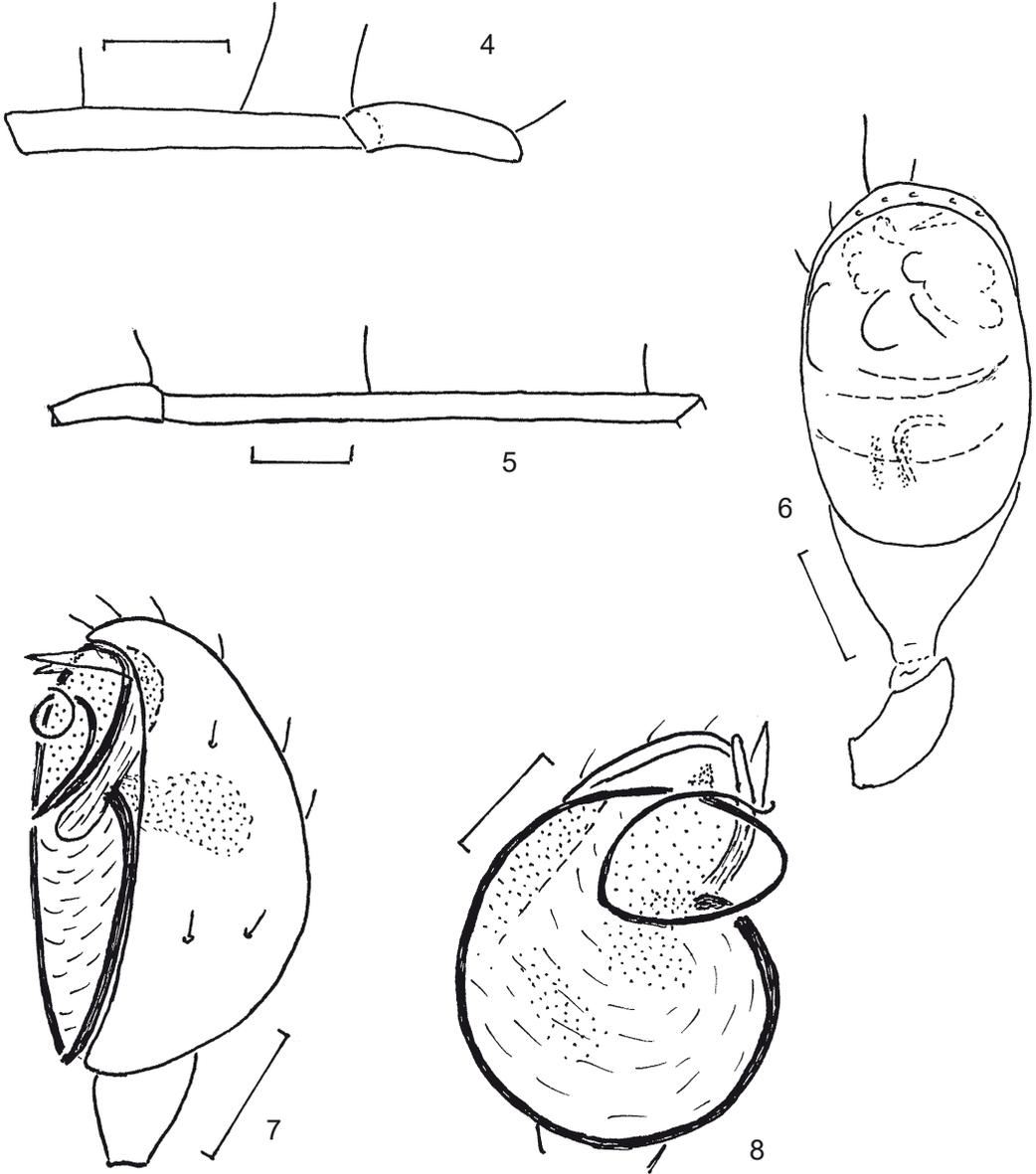
WUNDERLICH, J. (2004): Subrecent spiders (Araneae) in copal from Madagascar, with description of new species. – *Beitr. Araneol.*, 3: 1830–1853.

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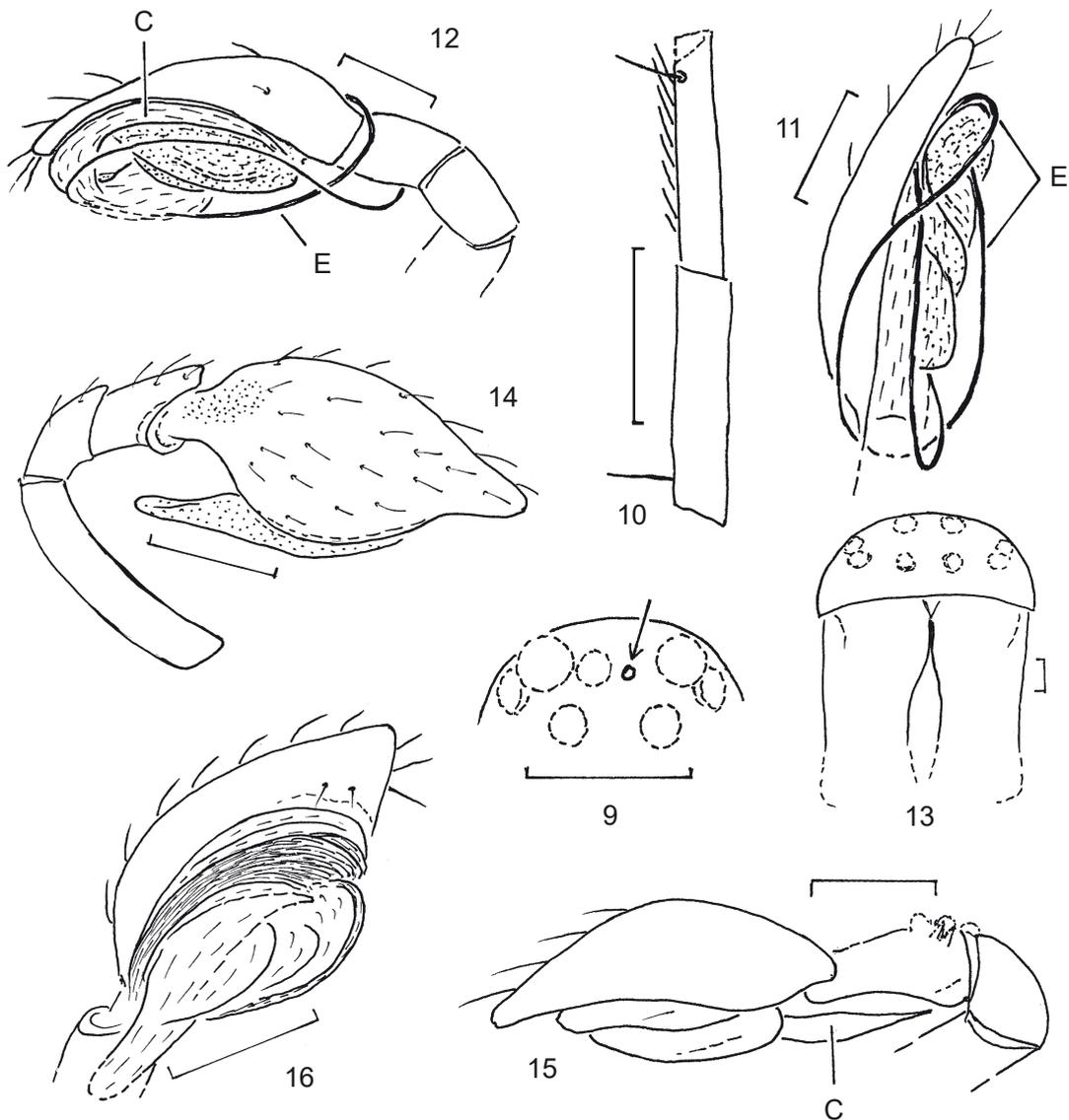


Figs. 1-3: *Madagascarphantes vomerans* n. gen. n. sp., ♂; 1) dorsal aspect of the left pedipalpus; 2) retrolateral aspect of the right pedipalpus; 3) ventral aspect of the left pedipalpus. The distal structures of the bulbus are difficult to observe. O = proventral posterior outgrowth of the cymbium. P = paracymbium. Scale bar 0.1 mm;



figs. 4-5: *Lasaeola (Phycosoma) inclinata* n. sp., ♂, holotype; 4) retrolateral aspect of the left patella and tibia I. Trichobothria and normal hairs are not drawn. Note the long bristles; 5) ventral aspect of the left pedipalpus. The structures of the bulbus are only insufficiently observable and partly hidden by a leg and a tiny bubble. Note the strong apical cymbial hair. Scale bars 0.1 and 0.2;

figs. 6-8: *Platnickina duosetae* n. sp., ♂; 6) Prolateral aspect of the left patella and tibia I. Hairs are not drawn; 7-8) retrolateral and ventral aspect of the left pedipalpus. Scale bars 0.2 in fig 6, 0.1 in figs. 7-8;



figs. 9-12: *Flagelldictyna copalis* n. gen. n. sp., ♂; 9) dorsal aspect of the eyes. Most eyes are covered with emulsions/bubbles. Note the questionable tiny right anterior median eye (arrow); 10) prodorsal aspect of the left tibia and metatarsus IV. Note the ret-rodorsal-basal tibial bristle, and the long distal metatarsal trichobothrium. Normal hairs and tibial trichobothria are not drawn; 11-12) prolateral aspect of the left and prolateral aspect of the right pedipalpus in slightly different positions. C = conductor, E = embolus. Scale bars 0.2 in figs. 9-10, 0.1 in figs. 11-12;

figs. 13-16: *Dictyna rufa* n. sp., ♂, fig. 15) paratype F2373, holotype: remaining figs.; 13) anterior aspect of the prosoma; 14) retrolateral aspect of the right pedipalpus; 15) prolateral aspect of the right pedipalpus; 16) oblique ventral-apical aspect of the right pedipalpus. C = conductor. Scale bar 0.1.

## NEW FOSSIL SPIDERS (ARANEAE) IN EOCENE AMBER FROM THE UKRAINE

JOERG WUNDERLICH, 69493 Hirschberg, Germany.

**Abstract:** Fossil spiders (Araneae: Deinopidae, Synotaxidae, Theridiidae, Dictynidae, Hahniidae) are reported from Eocene Ukrainian amber from Rovno. The families Hahniidae s. str. and Deinopidae are reported for the first time from this kind of amber.

**Acknowledgement:** I thank EVGENY PERKOVSKY for the loan of the fossil spider material. He recently told me in a personal note of the first report of a member of the family Deinopidae in Rovno amber.

The **material** is kept in the Schmalhausen Institute of Zoology of the Ukrainian National Academy of Sciences, Kiev, Ukraine.

In the Ukraine exist numerous Eocene amber deposits, e. g. in the North-Western region of the area of Rovno.

WUNDERLICH (2004) reported 13 spider families in Rovno amber, PERKOVSKY et al. listed 29 spider families; the report of several families appears quite unsure to me; competent revisional determinations are needed. In this paper I add the families Deinopidae (see above) and Hahniidae s. str. to the list of this kind of amber.

Several spider species are common to Baltic and Rovno amber as well, see WUNDERLICH (2004: 1822); in this paper I treat two more species from Rovno amber which probably were already known from Baltic amber.

## Family SYNOTYXIDAE

### Succinitaxus WUNDERLICH 2004

Two species of this extinct genus were described by WUNDERLICH (2004): *Brevis* (in Baltic and probably in Bitterfeld amber, 6♂), and *minutus* (a single male in Baltic amber). The structures of the bulbus of one of the Ukrainian males, K-9276 (fig. 1), are well observable in the ventral aspect. These structures may appear quite different because of the kind of preservation – see figs. 84–85, Beitr. Araneol., 3: 1237 –, and I am not quite sure about the conspecificity of the Ukrainian males. The genus is new to the Ukrainian amber.

### *Succinitaxus* (?)*brevis* WUNDERLICH 2004 (fig. 1)

**Material:** 2♂ in Rovno amber, K-25195 and K-9276.

#### **Preservation and short descriptions:**

Male K-25195: The male is completely preserved, mainly the opisthosoma including the epigaster are covered with a white emulsion, the prosomal length is 0.5 mm, the stridulatory tooth of coxa IV is observable, the tibiae (at least I and IV) bear at least a single bristle in the basal half, other bristles may be hidden or broken off. The ventral aspect of the pedipalpus is hidden, the parembolic process is pointed, bent forward.

Male K-9276: The male is only fairly well preserved except the left pedipalpus, most parts are covered with a white emulsion, the left leg III has been lost beyond the coxa by autotomy, the body length is 1.5 mm, the tibiae I, II and IV bear 2 dorsal bristles. Ventral aspect of the pedipalpus: Fig. 1.

**Distribution:** Eocene Ukrainian (Rovno) amber forest.

## Family THERIDIIDAE

### Clya KOCH & BERENDT 1854

The following genera of this diverse family are known from Rovno amber (and from Baltic amber as well):

*Clya* KOCH & BERENDT 1854, *Episinus* WALCKENAER 1804, *Pseudoteutana* WUNDERLICH 2008 and probably *Obscurpholcomma* WUNDERLICH 2008 (see below).

### *Clya lugubris* KOCH & BERENDT 1854

**Material:** 1♂ in Rovno amber, K-1598.

### Obscurpholcomma sp. indet.

**Material:** 1♂ in Rovno amber, KF-3.

**Remark:** The determination of the male is not quite sure because of its insufficient preservation.

## Family DICTYNIDAE: DICTYNINAE

The family is well-known from Baltic and Bitterfeld amber (5 extinct genera); it is quite rare in Rovno amber, listed (under Dycynidae) by PERKOVSKY et al. in PENNEY (2010). No taxon has been specified up to now. Here I treat a member of the subfamily Dictyninae.

## Dictynidae: Dictyninae indet.

**Material:** 1 subad. ♂ in Rovno amber, K-24973.

**Preservation and short description:** Most parts of the body are covered with a white emulsion, the body length is 2 mm, the 8 eyes are small, the posterior row is straight, the cephalic part is large, the basal cheliceral articles are large (long and thick) and not diverging, an opisthosomal scutum is absent, the calamistrum is almost as long as the basal half of the metatarsus IV.

Close **relationships** are unknown to me; the characters of the genus are different from the Eocene genera which are known from Baltic amber, see WUNDERLICH (2004: 1430–1431).

**Distribution:** Eocene Ukrainian amber of Rovno.

## Family HAHNIIDAE: HAHNIINAE

The family, subfamily and the monotypic genus *Cymbiohahnia* WUNDERLICH 2004 are known from Baltic and Bitterfeld ambers; they are new to the Rovno amber.

*Cymbiohahnia* (?) *parens* WUNDERLICH 2004

**Material:** 1♂ in Rovno amber, K-25865.

**Preservation and short description:** The spider is slightly deformed and completely preserved in a piece of amber which was heated. Most of its ventral parts are covered with a thick white emulsion, only a part of the right pedipalpus is free observable. The body length is 2 mm, the area of the tracheal spiracle is darkened probably by heating and probably sclerotized. Because of the heating and the emulsions on the pedipalpi the determination to the species level is not quite sure.

**Distribution:** Eocene Baltic, Bitterfeld, and probably Ukrainian (Rovno) amber.

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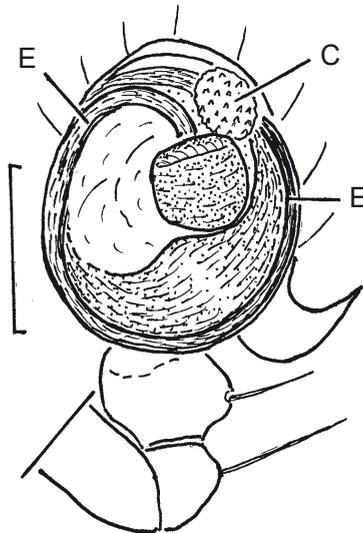


Fig. 1) *Succinitaxus (?) brevis* WUNDERLICH 2008, ♂ K-9276, ventral aspect of the left pedipalpus. C = conductor, E = embolus. Scale bar 0.1 mm.

## NEW FOSSIL SPIDERS (ARANEAE) OF EIGHT FAMILIES IN EOCENE BALTIC AMBER, AND REVISIONS OF SELECTED TAXA

JOERG WUNDERLICH, 69493 Hirschberg, Germany.

**Abstract:** Fossil spiders (Araneae) in Eocene Baltic amber are treated: The genera of the family Tetragnathidae are revised, *Samlandicmeta mutila* **n. gen. n. sp.** and *Baltleucauge propinqua* **n. sp.** are described. The tribe Praetheridiini WUNDERLICH 2004 from the family Protheridiidae WUNDERLICH 2004 (superfamily Araneoidea) is upgraded to the family rank (Praetheridiidae, **n. stat.**), and revised, the genus *Ero* C. L. KOCH 1837 is revised, *Succinero* WUNDERLICH 2004 and *Palaeoero* WUNDERLICH 2004 are regarded as subgenera of *Ero* (**n. stat.**), *Ero* (*Succinero*) *clunis* **n. sp.**, *E.* (*S.*) *gracilitibialis* **n. sp.**, and *E.* (*S.*) *veta* **n. sp.** are described, *Mimetes brevipes* WUNDERLICH 2004 is revived (**sp. resurr.**) from the synonymy with *M. longipes* WUNDERLICH 2004, the relationships of the family Mimetidae s. str. are discussed. *Graea magnoculi* **n. sp.** (Zygiellidae), *?Eophantes seorsum* **n. sp.** (Linyphiidae), *Succiniopsis runcinata* **n. sp.** (Zoropsidae s. l.: Eomatachiini WUNDERLICH 2004), *Ephalmator tredecim* **n. sp.** (Ephalmatoridae). The tribe Succinomini WUNDERLICH 2008 (RTA-clade, superfamily unsure) is upgraded to family rank (Succinomidae, **n. stat.**), and revised, including *?Succinomus gibbosus* **n. sp.**, *Eohalinobius calefacta* **n. sp.**, *E. hiddenseeensis* **n. sp.**, and *Eohalinobius patina* **n. sp.** (Succinomidae). *Eodoter longimammillae* **n. sp.** (Clubionidae) is described. – Furthermore descriptions and remarks are given on fossil taxa of the families Araneidae, Archaeidae, Dictynidae, Linyphiidae, Nephilidae, Segestriidae, Sparassidae, Thomisidae and Zoropsidae, as well as on some higher spider taxa in Baltic amber which became probably extinct at the end of the Eocene.

Key words: Amber, Araneae, Baltic, Cretaceous, Eocene, fossils, new taxa, spiders.

Recently discovered and well preserved Eocene fossils allow new conclusions on the relationships of higher taxa, see below, e. g., Praetheridiidae. First reports of tribes in the Baltic amber indicate the existence of still more unknown higher taxa in the Eocene than already known. – Photos: Part I B, p. 339–345.

## Family **SEGESTRIIDAE**

Three fossil species of the genus *Segestria* LATREILLE 1804 in Baltic amber were described and named by WUNDERLICH (2004). The species are well distinguishable by the shape of their embolus, less by the length of their prosoma.

The prosomal length of a recently studied male (F2286/BB/AR/CJW), photo 1, 1.65 mm, lies between *S. mortalis* and *flexio*, but the strongly bent distal part of the embolus indicates a conspecificity with *flexio*. The present specimen is the largest one of seven males known to me, and its large prosomal length has to add in the paper by WUNDERLICH (2004: 660 and 663).

## Family **TETRAGNATHIDAE**

Tetragnathidae was a diverse family in the Eocene Baltic amber forest although most taxa are rarely preserved in the fossil resin; the genus *Priscometa* is most frequent. Seven genera of the subfamilies Diphyinae, Leucauginae, Metinae (Metainae), and *Anameta* (questionable subfamily) were described by WUNDERLICH (2004: 899–947, 2008: 81–103, and 2011: 507–510). The subfamily Tetragnathinae – very diverse today and known from the Miocene Dominican amber – is not reported. All fossil genera in Baltic amber except *Meta* s. l. are extinct.

Today four genera are known from Europe – only half as many as existed in the Baltic amber forest.

Here I add a further genus, two new species, a questionable taxon, a table, and a completed key to the fossil genera in Baltic amber.

Genus	dorsal-basal bristle(s) on metatarsus I–II	short ventral spines of legs I–II	widely spaced lateral eyes
<i>Anameta</i>	a pair	–	+
<i>Corneometa</i>	a pair	variable (*)	–
<i>Eometa</i>	a pair	–	+
<i>Meta (Praetermeta)</i>	a single one	–	–
<i>Samlandicmeta</i>	a single one	–	–
<i>Priscometa</i>	a pair	on tibia I (*)	–
<i>Balticgnatha</i>	a pair	–	–
<i>Baltleucauge</i> (**)	a pair	–	+

(\*) Frequently existing.

(\*\*) Trichobothria exist on the femora (fig. 10).

Tab.: Selected characters of the tetragnathid genera in Baltic amber  
(in addition and with corrections to the tab. p. 909 by WUNDERLICH (2004))

**Key to the genera of the family Tetragnathidae in Baltic amber (♂):**

- 1 The femora bear dorsal trichobothria (fig. 10). Leucauginae . . . . . *Baltleucauge*
- Femoral trichobothria absent. . . . . 2
- 2(1) Metatarsus I (and usually II) bear a single dorsal-basal bristle (fig. 1). Lateral eyes close together. Metinae . . . . . 3
- Metatarsus I–II bears a pair of dorsal-basal bristles (fig. 7). Lateral eyes close together or distinctly spaced. Diphyinae and *Anameta* . . . . . 4
- 3(2) Pedipalpus (figs. 4–6): Tibia long, paracymbium small and simple *Samlandicmeta*
- Pedipalpus: Tibia short, paracymbium consisting of two large branches, see Beitr. Araneol., 3: 947, fig. 32. Subgenus *Praetermeta* . . . . . *Meta*
- 4(2) Cymbium dorsally with cuspules-bearing outgrowths, see Beitr. Araneol., 3: 941, fig. 2. . . . . *Anameta*
- Cymbial cuspules absent . . . . . 5

- 5(4) Lateral eyes distinctly spaced from each other, posterior eye row recurved. The erect hairs of the legs I–II are shorter than in other genera . . . . . Eometa
- Lateral eyes almost contiguous. . . . . 6
- 6(5) Femur and/or tibia and/or metatarsus I (II) with ventral/ prolateral thorns or short spines, see Beitr. Araneol., 3: 943, fig. 10. . . . . 7
- No such thorns/spines. Pedipalpus: Fig. 8 . . . . . Balticgnatha
- 7(6) Cymbium with an erect dorsal-basal horn . . . . . Corneometa
- Cymbial horn absent . . . . . Priscometa

(a) Subfamily **METINAE** (name in the future most probably Metainae)

**Samlandicmeta n. gen.**

The name of the genus is based on the origin of the holotype, the Samlandic coast, and the name of the related genus *Meta*. The gender of the name is feminine.

Type species (by monotypy): *Samlandicmeta mutila* n. sp.

**Diagnosis** (♂; ♀ unknown): Lateral eyes close together, femora I–II bear a single bristle only, metatarsi I–II bear a single dorsal-basal bristle (figs. 1–2), prosoma finely corniculate, opisthosoma 1.3 times longer than wide, pedipalpus (figs. 4–6): Paracymbium simple and almost sickle-shaped, cymbium with a retrobasal outgrowth.

Further characters: Femoral trichobothria and short ventral leg spines absent.

**Relationships**: According to the weakly spaced lateral eyes, the chaetotaxy and the stout opisthosoma I regard *Samlandicmeta* as a member of the subfamily Metinae (Metainae). I do not know a close extant relative. In the remaining Eocene genera except *Meta* (*Praetermeta*) the metatarsi I–II bear dorsally-basally A PAIR of bristles, see the tab. below, the prosoma is not corniculate, and the paracymbium is large and more complex.

**Distribution**: Eocene Baltic amber forest.

***Samlandicmeta mutila* n. gen. n. sp.** (figs. 1–6) photos 2–4

The name of the species points to the amputated patella IV; *mutilus* (lat.) = mutilated.

**Material:** Holotype ♂ in Eocene Baltic amber, F2354/BB/AR/CJW.

**Preservation and syninclusions:** The spider is well and almost completely preserved in a clear piece of amber which was slightly heated. The right patella I is cut off, the left leg IV has been amputated through the end of the patella, the opisthosoma is depressed dorsoventrally. Thin hyphae are preserved left of the spider; a thin light and a transparent structure exist right in contact to the spiders body.

**Diagnosis** (♂; ♀ unknown): See the genus.

**Description** (♂):

Measurements (in mm): Body length 2.6, prosoma: Length 1.3, width 1.1, opisthosoma: Length 1.55, width 1.2; leg I: Femur 2.4, patella 0.6, tibia 2.0, metatarsus almost 2.5, tarsus ca. 0.8; tibia II 1.4, tibia III 0.58, tibia IV 1.4; pedipalpus: Femur 0.95, tibia 0.35.

Colour: Prosoma dark brown, legs mainly medium brown, opisthosoma light brown. Prosoma (photo) 1.2 times longer than wide. finely corniculate (mainly anteriorly-laterally), few short hairs, fovea well developed, eyes fairly large, posterior row fairly procurved, posterior median eyes spaced by their diameter, slightly more from the posterior lateral eyes, lateral eyes close together, anterior medians largest, only fairly protruding, clypeus short, basal cheliceral articles only fairly large, not diverging, lateral files absent, teeth hidden, fangs long and strongly bent, gnathocoxae large and parallel, labium strongly rebordered. – Legs (figs. 1–3, photo) slender, order I/II/IV/III, I distinctly longest, III distinctly shortest; tibia I–II bear longer erect hairs, bristles numerous and long, femora a single one on I–II retrodistally, 1 dorsally on III, 1/1 dorsally on IV, all patellae dorsally 1/1, tibia I dorsally 1/1 and 2 lateral pairs, IV probably the same, all metatarsi bear a single dorsal-basal one; position of the metatarsal trichobothria unknown. – Opisthosoma (photo) 1.3 times longer than wide, widest in the basal half, hairs indistinct, probably 2 pairs of dorsal sigillae, spinnerets stout. – Pedipalpus (figs. 4–6, photo, see also above): Femur long and slender, patella short, bearing a long and a short bristle, tibia long, bearing a retroapical apophysis and at least 3 trichobothria.

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

(b) Subfamily **DIPHYINAE**

***Balticgnatha*** WUNDERLICH 2011

***Balticgnatha projectens*** WUNDERLICH 2011 (figs. 7–8)

Here I add two figures of the holotype: The dorsal aspect of the basal part of the right metatarsus I (fig. 7), and the redrawn retrolateral aspect of the left pedipalpus (fig. 8). The real shape of the paracymbium appears different in the re-study in a slight different aspect and lilluminating compared to the previous drawing; therefore is has been redrawn.

(c) Subfamily **LEUCAUGINAE**

***Baltleucauge propinqua*** n. sp. (figs. 9–13) photos 5–6

The name of the species points to the related *Baltleucauge gillespieae* WUNDERLICH 2008; propinquus Latin = related, similar. The name *Baltleucauge* is feminine.

**Material:** Holotype ♂ in Eocene Baltic amber, F2355/BB/AR/CJW.

**Preservation and syninclusions:** The spider is excellently and almost completely preserved in a clear yellowish piece of amber which was slightly heated, only both patellae I and the right metatarsus and tarsus I are cut off; parts of the body are partly covered with a white emulsion. – A Diptera, some hyphae, some thin spiders threads, few stellate hairs and detritus are preserved in the same piece of amber. Two questionable

Nematoda: Rhabditida are preserved furthermore, one in contact with the left tibia I and a thin spiders thread.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (figs. 10–13): Tibia strongly bulging ventrally in the middle, cymbium with a dorsal-basal “tooth” and retrobasal spines on a shallow depression.

**Description** (♂):

Measurements (in mm): Body length 4.0, prosoma: Length 1.8, width 1.3, opisthosoma: Length 2.4, width 1.2; Leg I: Femur 3.4, patella ca. 0.8, tibia 4.3, metatarsus 4.3, tarsus 1.5, tibia II 3.2, tibia III 1.1, pedipalpal femur ca. 1.1.

Colour: Prosoma and legs medium brown, legs not annulated, opisthosoma grey brown.

Prosoma (photos) 1.4 times longer than wide, hairs short and indistinct, fovea low, eyes large, posterior row recurved, posterior median eyes spaced by less than their diameter, lateral eyes spaced from each other by about their radius, clypeus about as long as the diameter of an anterior median eye, basal cheliceral articles large, only slightly diverging, lateral files absent, teeth hidden, fangs long, position of the gnathocoxae parallel, labium slightly rebordered, coxae IV not widely separated. – Legs (photos, fig. 9) long and slender, order I/II/IV/III, I distinctly longest, III distinctly shortest; the tibiae I–II bear long, thin and erect hairs, femora with trichobothria, I with 5 basal ones in two rows, IV bears 4 ones in the basal half, bristle long and slender, similar to *B. gillespiae* (probably variable intraspecificly); femora: I–II 1 dorsally, III–IV 1/1 dorsally and additional in the distal half, tibia I bears 8 bristles, metatarsus I a dorsal-basal pair, tibia IV 5 ones. Position of the metatarsal trichobothria unknown. – Opisthosoma (photos) twice as long as wide, covered with short hairs, spinnerets short. – Pedipalpus (figs. 10–13): See the diagnosis; femur long and slender, patella short, tibia long, bearing at least 4 trichobothria and several apophyses, cymbium with a dorsal-basal “tooth” and a shallow retrobasal depression which bears short spines, paracymbium simple and sickle-shaped, blunt, bulbus fairly flat, subtegulum and tegulum long, most parts of the embolus hidden.

**Relationships:** The shape of the body, the position of the eyes, chaetotaxy, trichobothriotaxy, and the conformation of the structures of the bulbus are like in the only other known congeneric species, *B. gillespiae* WUNDERLICH 2008 in Baltic amber. In *gillespiae* femur IV bears 5 trichobothria (4 in *propinqua*) (an intraspecific variability may exist!), the pedipalpal tibia is thickened ventrally-distally (not in the middle), its apophyses are different, and the cymbium bears a larger retrobasal depression.

**Distribution:** Eocene Baltic amber forest.

## Family ZYGIELLIDAE

Members of Eocene Zygiellidae s. str. are not rare in Baltic amber, autotomy beyond the coxa is frequent. Species of this family were treated, e. g., by WUNDERLICH (2004: 924–937): Two species of the genus *Eozygiella* WUNDERLICH 2004, and seven species of *Graea* THORELL 1869. Here I add a further species of the genus *Graea*:

### *Graea magnocoli* n. sp. (figs. 14–15) photos 7–8

The name of the species points to the existence of its large anterior median eyes.

**Material:** Holotype ♂ in Eocene Baltic amber and two separated pieces of amber, F2322/BB/AR/CJW.

**Preservation and syninclusions:** The spider is well preserved in a yellowish piece of amber which was slightly heated. The right leg II and the left leg III are lost beyond the coxa by autotomy, the distal parts of the left metatarsus/tarsus I–II are cut off, remains of a white emulsion exist on some ventral parts of the body, a bubble is preserved on a ventral depression of the opisthosoma. – Long and thin leg parts of the member of an Opiliones and remains of a plant are preserved in the larger separated piece of amber, stellate hairs exist within the three pieces. Right above the spiders prosoma a tiny questionable beetle is preserved which body length is only 0.25 mm. Few tiny Nematoda: Rhabditida are preserved, e. g., left above the spiders prosoma, a thin spiders thread is running from the right eyes sideward.

**Diagnosis** (♂; ♀ unknown): Anterior median eyes large (photo) (but see below), paracymbium with a pointed branch which is directed to the cymbium, embolus hidden.

### **Description** (♂):

Measurements (in mm): Body length 3.5, prosoma: Length 1.8, width ca. 1.4; leg I: Femur 1.9, patella 0.7, tibia 1.6, metatarsus 1.05, tarsus 0.9, tibia III 0.65, tibia IV 0.9. Diameter of an anterior median eye up to 0.2 mm.

Colour medium to light brown, legs not or only slightly annulated.

Prosoma (photo) 1.2 times longer than wide, narrow anteriorly, most hairs are short, thoracic furrow well developed, eyes large, posterior straight, posterior median eyes spaced by 2/3 of their diameter, lenses of the anterior median eyes apparently quite large, but they probably are covered with a thin emulsion, clypeus short, basal cheliceral articles only fairly large, fangs (the left one is spread off) slender, fang margins toothed, labium free and wide, gnathocoxae stout, coxae IV close together. – Legs (photo) stout, I longest, III distinctly shortest; numerous bristles, most are long and fairly thin; leg I: Femur 3 near the end, 1/1 dorsally, patella 1/1 (the basal one quite thin),

and a retrolateral one in the distal half, tibial bristle in various positions, metatarsus 1 dorsally in the basal half, and 1/1 retrolaterally, leg IV similar but metatarsus with an additional short ventral-apical bristle. Position of the metatarsal trichobothria unknown. – Opisthosoma oval, widest in the basal half, dorsally covered with relatively few long and bristle-shaped hairs, colulus large, bearing ca. 5 hairs, anterior spinnerets stout and close together. – Pedipalpus (figs. 14–15): Patella and tibia only fairly long, each with a long dorsal bristle, tibia slightly elongated dorsally-apically, cymbium wide, paracymbium with two distal branches, strongly sclerotized, a free or almost free sclerite, see also the diagnosis.

**Relationships:** The shape of the paracymbium is probably unique in this species, its eyes are larger than in most related species.

**Distribution:** Eocene Baltic amber forest.

## Family NEPHILIDAE

The Nephilidae – under Araneidae: Nephilinae – in Baltic amber were treated by WUNDERLICH (2004: 963–978). The specimen described below is the first known LARGE nephilid female in Baltic amber. It may be a member of the – in the geological sense – very old genus *Nephila* LEACH 1815 (or a strongly related genus), which has been reported even from the Jurassic, see SELDEN et al. (2011).

Leg tufts (figs. 16–17) are known to me from three families within the superfamily Araneoidea s. l. (= Orbiculariae), only from females of certain species of each genus, from the Uloboridae: *Uloborus*, the Tetragnathidae: *Leucauge*, and the Nephilidae: *Nephila*. The tufts are located mainly on the tibiae and metatarsi, and usually more distally. Their function is unknown; I would not exclude a kind of camouflage which existed already in the Jurassic.

**Nephilidae indet.** (fig. 16) (compare fig. 17)

**Material:** 1 ?inad. ♀ in Eocene Baltic amber, F2323/BB/AR/CJW.

**Preservation and syninclusions:** The spider is badly preserved in a larger piece of amber which has been heated; its ventral side bears fissures in the amber and is partly observable, the dorsal side is hidden by an oxidated layer within the amber, the distal

parts of the right legs are cut off, the tips of the left legs I, II and IV are also cut off, the left leg III is completely preserved. – In the same piece of amber are preserved: A large inad. female of the Araneidae: Araneinae (?*Araneus* sp.), body length 10.5 mm, see below, Acari, Coleoptera, an Aphidina larva, Hymenoptera including Formicidae, remains of a Blattaria, stellate hairs, insects excrement, as well as a lot of detritus particles and soil.

**Description** (♀):

Measurements (in mm): Body length 8.5, prosomal length ca. 4.0, femur I 3.7, tibia IV 2.4.

Colour: Legs dark brown (darkened by heating), prosoma medium brown, opisthosoma light grey brown.

Prosoma (most parts are hidden): Eyes small, their position araneinae-like: Median eyes close together, and widely spaced from the laterals, lateral eyes close together, basal cheliceral articles large and robust, claw of the pedipalpus well developed. – Legs fairly stout, numerous bristles, most are long and slender but few are spine-shaped. The tibiae I, II and IV bear dense hairs in their distal half (fig. 16), apparently tufts, similar to extant members of the genus *Nephila* LEACH (fig. 17) and other taxa, see above.

**Relationships:** Hair brushes (tufts) are known from certain extant females of the genus *Nephila* on various leg articles, see, e. g., fig. 17. In *Luxurionephila* WUNDERLICH 2004 males (females are unknown) exists a wide eye field, too, and I do not want to exclude relationships to this genus, in which a distinct sexual size dimorphism exists. Uloboridae are cribellate spiders in which the femora bear trichobothria like in the Tetragnathidae: Leucauginae in contrast to the ecribellate Nephilidae.

**Distribution:** Eocene Baltic amber forest.

Family **ARANEIDAE**

The Eocene member of this family in Baltic amber were treated by WUNDERLICH (2004: 978–997) and (2011: 103–107). Here I describe a remarkable female which may be the member of the extant genus *Araneus* CLERCK 1757 or related to it.

?*Araneus* sp. (fig. 18) (compare fig. 19), photo 9

**Material:** 1 inad. ♀ in Eocene Baltic amber, F2323/BB/AR/CJW.

**Preservation:** The spider is completely and fairly well preserved in a heated and darkened piece of amber which is up to 3.5 cm long. Some bubbles are preserved on the spiders opisthosoma.

**Syninclusions:** See above, Nephilidae indet.

**Description** (inad. ♀):

Measurements (in mm): Body length 10.5, prosoma: Length 4.5, width 4.0, opisthosoma: Length 7.0, width 7.7; leg I: Femur 4.8 (height 1.3), patella and tibia ca. 3.2, leg II: Tibia 2.8, metatarsus 3.0, tarsus 1.2.

Colour medium grey.

Prosoma not much longer than wide, cephalic part posteriorly very high compared to the low thoracic part, bearing longer hairs, fovea low, eyes (fig. 18, photo 9) small, field very wide, position of the lateral eyes far from the medians, clypeus short, basal cheliceral articles stout, other mouth parts hidden. – Claw of the pedipalpus well developed, bearing several long teeth. – Legs stout, bearing numerous thin (!) bristles, tibia I bears more than a dozens ones. – Opisthosoma 1.1 times wider than long, bearing numerous short hairs and a pair of widely spaced humps in the anterior half (photo).

**Relationships:** The anterior median eyes are probably slightly larger than the posterior median eyes, and so the female may be a member of the extant genus *Araneus* CLERCK 1757 but not of *Gibbaranea* ARCHER 1951. In the female of ?*Araneus* sp. indet. in Baltic amber – see WUNDERLICH (2004: 983, fig. 47) – exists also a pair of opisthosomal humps but the body length of that female is only 4.5 mm. An extant male of the genus *Araneus* is shown in fig. 19. A fossil male is needed for a more close determination. – The juv. female of *Araneus defunctus* PETRUNKEVITCH 1958 is only 3.43 mm long.

**Distribution:** Eocene Baltic amber forest.

Family **MIMETIDAE: Subfamily Mimetinae**

Remark: The Subfamily Protomimetinae WUNDERLICH 2011 (p. 522) in Baltic amber (extinct, Eocene) has been provisionally regarded as a taxon of the Mimetidae.

Baltic amber fossils of the spider eating mimetids – members of the diverse genus *Ero* C. L. KOCH 1837 (8 species) and of the the rare members of the genus *Mimetus* HENTZ 1832 (only 2 species are known) – has been treated at last by HARMS & DUNLOP (2009) and WUNDERLICH (2004: 1260–1278) as well (2011: 526–531), some extant members of *Ero* by THALER et al. (2004).

HARMS & DUNLOP tried to revise members of *Ero* in Baltic amber, ignoring the chaetotaxy of the spiders, without giving a key to the species or a drawing of a bulbus in the important ventral aspect, see the figs. 33 and 35 in the present paper. *Ero aberrans* PETRUNKEVITCH 1958 has mistaken by these authors as a nomen dubium, see below, and a species of *Mimetus* has been erroneously synonymized, see below. During the last years I got new material of *Ero* in Baltic amber, including three new species which are described below; these species are based on excellently preserved males which possess very well observable structures of body, legs and pedipalpi. This new material and the errors of the revision – see above – stimulated me to carry out the present revision.

*Mimetus longipes* WUNDERLICH 2004 and *M. brevipes* WUNDERLICH 2004 (sp. resurr.)

Remarkably HARMS & DUNLOP – 2009: p. 779 within the abstract and p. 796 – synonymized *M. brevipes* with *longipes*, but p. 795 the same authors wrote “both species are probably <!> conspecific.”. These authors mistook the name of the species – it was given after its legs (leg Latin = “pes”), see WUNDERLICH (2004: 1263): the diagnosis of the species – for its pedipalpal articles, although legs and pedipalpi are well-known different kinds of extremities. (*M. longipes* has longer legs than *brevipes* but has a relatively shorter pedipalpal tibia). Furthermore HARMS & DUNLOP did not discuss (or even note) the quite different number of cheliceral “peg teeth” of both species. The authors published the synonymy of these species although they noted that the structures of the bulbus can not compared in all aspects. Therefore the synonymizing of these species appears not at all justified, and the name *Mimetus brevipes* is revived here (sp. resurr.). See WUNDERLICH (2011: 528).

*Ero* C. L. KOCH 1837

The taxonomical situation of this genus is difficult, and although a worldwide revision has not been carried out, HARMS & DUNLOP (2009) synonymized the fossil genera *Succinero* WUNDERLICH 2004 and *Palaeoero* WUNDERLICH 2004 with *Ero* C. L. KOCH 1837. In the generotype of *Ero* – *Ero tuberculata* (DE GEER 1775) – and the related European species exist lateral stridulatory cheliceral files, see WUNDERLICH (2004: 1271, fig. 2) as well as opisthosomal humps in contrast to all known fossil species of “*Ero*” in Baltic amber. Furthermore tiny cymbial/paracymbial cusps exist in the fossil species (see e. g. figs. 31–32).

Because of the unknown important ventral aspect of the bulbi in most fossil species in Baltic amber – and lacking a worldwide revision of the species described under *Ero* – I am quite unsure about the synonymy of *Succinero* and *Palaeoero* with *Ero*, and I regard both provisionally as subgenera of *Ero* s. l. (**n. stat.**).

Note on *Ero aberrans* PETRUNKEVITCH 1958: Remarkably in the revision of *Ero* by HARMS & DUNLOP (2009) the valid species *Ero aberrans* is not treated within the species of *Ero*, but (p. 796) – due to the bad condition of the partly oxidated holotype – under “Nomina dubia”. These authors stated in the abstract that the holotype “lacks useful taxonomically characters” although fig. 2A p. 789 (figs. 20–23 in the present paper) shows important taxonomical characters of the ♂-pedipalpus with a distinctive large and pointed distal tegular apophysis in contrast to related species. PETRUNKEVITCH (1958) noted in his useful and clear-cut original diagnosis of this species that (a) metatarsus II lacks short spines between the long prolateral bristles (\*) (fig. 23 in the present paper) (compare the existence of short spines on metatarsus I, fig. 22), and (b) that the shape of the pedipalpal tibia is club-shaped (fig. 20 in the present paper).

The fig. 2A given by HARMS & DUNLOP of the holotype of *E. aberrans* (= fig. 21 in the present paper) is quite similar to fig. 4a of the holotype which was published by WUNDERLICH (2004: 1272). In both figures of the – right – male pedipalpus the tibia is NOT club-shaped (fig. 21) in contrast to the left pedipalpus (fig. 20) in which it is clearly club-shaped. The simple reason for this difference according to my investigation of the holotype: Its right pedipalpal tibia is deformed in contrast to the left tibia.

Remark: A fairly bad condition of a holotype cannot justify the assignment to a dubious species, especially not in the case in which the genital structures are partly well preserved.

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(\* ) The (in *Ero*) unusual absence of such short bristles was apparently the reason for naming the species “*aberrans*”.

### Key to the fossil species of the genus *Ero* s. l. in Eocene European ambers (♂):

Remarks: The most frequent species is *carboneana*. The only known species of the Ukrainian Rovno amber is *rovnoensis*. – The determination – even of males – is quite difficult because (a) usually their pedipalpi cannot be compared in the same position, and (b) the structures of the bulbus are only rarely observable in the important ventral aspect, see figs. 33 and 35.

- 1 Tarsus I almost twice as long as metatarsus I (fig. 24). Pedipalpus: Fig. 25; tibia only as long as wide . . . . . longitarsus (WUNDERLICH 2004)
- Tarsus I about as long as metatarsus I. Pedipalpal tibia (figs. 20, 27, 31) about 2–3½ as long as wide . . . . . 2
- 2(1) Pedipalpus: Fig. 27. Rovno (Ukrainian) amber . . . . . rovnoensis (WUNDERLICH 2004)
- Pedipalpus different (e. g. figs. 28, 31). Not Ukrainian amber. . . . . 3
- 3(2) Pedipalpus (fig. 26): Paracymbium long, slender, erect and thickened near its end, tibia about 3 ½ times longer than wide, distal tegular apophysis pointed dorsally. Most frequent species of *Ero* in the Baltic amber forest. . . . . carboneana PETRUNKEVITCH 1942
- Pedipalpus (fig. 30–33): Paracymbium low, tibia also 3 ½ times longer than wide . . . . . gracilitibialis n. sp.
- Pedipalpus (figs. 20–21, 28–35): Paracymbium different, tibia 2–2 ½ times longer than wide, more or less thickened in the distal half. . . . . 4
- 4(3) Pedipalpus (figs. 29–30): Paracymbium complicated, long and elevated, ventral aspect of the bulbus unknown, tibia less thickened distally . . . . . clunis n. sp.
- Pedipalpus (figs. 20–21, 28, 31–35): Paracymbium more simple, low or elevated (in *aberrans*), tibia stronger thickened in the distal half, club-shaped . . . . . 5
- 5(4) Tibia and metatarsus of only the first pair of legs provided with short curved spines between the long prolateral bristles (fig. 22) which are typical for the family Mimetidae, in contrast to the second leg (fig. 23). Pedipalpus (figs. 20–21): Bulbus with a large and pointed distal tegular apophysis (DS) . . . . . aberrans PETRUNKEVITCH 1958
- Tibia and metatarsus of legs I AND II provided with short curved spines between the long prolateral bristles (as in fig. 22). Pedipalpus (figs. 28, 34–35): Bulbus without such a large and pointed distal tegular apophysis . . . . . 6
- 6(5) Pedipalpus (figs. 34–35): Cymbium with a retrolateral outgrowth near the paracymbium (O in fig. 34), paracymbial lateral lobe convex apically . . . . . veta n. sp.
- Pedipalpus (fig. 28): Cymbium – according to HARMS & DUNLOP – without such an outgrowth, paracymbial lateral lobe straight or even concave apically . . . . . permunda PETRUNKEVITCH 1942

## **Descriptions of the new species of *Ero*:**

***Ero (Succinero) clunis* n. sp.** (fig. 29–30) photo 10

The name of the species points to its club-shaped (Latin = clunis) pedipalpal tibia.

**Material:** Holotype (♂) in Eocene Baltic amber and 3 separated pieces of amber, F2029/BB/AR/CJW.

**Preservation and syninclusions:** The spider is very well preserved in a clear yellow piece of amber which was slightly heated; the left side of the prosoma below the peltidium and of leg articles are covered with a white emulsion, parts of the left side of the opisthosoma are cut off. – Thin spiders threads exist between some leg articles, numerous particles of detritus are also preserved.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (figs. 29–30): Tibia about 2.3 times longer than wide, paracymbium large, high and complicated, bearing a large lateral lobe.

### **Description** (♂):

Measurements (in mm): Body length about 3.0, prosoma: Length 1.5, width 1.2, height 0.7; leg I: Femur 2.6, patella 0.65, tibia 2.7, metatarsus 2.1, tarsus 1.4, tibia II 2.1, tibia III 1.1, tibia IV 1.5.

Colour mainly yellowish brown, legs annulated, prosoma bearing a pair of light brown longitudinal bands in some distance of its margin.

Prosoma (photo) smooth, high, profile distinctly convex, fovea well developed and almost circular, eyes large, anterior medians largest and protruding, posterior row procurved, posterior medians spaced by ca. 3/4 of their diameter. Clypeus concave, distinctly longer than the field of the median eyes, basal cheliceral articles fairly large, lateral files absent, fangs fairly long, other mouth parts hidden. – Legs long and slender, order I/II/IV/III, hairs indistinct, bristles long and numerous, femur I and IV bear 7 bristles, all patellae dorsally 1/1, tibia I with 7 long bristles, short spines between them, metatarsus I with 8 long bristles, some hair-shaped between them. Position of the metatarsal I trichobothrium just before the end of the article. – Opisthosoma egg-shaped, hairs short and indistinct, spinnerets short. – Pedipalpus (figs. 29–30) with a long and slender femur, a short patella which bears a long dorsal-distal bristle, tibia distinctly widened in the distal half, ca. 2.3 times longer than wide, bearing some bristle-shaped hairs and 3 or 4 trichobothria, paracymbium large, high and complicated, its lateral lobe large, distal tegular apophysis blunt, not strongly protruding.

**Relationships:** See the key to the fossil species. In *E. permunda* the pedipalpal tibia (fig. 28) has a similar shape but the paracymbium and its lobe are smaller and lower, the shape of the lobe is different.

**Distribution:** Eocene Baltic amber forest.

***Ero (Succinero) gracilitibialis* n. sp.** (figs. 31–33) photos 11–13

The name of the species points to the slender pedipalpal tibia (*gracilis* Latin = slender).

**Material:** Holotype in Eocene Baltic amber, F2352/BB/AR/CJW.

**Preservation and syninclusions:** The spider is very well preserved in a small yellowish piece of amber, a white emulsion exists on the right side of the prosoma and few leg articles, the right tarsus and metatarsus I are cut off, the left legs I and II are cut off beyond their femur resp. patella. – A mite, a Nematoda: Rhabditida and a stellate hair are preserved below the spider, some thin spiders threads are preserved near to the spider.

**Diagnosis** (♂; ♀ unknown): Legs very long, pedipalpus (figs. 31–33): Tibia ca. 3 ½ times longer than wide, apically-ventrally with complicated apophyses, bulbus oval, distal tegular apophysis short.

**Description** (♂):

Measurements (in mm): Body length 3.2, prosoma: Length 1.6, width 1.2, height 0.5; leg I: Femur 3.0, patella 0.7, tibia ca. 3.3, leg II: Tibia 2.7, metatarsus 2.2, tarsus 1.1, tibia III 1.2, tibia IV 1.7; longest bristle on tibia III 0.95.

Colour mainly light grey brown, legs apparently annulated, prosoma bearing a pair of wide dark brown lateral bands.

Prosoma (photo) 1.3 times longer than wide, few hairs, fovea hidden, eyes large, similar to *E. veta* n. sp., but posterior median eyes spaced by their diameter, clypeus long, basal cheliceral articles long, fused basally, lateral files absent, peg teeth long, gnathocoxae and labium long, coxae IV spaced by the sternum by less than their diameter. – Legs (photo) very long and slender, order I/II/IV/III, bristles long and numerous, femur I and IV bear 6–7 bristles, tibia I bears 13 bristles, all metatarsi bear a trichobothrium, its position on IV in 0.9. – Opisthosoma oval, hairs fairly long, spinnerets short, genital area with a transverse row of long epiandrous spigots. – Pedipalpus (figs. 31–33, photo): Femur long and slender, patella short, bearing a long dorsal-distal bristle, tibia slender, 3 ½ times longer than wide, bearing 4–6 (?) trichobothria, cymbium and paracymbium finely corniculate like in related species, paracymbium with a rounded basal part, its lobe large, bulbus oval, distal tegular apophysis relatively small, embolus originating at the basal part of the bulbus, describing half of a circle, distally hidden by a conductor.

**Relationships:** See the key to the species. The pedipalpal tibia is as long as in *E. carboniana*.

**Distribution:** Eocene Baltic amber forest.

***Ero (Succinero) veta* n. sp.** (figs. 34–35) photos 14–16

Derivatio nominis: The species is dedicated to MARIUS VETA in Palanga (Lithuania) who sent me the holotype.

**Material**: Holotype ♂ in Eocene Baltic amber (most probably from the Kaliningrad area), F2353/BB/AR/CJW.

**Preservation and syninclusions**: The spider is excellently and almost completely preserved in a small clear yellowish piece of amber which was fairly heated, a white emulsion is absent except the right ventral part of the opisthosoma, the tips of all left tarsi are cut off as well as the right tarsus II and half of its metatarsus, and parts of the left patella I. – Small bubbles are preserved on some leg articles, stellate hairs are absent.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (figs. 34–35): Tibia 2.25 times longer than wide, distinctly thickened in the distal half (almost club-shaped), cymbium with an indistinct outgrowth near the paracymbium, shape of the bulbus circular, subtegulum with a large retrobasal outgrowth, tegular apophysis large.

**Description** (♂):

Measurements (in mm): Body length ca. 3.5, prosoma: Length 2.0, width 1.5; leg I: Femur 2.6, patella 0.8, tibia 2.8, metatarsus 2.6, tarsus 1.5, tibia II 2.0, tibia III 1.35, tibia IV 1.6.

Colour (photo): Prosoma and legs dark brown (darkened by heating), opisthosoma light grey brown.

Prosoma 1.3 times longer than wide, covered with few longer hairs, fovea deep and circular, eyes fairly large, anterior median eyes weakly protruding, posterior row procurved, posterior median eyes spaced by less than their diameter, clypeus long, basal cheliceral articles slender, lateral files absent, “peg teeth” long, fangs hidden, position of the gnathocoxae parallel, labium probably about as long as wide, coxae IV spaced by the sternum by less of their diameter. – Legs long and slender, order I/II/IV/III, hairs indistinct, bristles long and numerous, femur I and IV bear 6–7 bristles, tibia I with 11 long bristles, metatarsus I with 5 long prolateral bristles and short spines between them, position of the metatarsal trichobothria unknown. – Opisthosoma egg-shaped, hairs fairly long, spinnerets short, photo 16. – Pedipalpus (fig. 34–35, photo 15): Femur long and slender, patella short, bearing a long bristle, tibia 2.25 longer than wide, almost club-shaped, bearing at least 3 trichobothria; cymbium, paracymbium and bulbus: See the diagnosis.

**Relationships**: See the key; *E. permunda* is most related.

**Distribution**: Eocene Baltic amber forest.

## Relationships of the family Mimetidae s.str. (= Mimetinae sensu WUNDERLICH (2011: 528)):

Certain former (and few recent) authors regard the Mimetidae as related to the haplogyne (!) Palpimanidae, superfamily Arachaeoidea/Palpimanoidea in which a capture web is absent like in the Mimetidae, the chelicerae bear “peg teeth” – like certain Theridiidae (*Borneoridion* WUNDERLICH 2011), and certain Thomisidae as well –, and the spiders of both taxa feed on spiders. On the other hand the Mimetidae are entelegyne and possesses a retrobasal paracymbium which is a basic character of the superfamily Araneoidea s. str. (the ecribellate branch). The “triad complex” of the spinnerets – a further important character of the ecribellate Araneoidea s. str. – has been lost in the Mimetidae – apparently in connection with the loss of the capture web.

The unique kind of the capture web of the basal Araneoidea s. l. (e. g. of the ecribellate Araneidae and the cribellate Uloboridae), THE ORB WEB, is an old and apomorphic character of this superfamily (\*), and has completely been lost several times (e. g. in the Mimetidae, in adults of *Pachygnatha* (Tetragnathidae), and several times in the Theridiidae like most Argyrodinae and Hadrotarsinae or has been “changed” to (replaced by) so-called “irregular” types of capture webs. This “changings” happened one or two times within the ecribellate Araneoidea; it is known (a) in the “spineless femur clade”, and (b) in the “linyphioid branch” sensu WUNDERLICH (2008: 118).

It would be of interest to know if the family Mimetidae is more related to branch (a) or (b) – or (c) to orb weavers like Araneidae, Nephilidae, Tetragnathidae, Theridiosomatidae, and Zygeliidae. The possibility (c) is not closely discussed here except the Theridiosomatidae, see the end of the discussion.

Discussion of the mimetid relationships:

– Long and strong bristles exist on femora, tibiae laterally and metatarsi in the Mimetidae as in almost all members of branch (b) but not in members of branch (a).

– Lateral cheliceral stridulatory files exist in certain taxa of the Mimetidae and are frequent in taxa of branch (b) but are totally absent in branch (a) (and in (c) with extremely rare exceptions).

– A sickle-shaped retrobasal paracymbium in a position close to the cymbium exists in (b) in contrast to (a) (and most (c)).

– In the Mimetidae the kind of leg autotomy between patella and tibia (\*\*) – which is frequent in members of branch (b) – is absent; in branch (a) exists an autotomy between coxa and trochanter like in most (c) (absent e. g. in the Tetragnathidae and in the Theridiosomatidae; see below and WUNDERLICH (2004: 148), Beitr. Araneol., 3).

– In the genus *Chthonos* CODDINGTON 1986 of the orb-web building family Theridiosomatidae exist rows of conspicuous long prolateral bristles on tibiae and metatarsi I–II, but short curved spines between these bristles – as well as cheliceral peg teeth – are absent. *Chthonos* is not a basal genus of the Theridiosomatidae. I regard the long leg bristles as convergently evolved, and both taxa most probably as not closely related. Similar strong prolateral bristles of the anterior legs exist in certain Theridiidae, too.

Putting together the pattern of these characters it appears likely to me that the family Mimetidae may be (a) more closely related to the “linyphioid branch” than to the “spineless femur clade”. (b) According to the chaetotaxy and leg autotomy the orb-web building family Tetragnathidae could well be most closely related to the Mimetidae.

Hopefully findings regarding (e. g.) structures of the spermatozoa and of genetic characters will help to answer the questionable relationships definitely. Such investigations are in progress by several authors.

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(\* ) Orb-building taxa are known already from the Jurassic. The oldest report of the family Mimetidae comes from the Tertiary Palaeogene, the Eocene.

(\*\* ) Probably a leg autotomy is completely absent in this family.

Family **LINYPHIIDAE**, subfamily Linyphiinae

The members of this family in Baltic amber were treated by WUNDERLICH (2004: 1298–1373). Here I add the descriptions of males of two further taxa.

***Paralabulla* sp. indet.** (fig. 36)

**Material:** 1♂ in Baltic amber from the Bitterfeld deposit, F 2301/BB/AR/CJW. Two tiny mites are preserved in the same piece of amber.

The body of the spider is only fairly well preserved, 1.5 mm long. Fig. 36 shows the apical aspect of the left pedipalpus with its embolus and conductor in an almost spiral position. The male may be the member of an undescribed species of the genus *Paralabulla* WUNDERLICH 2004.

?***Eophantes seorsum* n. sp.** (figs. 37–40) photos 17–18

Etymology: Seorsum (Lat.) means to be special.

**Material:** Holotype ♂ in Eocene Baltic amber, F2321/BB/AR/CJW.

**Preservation and syninclusions:** The spider is completely and very well preserved in a small yellow-orange piece of amber which was slightly heated; weak white emulsions exist anteriorly on the body, a large bubble on the opisthosoma. – Several stellate hairs and bubbles are also preserved.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (figs. 37–40): Patella bearing a very long bristle, cymbium with two dorsal-basal humps, questionable lamella characteristica very long and undivided, questionable embolus fairly long, suprategular structures very complicated.

**Description** (♂):

Measurements (in mm): Body length 1.8, prosoma: Length 1.0, width 0.9; leg I: Femur 1.1, patella 0.25, tibia ca. 1.2, metatarsus 1.15, tarsus 0.85, tibia III 0.7.

Colour: Prosoma and legs medium brown, opisthosoma light brown.

Prosoma (photo 17) 1.1 times longer than wide, hairs indistinct, fovea well developed, eyes fairly large, posterior row slightly procurved, posterior median eyes spaced by less than one diameter, clypeus about as long as the field of the median eyes, basal cheliceral articles fairly large and slender, lateral files widely spaced, fangs long, its furrows toothed, labium free, rebordered, wider than long, coxae IV spaced by almost their diameter. – Legs long and slender, order I/IV/II/III, bristles long and thin: Femora 1 dorsally (near the middle on I, in the basal half on III), I additionally with a prolateral one in the distal half, patellae dorsally 1/1 (the basal one quite short), tibiae dorsally 1/1, I–II additionally 1 ventrally near the middle as well as a lateral pair in the distal half. Position of the metatarsal I trichobothrium in 0.17. – Opisthosoma long oval, covered with few short hairs. – Pedipalpus (figs. 37–40, photo 18): Patella and tibia short, both bearing a long dorsal bristle, tibia bulging ventrally in the basal half, cymbium wide, dorsally-basally with a divided and finely corniculate outgrowth, paracymbium long, simple, without outgrowth, suprategulum complicated, bearing several apophyses, a longer conductor and an embolus (?) which is free observable in its distal part and bent.

**Relationships:** Probably a member of the genus *Eophantes* WUNDERLICH 2004. In *E. complicatus* WUNDERLICH 2004 in Baltic amber the bristle of the pedipalpal patella is much shorter, the lamella characteristica is divided, short and strongly bent, the structures of the ♂-pedipalpus are quite different except the long and simple paracymbium; both species are probably not congeneric.

**Distribution:** Eocene Baltic amber forest.

Family **PRAETHERIDIIDAE** (n. stat.)

From the tribe Praetheridiini WUNDERLICH 2004 of the family Protheridiidae WUNDERLICH 2004

The find of a second male of the monotypic type genus *Praetheridion* WUNDERLICH 2004 in the Eocene Baltic amber – F2273/BB/AR/CJW – allows a closer study of the relationships of this remarkable genus and the extinct monotypic family Praetheridiidae as well.

I found only two male specimens among ten thousands of adult males. Why is this species so extremely rare in Baltic amber? Has it been photophilous, living in a sunny area outside the amber forest?

***Praetheridion fleissneri*** WUNDERLICH 2004: 1141–1142, 1153–1154, figs. 35–40, photo 188.  
Photos 19–20.

The male spider – F2273/BB/CJW – is well preserved in a piece of amber which is 4.2 cm long and was heated. Few thin spider's threads exist, too; one of them is in contact to the tip of the left tarsus II. These threads are probably part of the capture web of the spider; sticky droplets are absent.

The right leg I and the left legs I and IV of the spider are lost beyond the coxa by autotomy, both bulbi are slightly expanded. Measurements (in mm): Body length 2.1, prosoma: Length 1.0, width 0.8; tibia II 1.1, tibia IV 1.0.

In the extinct family Protheridiidae – preserved in Eocene Baltic amber – were originally included:

(a) the monotypic tribe Protheridiini (type genus *Protheridion* WUNDERLICH 2004, 5 species), and

(b) the monotypic tribe Praetheridiini WUNDERLICH 2004 (only *Praetheridion fleissneri* WUNDERLICH). This tribe is excluded now from the family Protheridiidae, see below. Later on

(c) the monotypic tribe Zarqaraneini WUNDERLICH 2008 from the Lowest Cretaceous Jordan amber were added with some hesitation to the family Protheridiidae in which the paired tarsal claws are smooth, too, a long clypeus, a convex profile of the prosoma, and a large erect paracymbium exist as well; metatarsal bristles are absent as in the Praetheridiini. The structures of the bulbus are insufficiently preserved and apparently quite different from the other two tribes, and close relationships are still unsure. A similar cymbial “horn” exists in certain Tetragnathidae.

Both nominal tribes of the family Protheridiidae in Baltic amber were united by a relative long clypeus (about as long as the field of the median eyes), numerous thin leg bristles (including femoral and – in *Protheridion* – metatarsal and tarsal ones, too), smooth paired tarsal claws (in the present male of *Praetheridion fleissneri* I found a single tooth, a large fused paracymbium, a coxa-trochanter autotomy, and the absence of cheliceral stridulatory files. – These two taxa may represent a third – ancient and extinct – branch of the ecribellate Araneoidea which are not orb-weavers, besides the “linyphiid branch” (in this branch exist basically a coxa-trochanter autotomy and cheliceral stridulatory files), and the “spineless femur clade” in which femoral, metatarsal and lateral tibial bristles are absent.

Upgrading: Because of the great morphological differences and differences in the structures of the male pedipalpus I elevate the tribe Praetheridiini WUNDERLICH 2004 to the family rank (**n. stat.**), and regard the Praetheridiidae and the Protheridiidae as related but different families. The type genus is *Praetheridion* WUNDERLICH 2004.

**Revised diagnosis of the upgraded family Praetheridiidae** (♂; ♀ unknown): Metatarsal and tarsal bristles absent, paired tarsal claws with a single tooth only, paracymbium standing out in a right angle, bulbous with a basal and a distal tegular apophysis, a large conductor, and a quite long embolus, see WUNDERLICH (2004: 1154, fig. 39).

Further characters: Coxa-trochanter autotomy, clypeus as long as the field of the median eyes, prosomal profile not convex, cheliceral stridulatory files absent legs and their bristles long and slender, sustentaculum absent, paired tarsal claws apparently with a single tooth, accessory (auxiliary) hairs thin, paracymbium fused to the cymbium.

Basic patterns are the characters of the ecribellate branch of the superfamily Araneoidea.

**Relationships**: In the Protheridiidae the prosomal profile is convex (similar to most Cyatholipidae), the legs and the leg bristles are fairly stout, ventral metatarsal and tarsal bristles as well as a sustentaculum exist, the unpaired tarsal claw may bear a small tooth (fig. 41), tibia of the male pedipalpus strongly elongated, cymbium small, bearing an erect paracymbium, tegulum with a large retrolateral apophysis, conductor large and denticulate, see WUNDERLICH (2004: 1150–1152, figs. 18–32).

**Distribution**: Eocene Baltic amber forest.

## Family **DICTYNIDAE**

Remark on *Chelicirrum stridulans* WUNDERLICH 2004: 1434, 1473, figs. 85–92:

A very well preserved male of this enigmatic taxon, F2375/BB/AR/CJW, which I studied recently, lead me to new conclusions (a revision of the species is in preparation):

- (1) The divided “paracymbium” is more likely an apophysis of the pedipalpal tibia;
- (2) the “conductor” may well be a median apophysis similar to the genus *Anuvinda* of the family Titanoecidae. This divided structure (see fig. 91 in the original description) is quite typical for this taxon.

## Family **ZOROPSIDAE s. l.**

(a) Tribe **Eoprychiini** WUNDERLICH 2004

Three species of the genus *Eoprychia* PETRUNKEVITCH 1958 – the only known genus of the tribe – were treated by WUNDERLICH (2004: 1509–1512); the female of the genus has been unknown, *E. succini* is not so rare as the remaining species. Besides the adult female (see below) I got the following spiders during the last few years which all may be members of *E. succini*: A juvenile female, F 2326/BB/AR/CJW, body length 5.8 mm; three males: F1655/BB/ AR/CJW body length 10 mm; F2324/BB/AR/CJW, body length 6.8 mm. The tarsal claws of the left leg III are well observable, an unpaired claw is absent; F2325/BB/ AR/CJW, body length ca. 6 mm.

***Eoprychia ?succini*** PETRUNKEVITCH 1958 (fig. 42) photos 21–22

**Material:** 1♀ in Eocene Baltic amber, embedded in artificial resin, private coll. of FRIEDRICH KERNEGGER in Hamburg.

The body length of the completely preserved spider is 10 mm, mainly dorsally it is covered with a white emulsion, the claw of the pedipalpus bears several short teeth, the spinnerets and the large divided cribellum are well observable (photos 21–22). The calamistrum is a well developed field, the epigyne (fig. 42) is distinctly wider than long, a pair of questionable receptacula seminis is observable, a pair of sickle-shaped structures and a large anterior pair of indistinct depressions exist, too.

(b) Tribe **Eomatachiini** WUNDERLICH 2004

### **Succiniropsis** WUNDERLICH 2004

The gender of the name of the genus is feminine.

Members of the extinct genus *Succiniropsis* are rare, small and cribellate spiders; their tibiae possess a basal suture, see WUNDERLICH (2004: 1519, fig. 27) which may be quite indistinct in fossils. The larger members of the related genus *Eomatachia* PETRUNKEVITCH 1942 are not rare in Baltic amber.

In 2004 I described two species of the genus; here a third species is added.

### ***Succiniropsis runcinata* n. sp.** (figs. 43–45) photo 23

The name of the species points to the incomplete (planed) dorsal parts of its body, from latin runcinare = plane.

**Material:** Holotype ♂ in Eocene Baltic amber, F2357/BB/AR/CJW.

**Preservation and syninclusions:** The spider – except its pedipalpi – is badly and incompletely preserved in a piece of amber which was heated and put in Benzylum benzoicum for a short time. Most ventral parts of the spider are covered with a white emulsion. The dorsal parts of prosoma and opisthosoma have been cut off on the previous surface of the fossil resin before the spider was embedded finely by a further flood of the resin. The left legs are complete, several parts of the right legs are lost, articles of two legs are preserved right in front of the spider, the right leg III is complete. A small mite, remains of an oxidated insect and some bubbles are preserved in the same piece of amber.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (figs. 43–45) The tibia bears 3 large(r) apophyses, the prolateral one is the largest, the median one is of medium length, the bulbus is strongly protruding.

**Description** (♂):

Measurements (in mm): Body length 2.6, prosomal length 1.4; leg I: Tibia 1.15, metatarsus 0.9, tarsus 0.6, tibia IV 0.9.

Colour dark brown (darkened by heating).

Prosoma: Most parts are cut off or hidden. – Legs fairly stout, I and IV longest, III distinctly shortest; bristles (most are hidden) slender, tibia I bears ventrally apparently a single pair. The tibial suture is well observable at the left tibia I. Tibia IV is straight, the hairs of the calamistrum in the basal half are short. Scopulae, metatarsal preening comb and claw tufts are absent. The paired claws bear long teeth; unpaired claw existing but difficult to observe. – Opisthosoma (photo 23) oval, hairs short, anterior spinnerets stout, I did not find median spinnerets which may be absent. Cribellum deformed, wide. – Pedipalpus: See the diagnosis; embolus unknown.

**Relationships:** In *S. kutscheri* WUNDERLICH 2004 and *S. samlandica* WUNDERLICH 2004 (which is most related) the bulbus is much less bulging, and the padipalpal tibial apophyses are different. The body length of these species is only 1.7–1.8 mm.

**Distribution:** Eocene Baltic amber forest.

Family **SUCCINOMIDAE** WUNDERLICH 2008 (**n. stat.**)

In this chapter I will combine two previously described genera (which were based on material which is not well and only incompletely preserved) to the new family Succinomidae (**n. stat.**) In 2008 I regarded these taxa as members of different families and superfamilies: *Eohalinobius* WUNDERLICH 2008 (?Lycosoidea), and *Succinopus* WUNDERLICH 2008 (Zoridae/Liocranidae, Clubionoidea/Gnaphosoidea within the monotypic tribe Succinomini). I now consider the family Succinomidae as probably related to the families Ephalmatoridae (extinct) and Chummidae. These are three members of small cribellate and three-clawed families of the RTA-clade.

As pointed out by me previously (2008: 473) the type genus “*Eohalinobius* may be the member of an unknown extinct family.” The discovery of new material – including the identification of a cymbial outgrowth (arrows in the figs.) which is largely hidden in the single previously known specimen of this genus – indicates that these spiders do not fit in any of the described extant or fossil families. In the genus *Succinopus* the same cymbial outgrowth exists as well as the same raised thoracic elevation and fovea/fissure (fig. 62) like in *Eohalinobius*. The female of the family is still unknown and may be

recognized by the raised thoracic region and the strongly developed thoracic fovea/fissure.

Upgrading: The family Succinomidae (**n. stat.** & **n. relat.**) is elevated from the tribe Succinomini WUNDERLICH 2008: 502 which has previously been regarded by me as a member of the family Zoridae/Liocranidae.

Type genus: *Succinomus* WUNDERLICH 2008 of the type tribe Succinomini WUNDERLICH 2008: 502, the only known tribe of this family.

Further genus: *Eohalinobius* WUNDERLICH 2008: 472 which is regarded now as a member of the type tribe (**n. relat.**).

**Diagnosis of the family Succinomidae** (♂; ♀ unknown): Thoracic region strongly raised, bearing a large and deep fovea/fissure (fig. 62, photo 25), quite small anterior median eyes in contrast to the large remaining eyes (fig. 47). Pedipalpus (see the figs.): Cymbium with a large dorsal outgrowth in its distal half (straight arrows in the figs. 48, 54, 56), bulbus with two almost needle-shaped apophyses of the tegulum which stand widely out from the bulbus in an almost parallel position, and a long embolus which is widely looped.

Further characters: Prosomal cuticula usually furrowed, eyes not on humps, posterior eye row procurved (fig. 62), anterior margin of the fang furrow with teeth and long plumose hairs (fig. 47), condylus existing (fig. 47), labium free, gnathocoxae not converging, serrula existing, opisthosoma with a dorsal scutum at least in the male (fig. 57, photos), one, two or three pairs of spinnerets (figs. 51, 67, 75), colulus existing (fig. 51), trochantera not notched, patellar bristles existing, few long metatarsal and tarsal trichobothria (fig. 64), tibia I – II bearing pairs of ventral bristles close to the article (fig. 63), leg scopulae, claw tufts, metatarsal preening combs, and feathery hairs absent, insertion of the teeth of the paired tarsal claws medially, cymbium short besides the dorsal outgrowth (figs. 48, 54, 56, see the diagnosis), pedipalpal tibia with several apophyses, body length only about 3–5 mm, leg autotomy unknown, probably absent.

Basic characters: One pair of lungs, ecribellate, unpaired tarsal claw existing, metatarsi and tarsi bearing trichobothria.

**Relationships and phylogenetics:** The family is a member of the Trionycha of the RTA-clade; it does not fit in any of the families of this branch, see WUNDERLICH (2008: 472–473). According to several characters – the characters of the legs, the eyes, the plumose cheliceral hairs, the opisthosomal scutum, and the small body size – Succinomidae may be related to the families Chummidae JOCQUE 2001 (extant, South Africa) and Ephalmatoridae PETRUNKEVITCH 1950 (extinct, Eocene Baltic amber forest); main differences: See tab. 1. These three families may be related to the Dictynidae s. l. or to the Zodariidae or may be members of a branch of its own, probably of a – in the geological sense – very old branch of hunting spiders of the RTA-clade, members of the Trionycha which lost their cribellum and capture web, but still possesses their unpaired tarsal claw, which became extinct at the end of the Palaeogene, displaced probably by competitors like Corinnidae and Zoridae/Liocranidae.

According to the branched lateral tracheae and the reduced median and posterior spinnerets Chummidae has been regarded as related to the Zodariidae by JOCQUE (2001) although reduced median and posterior spinnerets are not so rare, and exist e. g. in the extant genus *Ablator* within the family Corinnidae besides the Chummidae and Succinomidae as well as in several Zodariidae. According to certain characters – like the plumose cheliceral hairs (fig. 47) Chummidae may be more related to the Dictynoidea than to the Zodariidae, but long tarsal trichobothria and an opisthosomal scutum are quite unusual in the Dictynidae.

Diversity and rarity: I know 6 species of 2 genera; every species is represented by only a single specimen. Thus Succinomidae apparently was a fairly diverse taxon in the Eocene but – because of its soil habitat, see directly below – its members got only rarely in contact with the fossil resin. The relative diversity of species and the rarity of specimens is remarkable and may indicate that the family Succinomidae has been a relict already in the Eocene.

**Ecology and behaviour**: Paired long ventral bristles in a position close to their articles of tibiae and metatarsi I–II (fig. 58) are common in ground living hunting spiders but not in spiders which construct capture webs. The reduction of the number of spinnerets contradicts the ability to construct a capture web (\*). A ground living life style would explain the rarity (see above) of these spiders in the fossil resin. (The probably related extant spiders of the family Chummidae are groundliving hunters). The thick bristles of legs III–IV in ?*Succinomus gibbosus* (fig. 65) may be in connection with dwelling in dense litter. – What may be the function of the strongly raised thoracic part (fig. 62, photo 25) and what may it contain?

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(\* ) From Eocene spiders in Baltic amber I know of such a strong reduction of the number of spinnerets also in *Ablator* PETRUNKEVITCH 1942 of the family Corinnidae and in male *Anniculus* PETRUNKEVITCH 1942 of the family Zodariidae. These spiders are not capture web building hunters, too, and also members of the RTA-clade; see also above.

**Distribution**: Eocene Baltic amber forest.

Character	Chummidae	Ephalmatoridae	Succinomidae
thoracic part	fairly low (fig. 62)	fairly low	strongly raised, fig. 62
fovea	absent	present	very deep, fig.62
leg bristles	absent	present	present
promarginal teeth of the fang furrow	present	absent	present
spinnerets	reduced medians and posteriors	three pairs	a single pair, fig.62, 2 or 3 pairs, fig. 51
pedipalpal articles	short	short	long, figs. 49, 70
cymbium	elongated	short	elongated erect outgrowth, figs. 49, 56
embolus	short/stout	long	long, fig. 54
genera	<i>Chumma</i>	<i>Ephalmator</i>	<i>Eohalinobius</i> , <i>Succinomos</i>
distribution	South Africa (extant)	Eocene Baltic amber forest	Eocene Baltic amber forest

Tab. 1. Differences of three families which may be related (♂).

Character	<i>Eohalinobius</i>	<i>Succinomos</i>
tibia I	more slender, bent, 2 pairs of ventral-distal bristles, fig. 58	straight, 4–5 pairs of ventral bristles, fig.63
distal femoral bristles	absent	present
spinnerets	3 pairs, fig. 51	large anteriors, reduced remainings, figs. 67, 75
colulus	large, wide, fig. 51	small, fig. 67
pedipalpal femur	hairy (normal)	spiny, fig. 68

Tab. 2. Differences of the Succinomidae genera *Eohalinobius* and *Succinomos* (♂).

**Succinomus** WUNDERLICH 2008

Type species (by monotypy): *Succinomus duomammillae* WUNDERLICH 2008.

**Diagnosis:** See tab. 2.

Further characters: See the family (above).

**Relationships:** See tab. 2.

**Distribution:** Eocene Baltic amber forest.

?*Succinomus gibbosus* n. sp. (figs. 62–74), photos 24–27

Etymology: The species name – from gibbus (lat.) – points to the strongly raised thoracic part of the spiders.

**Material:** Holotype ♂ in Eocene Baltic amber and a separated piece of amber, F2327/BB/AR/CJW.

**Preservation and syninclusions:** The spider is fairly well and almost completely preserved, parts of the right patella and tibia I–II are cut off, few ventral parts are covered with a white emulsion. – Three larger fissures exist in the piece of amber, astellate hair is preserved in the separated piece.

**Diagnosis** (♂; ♀ unknown): Median and posterior spinnerets absent (fig. 67), pedipalpus (figs. 68–74): Patella with a short and blunt erect dorsal spine, tibia with a long erect apophysis which is bent distally to the cymbium, ventral tegular apophysis wide basally.

**Description** (♂):

Measurements (in mm): Body length 3.0, prosoma: Length 1.7, width 1.6; leg I: Femur 1.7, patella 0.65, tibia 1.8, metatarsus 1.6, tarsus 0.45, tibia II 1.4, tibia III 0.8, tibia IV 1.45, pedipalpal femur 1.4.

Colour light brown, legs not annulated.

Prosoma (fig. 62, photos) almost as wide as long, finely furrowed, hairs very short, thoracic part strongly raised, posteriorly strongly inclined to a striking fissure. Eyes: Anteriors small (similar to *Eohalinobius hiddenseensis* n. sp., see the fig. 47), remainings large and not on humps, posterior row recurved, posterior median eyes spaced by

less than their diameter, posterior lateral eyes largest. Clypeus short, basal cheliceral articles of medium size, distal plumose hairs present similar to *Eohalinobius hiddenseeensis*, most mouth parts and parts of the sternum are hidden by a white emulsion, the gnathocoxae are not converging. – Legs (figs. 63–75) only fairly long, hairs not distinct; bristles numerous, femora dorsally 1–2, femur IV bears an additional retrobasal bristle, patellae dorsally 1/1 (small on I–II), III–IV with few additional dorsal bristles, tibia I–II bears 1/1 thin dorsal bristles and 5 long ventral pairs close to the article, metatarsus I bears 3 pairs of long bristles close to the article and a retrolateral one in the basal half, tibia III a ventral bristle, and – like tibia IV – a row of dorsal bristles which are longer basally, metatarsi III–IV with numerous ventral, lateral and dorsal bristles. The tarsi are distinctly bent and bear an unpaired claw. Scopulae, metatarsal preening combs and claw tufts are absent. – Opisthosoma (figs. 66–67) oval, with short hairs and a large scutum, colulus small, anal tubercle large, anterior spinnerets stout and two-segmented, no other spinnerets are observable. – Pedipalpus (figs. 68–74, see above) with a long, straight and spiny femur, patella blunt, bearing a short dorsal-basal bristle, tibia with a long, erect and bent apophysis distally of a longer bristle, additional retroventral apophyses are partly hidden, cymbium short, bearing a long dorsal outgrowth in the distal half (arrow in the figs.), tegulum with several short and long apophyses, a long and slender median apophysis and a basally wide ventral tegular apophysis, the embolus is hidden in this specimen.

**Relationships:** *Succinomos duomammillae* WUNDERLICH 2008 is probably congeneric but the differences are distinct: Reduced posterior spinnerets exist in *duomammillae*, the pedipalpal tibial apophyses are quite different, the embolus of *gibbosus* is unknown, the ventral aspect of the bulbus of *duomammillae* is unknown, too; a better preserved male of *duomammillae* is needed. In *duomammillae* exist four pairs of ventral tibial bristles, in *gibbosus* five.

**Distribution:** Eocene Baltic amber forest.

### *Eohalinobius* WUNDERLICH 2008

Type species (by monotypy): *Eohalinobius scutatus* WUNDERLICH 2008 (figs. 49–50).

**Diagnosis:** See tab. 2. Note: Tibia I bears two pairs of ventral bristles in the distal half in all known species which were not recognized by me (2008) in the type species.

Further characters: See the family above.

**Relationships:** See tab. 2.

**Distribution:** Eocene Baltic amber forest.

**Key to the species of the genus *Eohalinobius* (♂):**

- 1 Pedipalpal tibia dorsally-basally with a long, strong, and erect bristle which is strongly bent at his end besides a shorter bristle on a hump (fig. 49) . . . . . *scutatus*
- Pedipalpal tibia dorsally-distally with a similar bristle in the DISTAL half (fig. 61). . . . . *calectatus*
- Pedipalpal tibia dorsally-basally only with a short and straight bristle on a hump. (fig. 48) . . . . . 2
- 2(1) Retroventral tibial apophysis (fig. 48) with a distally distinctly widened ventral branch and a shorter and relatively wide dorsal branch . . . . . *hiddenseeensis*
- Ventral branch of the retroventral tibial apophysis not widened, dorsal branch long and slender (fig. 55). . . . . *patina*

***Eohalinobius patina* n. sp.** (figs. 51–56), photos 28–29

**Etymology:** The name of the species – patina (lat. = basin) – points to the artificial depression of the opisthosoma of the holotype.

**Material:** Holotype ♂ in Eocene Baltic amber, F2328/BB/AR/CJW.

**Preservation and syninclusions:** The spider is well preserved, especially the pedipalpi; several leg articles are cut off, 4 legs are complete, basal articles of both pedipalpi are partly cut off, the opisthosoma has a large dorsal artificial depression, a white emulsion is absent. – A tiny mite is preserved below the mouth parts of the spider, parts of a Diptera exist left of the spider, some stellate hairs and other plant parts are present in the small piece of amber which has been slightly heated.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (figs. 52–56, photos): Tibia retroventrally with a long and divided apophysis which has a long and slender dorsal branch and a ventral branch which is not widened distally.

**Description** (♂):

Measurements (in mm): Body length ca. 3.4, prosomal length ca. 1.5; leg I: Femur 2.0, patella 0.7, tibia 2.0, metatarsus 1.7, tarsus 0.55, tibia IV 1.8.

Colour light brown, legs not annulated.

Prosoma with a strongly raised thoracic part and a deep fissure similar to fig. 62, hairs short, cuticula furrowed; eyes (similar to fig. 47): Anteriors small, the remainings large, situated not on humps, posterior row distinctly recurved, similar to fig. 62, posterior lat-

eral eyes largest, posterior median eyes spaced by about their radius, clypeus longer than the diameter of the anterior median eyes, basal cheliceral articles and fangs each long and slender, plumose hairs as in *E. hiddenseeensis*, labium slightly wider than long, gnathocoxae longer than wide, not converging, serrula existing, coxae IV close together. – Legs fairly long, several bristles, tibia I not strongly bent, bearing 2 pairs of ventral bristles in the distal half; femora: a dorsal one in the basal half (distal/apical bristles are absent), patellae dorsally 1/1, tibia II ventrally with 5 pairs of long bristles close to the article, tibia III–IV 1/1 dorsally and 1 ventrally. Metatarsi I–II ventrally 3–4 pairs of ventral bristles close to the articles, metatarsi III–IV with several bristles. No scopulae, metatarsal preening combs or claw tufts, unpaired tarsal claw existing, tarsi and metatarsi probably all with two long trichobothria. – Opisthosoma oval, hairs short, dorsal scutum less than half of the opisthosomal length, colulus large, three pairs of spinnerets which are not reduced, anterior spinnerets stout (fig. 51). – Pedipalpus (figs. 52–56; see also the diagnosis): Dorsal cymbial outgrowth large, median apophysis more slender than the ventral tegular apophysis, two shorter tegular apophyses exist in a more distal position. Embolus long, describing probably two wide loops, hidden distally by the conductor.

**Relationships:** See the key to the species. *E. hiddenseeensis* is closely related.

**Distribution:** Eocene Baltic amber forest.

***Eohalinobius hiddenseeensis* n. sp.** (figs. 47–48), photos 30–32

**Etymology:** The species name points to the type locality of the species, the German island Hiddensee near Rügen.

**Material:** Holotype ♂ in Eocene Baltic amber, N-Germany island Hiddensee E Rügen, few km S Vitte, at the beach, FRIEDHELM EICHMANN leg. October 2006, coll. F. EICHMANN in Hannover, no. Ar 88.

**Preservation and syninclusions:** The spider is ventrally covered with a white emulsion, several leg articles are cut off, the right legs III–IV and the left legs I–III are complete. – Numerous hyphae are preserved on several leg articles, on the prosoma and near the spider. – Stellate hairs are also preserved and a mite behind the spider.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (fig. 48): Retroventral tibial apophysis (fig. 48) with a distally distinctly widened ventral branch and a shorter and relatively wide dorsal branch.

**Description** (♂):

Measurements (in mm): Body length 3.5, prosoma: Length 1.9, width 1.7; leg I: Femur 1.9, patella 0.8, tibia 2.0, metatarsus 2.0, tarsus 0.55.

Colour light brown, legs not annulated.

Prosoma (fig. 47, photos) like in *E. patina*, with a strongly raised thoracic part, anterior median eyes small (photo 32), most mouth parts and the sternum are hidden. The ante-

rior margin of the fang furrow bears at least one tooth. – Legs as far as observable as in *E. patina*. – Opisthosoma oval, dorsal opisthosomal scutum about 1/3 of the opisthosomal length. – Pedipalpus (fig. 48; see the diagnosis): Cymbium with a long dorsal-distal outgrowth, median apophysis and ventral tegular apophyses long and slender, embolus (most parts are hidden) long, similar to *E. patina*.

**Relationships:** See the key to the species.

**Distribution:** Eocene Baltic amber forest.

***Eohalinobius calefactus* n. sp.** (figs. 57–61)

The name of the species points to the heated piece of amber in which the holotype is preserved; latin calefactus = heated.

**Material:** Holotype ♂ in Eocene Baltic amber, F2356/BB/AR/CJW.

**Preservation and syninclusions:** The spider is almost completely preserved in a larger flat piece of amber which has been heated, and put in Benzylium benzoicum for a short time. The dorsal parts of the left patellae I and IV and the left tarsus III are cut off, a white emulsion covers the ventral side of the spider. – A Diptera, numerous bubbles, remains of plants and spiders threads are preserved in the same piece of amber.

**Diagnosis** (♂;♀ unknown): Pedipalpus (figs. 59–61) with a large and bent erect dorsal tibial apophysis in front of a larger and long dorsal bristle; two apical and apparently two dorsal-basal tibial apophyses exist additionally.

**Description** (♂):

Measurements (in mm): Body length 2.9, prosoma: Length ca. 1.5, width ca. 1.2; opisthosoma: Length 1.5, width 1.1; leg I: Tibia >2.1, metatarsus 2.0, tarsus ca. 0.5.

Colour dark brown (the spider is darkened by heating).

Prosoma (most parts are hidden) ca. 1.25 times longer than wide. – Legs (fig. 58, photo) only fairly long, IV longest, tibia I distinctly bent, hairs indistinct; bristles (some are hidden or broken off): Most femora (e. g. IV) with 1/1 dorsally, patellae dorsally 1/1, tibia I 2 ventral pairs in the distal half, metatarsus I at least 2 ventral pairs in the basal third, metatarsus II 5 ventral pairs, tibiae III–IV 1/1 dorsal bristles and at least a single ventral one; three tarsal claws. – Opisthosoma (fig. 57) 1.36 times longer than wide, with a larger dorsal scutum, spinnerets stout. – Pedipalpus (figs. 59–61; see the diagnosis) with a dorsal-distal, two apical and two dorsal-basal apophyses. Bulbus (most parts are hidden by a white emulsion) strongly bulging, embolus long.

**Relationships:** A special bent and large dorsal-apical apophysis exists in *calefactus* in contrast to the related species, and the strong tibial bristle has a more distal position near the base of the dorsal-distal apophysis than in the related species.

**Distribution:** Eocene Baltic amber forest.

## Family **EPHALMATORIDAE**

Most of the small members of the monogeneric extinct family Ephalmatoridae PETRUNKEVITCH 1950 were treated by WUNDERLICH (2004: 1559–1577). Five more males – including a questionable one of *E. ruthildae* – are kept in my private collection (CJW), e. g. F2305/BB/AR/CKW. Here I describe a further species of this family:

### ***Ephalmator tredecim* n. sp.** (figs. 76–77) photos 33–34

The Latin name points to the 13th known species of the extinct genus *Ephalmator* PETRUNKEVITCH 1950.

**Material:** Holotype ♂ in Eocene Baltic amber, F2206/BB/AR/CJW.

**Preservation and syninclusions:** The spider is completely and well preserved in a small yellow piece of amber which was slightly heated. A small fissure in the amber exists right behind the opisthosoma, ventrally exists a white emulsion. A tiny Nematoda: Rhabditida is preserved above the prosoma behind the left pedipalpal patella; a second specimen is preserved just behind the patella IV. A thin spiders thread originates on the tip of the right tarsus IV.

**Diagnosis:** Tibia I bears 3 pairs of ventral bristles, the dorsal scutum (fig. 76) covers almost half of the opisthosoma, pedipalpal tibial apophysis (fig. 77) slender, erect and pointed.

### **Description** (♂):

Measurements (in mm): Body length 2.15, prosoma: Length 1.0, width 1.0; leg I: Femur ca. 0.5, patella 0.27, tibia 0.58, metatarsus 0.47, tarsus 0.27; tibia II 0.48, tibia III 0.4, tibia IV 0.6.

Colour medium brown, opisthosomal scutum dark brown.

Prosoma (fig. 76, photos) as long as wide, relatively high, distinctly wrinkled, few hairs which are fairly short, thiracic fissure quite indistinct, eyes of medium size, all about the same size, posterior row fairly procurved, posterior medium eyes spaced by ca. their diameter, clypeus short, basal cheliceral articles fairly stout, remaining mouth parts hidden, sternum slightly rugose, coxae IV spaced by less than their diameter by the sternum. – Legs (photos) fairly stout; bristles: Leg I: Femur a prolateral-distal one, tibia dorsally-basally a thin bristle and ventrally 3 pairs of long and strong bristles, the left tibia bears an additional prolateral bristle, metatarsus most probably 3 ventral pairs, femur II bears a dorsal bristle in the basal half in contrast to the remaining femora, patellae bristle-less, legs III–IV bristle-less, metatarsal preening comb, scopulae and claw

tufts absent, the paired tarsal claws bear several long teeth. – Opisthosoma (fig. 76, photos) oval, hairs short and indistinct, length of the scutum almost half of the opisthosomal length, epigaster apparently not scutate. – Pedipalpus (fig. 77) with stout articles, tibia fairly elongated apically-medially, retrolateral tibial apophysis slender, erect and pointed, its tip bent anteriorly, cymbium wide, bulbus flat, embolus describing a wide loop.

**Relationships:** The species fits in no. 5 of the key to the species, see WUNDERLICH (2004: 1563). The shape of the slender tibial apophysis is different in the remaining congeneric species.

**Distribution:** Eocene Baltic amber forest.

## Family CLUBIONIDAE

The members of this family are rare and not diverse in the Baltic amber; only a single genus of the subfamily Eodotinae WUNDERLICH 2011 is known, *Eodoter* PETRUNKEVITCH 1958.

The specimens which I (2004: 1616) regarded more or less questionable as conspecific with the generotype *magnificus* are partly surely members of different species; *E. ?magnificus*, F722/CJW, figs. 11–12 sensu WUNDERLICH (2004: 1621), is apparently the member of an unnamed species. The generotype has a proventral pedipalpal tibial apophysis, compare the RETROventral tibial apophysis in *longimammillae* n. sp. (figs. 80–81), in contrast to *magnificus* in which the apical article of the posterior spinnerets are retracted, see WUNDERLICH (2004: 1620: Fig. 7).

In this paper I describe a fifth species of the genus *Eodoter*. The single male bears two of the extremely rare parasitic larvae of the family Mantispidae (Neuroptera), whose larvae are ectoparasites of spiders; see the paper on these larvae in this volume.

Remark: I strongly disagree with the recent synonymations of the extant genera by MIKHAILOV (2012).

### *Eodoter longimammillae* n. sp. (figs. 78–81) photos 35–37

The name of the species points to the long – expanded – articles of the posterior spinnerets of the holotype (fig. 78).

**Material:** Holotype ♂ in Eocene Baltic amber, bearing two larvae of the family Mantispididae (Neuroptera), F2275/BB/AR/CJW.

**Preservation and syninclusions:** The spider is fairly well preserved in a yellow piece of amber which was slightly heated. The ventral side is covered with a white emulsion, the ventral part of the opisthosoma bears a larger gas bubble, the legs are folded above the body. The left legs III and IV and the right leg III are cut off through tibiae and metatarsi, the tip of the left tarsus I is also cut off. – Syninclusions are numerous: Plant particles including stellate hairs, detritus, a small Diptera right below the spider, the posterior part of a wingless larva of an Orthoptera which is strongly oxidated and may have been 6 mm long, two parasitic larvae of the Mantispididae (Neuroptera) (photos), less than 1 mm long, are preserved on the anterior part of the spiders opisthosoma, a third mantispid larva is preserved in a different layer, 1 cm away from the spiders body.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (figs. 79–81, photo 37): Tibia with a large retrodistal, a smaller retroventral apophysis, and two hook-shaped ventral-apical apophyses, median apophysis fairly stout, originating in the basal half of the bulbus.

**Description** (♂):

Measurements (in mm): Body length 5.2, prosomal length 2.2, opisthosoma: Length 3.0, width 1.7; tibia I 2.8, tibia IV 2.3, tarsus IV 1.05; length of the fang 0.1.

Colour grey brown, legs apparently annulated.

Prosoma (photo; parts are hidden) wide and fairly raised, eyes small, eye field almost as long as the short clypeus, posterior row recurved, its eyes widely spaced, lateral eyes touching. Basal cheliceral articles large, not diverging, fangs long; teeth of the fang furrow and ventral side of the remaining prosoma hidden. – Legs (photo) long and slender, prograde, I longest, II not much shorter, III shortest. No true scopulae, claw tufts well developed, bristles long and slender, legs I–II: Femur 1 dorsally in the basal half and 1 prolaterally in the distal half, patella none (like the remaining patellae), tibia 2 ventral pairs, metatarsus a single ventral one in the distal half (the numbers may be not konstant), tibia IV bears 2 ventral pairs, metatarsus IV bears an apical comb of „preening bristles“. – Opisthosoma 1.7 times longer than wide, covered with thin hairs, posterior spinnerets expanded (fig. 78), their articles long and slender. – Pedipalpus (figs. 78–81) (see the diagnosis): Femur slightly bent, tibia longer than the patella.

**Relationships:** The pedipalpal tibial apophyses are quite different in *E. scutatus* WUNDERLICH 2011 and *E. tibialis* WUNDERLICH 2011. A ventral pedipalpal tibial apophysis exists also in *E. magnificus*, but the retrodistal tibial apophysis is directed dorsally in this species, see WUNDERLICH (2004: 1620, fig. 9), in contrast to *E. longimammillae* in which it is longer and directed ventrally. Shape of the expanded spinnerets: See above.

**Distribution:** Eocene Baltic amber forest.

Family **SPARASSIDAE**, probably subfamily Eusparassinae

Sparassidae is a family which has a cosmopolitical (mainly tropical) distribution. Mainly because of its usually large specimens the reports in amber are quite rare, and juveniles may be not recognized. On the other hand the large members of the genus *Sosybius* KOCH & BERENDT 1854 (family Trochanteriidae) (\*) are frequent in Baltic amber, and its adult males are not too rare.

Fossil Sparassidae are known from the Miocene Dominican amber of Hispaniola and – the oldest ones – from the Palaeogene, the Eocene Baltic amber. Here I describe the second known male in Baltic amber. The species has originally been described by PETRUNKEVITCH erroneously under the genus name *Zachria*, an Australian genus.

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(\*) In the similar spiders of *Sosybius* – which also possess a laterigrade leg position – the lenses of the posterior median eyes are reduced, and the retroventral rows of the tibial and metatarsal I–II are absent in contrast to the Sparassidae in which paired ventral bristles exist.

Gen. indet., described under *Zachria desiderabilis* PETRUNKEVITCH 1950 (figs. 82–84) photos 38–40

1950 *Zachria desiderabilis* PETRUNKEVITCH, Bull. Mus. Comp. Zool., 103: 311, figs. 109–118, 205 (♂).

**Material:** 1♂ in Eocene Baltic amber, most probably from the area of Kaliningrad (Königsberg) in Russia, F2341/BB/AR/CJW.

**Preservation and syninclusions:** The spider (including its spinnerets) is very well and fairly darkened preserved together with two Diptera in a piece of amber which was slightly heated; its right legs II–IV are lost beyond the coxa by autotomy, a white emulsion is absent.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (figs. 83–84), photo: Tibia with a retroBASAL apophysis which bears two strong bristles; the embolus is fused basally to a parembolic apophysis which is not much shorter than the embolus.

**Description** (♂):

Measurements (in mm): Body length 7.5, prosoma: Length and width 3.5, opisthosoma: Length 3.6, width 2.2; leg I: Femur 3.8, patella 1.5, tibia 3.7, metatarsus 3.8, tarsus 1.6, tibia II 3.8, tibia III 3.2, tibia IV ca. 3.5.

Colour medium grey brown, legs not annulated.

Prosoma (photo) as wide as long, covered with short hairs, thoracal fissure very long, 8 eyes in two parallel rows, laterals distinctly larger than medians, median eyes spaced by ca. 1 1/4 times of their diameter, clypeus ca. 1 1/2 times longer than the diameter of the anterior median eyes, bearing long bristles, anterior cheliceral articles with long bristles, robust, anterior margin most probably bearing 3 teeth (or only 2?), fangs long, gnathocoxae not converging. Labium wider than long, sternum as wide as long, coxae IV spaced by less than their diameter. – Legs robust, position laterigrade, hairs short, order I–II/IV/III, bristles numerous, femur I with 1 dorsal bristle in the middle, 2 prodorsals in the basal half and 4 distals in a transverse row, tibia I 3 ventral pairs and apicals, metatarsus I 2 ventral pairs, claw tufts and scopulae well developed, trilobate metatarsal membrane as in fig. 82. – Opisthosoma 1.6 times longer than wide, hairs short one pair of epiandrous gland spigots, spinnerets short. – Pedipalpus (figs. 83–84, photo): See the diagnosis. The tibia has proapically a blunt outgrowth, the embolus and the sclerotized parembolic apophysis are fused basally, the sciny conductor is slightly longer than the embolus which is bent distally.

**Relationships** (I thank PETER JÄGER for a very helpful discussion): (1) The genus and the subfamily: With hesitation PETRUNKEVITCH (1950) placed *desiderabilis* in the endemic Australian genus *Zachria* L. KOCH 1875 (Eusparassinae), but *Zachria* is quite different, e. g., the eye position is different, and the anterior margin of the fang furrow bears only 2 teeth. The differentiation of the Sparassid subfamilies is – because of numerous convergences – quite difficult and just in progress. The large lateral eyes (compared to the medians), and the number of (probably) 3 teeth of the promargin of the fang furrow may point to the subfamily Heteropodinae, the low number of ventral bristles on tibia I is more frequent in the Eusparassinae than in the Heteropodinae. Eusparassinae are more frequent in dry biotopes than Heteropodinae, and dry biotopes may have been rare in the Baltic amber forest. A retrobasal position of the tibial apophysis and a parembolic apophysis exist in several subfamilies. According to the different shape of the trilobate metatarsal membrane and the short teeth of the paired tarsal claws *Eusparassus crassipes* (KOCH & BERENDT 1854) in Baltic amber is not closely related, see DUNLOP et al. (2011). Two specimens in Baltic amber, see WUNDERLICH (2008: 477–478) possess relative large median eyes and thus may be not strongly related. The present male may well represent an undescribed extinct genus. A worldwide revision of the Sparassid genera is needed. – (2) The species: The holotype of „*Zachria*“ *desiderabilis* is smaller (body length almost 5 1/2 mm), and the small basal tooth of the pedipalpal tibia is pointed; bulbous and embolus are apparently identical although a parembolic apophysis has not been reported by PETRUNKEVITCH.

**Distribution**: Eocene Baltic amber forest.

## Family THOMISIDAE

Juvenile spiders of this family are not so rare in Baltic amber but adult spiders are extremely rare; only 6 of about 50 specimens which are known to me are adult, that means 1/8. A provisional key to the fossil genera in Baltic amber has been published by WUNDERLICH (2004:1751).

Several doubtful fossil thomisid taxa exist in Baltic amber, see the part “fossils” in the World Spider Catalog by N. PLATNICK (internet), and the situation is somewhat confusing.

No taxon of the Eocene Baltic amber is known which possesses club-shaped spines on body and legs as known from numerous extant taxa like *Psammitis*.

### Taxa in Baltic amber:

(a) Subfamily STEPHANOPINAE (if this taxon is regarded as a member of the family Thomisidae and the Stephanopinae): Tribe Borboropactini; a synonym is Succiniraptorinae WUNDERLICH 2004: *Succiniraptor* WUNDERLICH 2004 with *S. radiatus* (KOCH & BERENDT 1854) (= *Succiniraptor paradoxus*, *Syphax radiatus*), see WUNDERLICH (2008: 484).

(b) The remaining taxa may all be members of the subfamily MISUMENINAE:

*Succinaenigma raptor* WUNDERLICH 2004;

*Thomisiraptor* WUNDERLICH 2004 with the type species *T. liedtkei*. *Syphax hirtus* MENGE in KOCH & BERENDT 1854: 21 – a nomen nudum – may be a member of *Thomisiraptor*, and probably conspecific;

*Syphax* KOCH & BERENDT 1854, see WUNDERLICH (2004: 1752), type species *S. megacephalus* KOCH & BERENDT 1854. Questionable synonym: *Facundia* PETRUNKEVITCH 1942. – Remark: A true leg scopula is apparently absent in *megacephalus*, and so this taxon is most likely not a member of the Stephanopinae; see WUNDERLICH (2004: 1752). Some juvenile specimens of my private collection may well be members of *megacephalus*, e. g., F633/BB/AR/CJW, and F2204/BB/AR/CJW. See the photos 41–42.

### New material:

*Thomisiraptor liedtkei* and *T. sp. indet.*: 1 ?ad. ♀ coll. A. BEIGEL BB-104, body length 3.5 mm, prosomal length ca. 1.7 mm; 1 juv. F 1503/BB/AR/CJW, body length ca. 1.8 mm; 1♂ from the Bitterfeld deposit, coll. H. GRABENHORST AR-168, body length ca. 2.2 mm. The posterior part of the opisthosoma is cut off. The spines of the body appear thicker than in the holotype, and therefore I am not sure about the conspecificity. The bulbi are not observable in the ventral aspect. The genus is new to the Bitterfeld deposit; 1♂ from the Bitterfeld deposit, coll. H. GRABENHORST AR-159, body length 2.9 mm, prosomal length 1.4 mm. A distinct opisthosomal hump is absent, the spines of the body are shorter than in the holotype of *liedtkei*, the bulbi are bent under the body, most parts are hidden. Therefore the determination is unsure.

Remarks – mainly on the relationships – on some suprageneric taxa of the Baltic amber forest which became probably extinct at the end of the Eocene:

Baltsuccinidae WUNDERLICH 2004, Eomactatorinae WUNDERLICH 2011 of the Gnaphosidae, Eotrechaleinae WUNDERLICH 2004 of the Trechaleidae, Ephalmatoridae PETRUNKEVITCH 191950, Miraraneinae WUNDERLICH 2004 of the Araneidae, Mizagallinae WUNDERLICH 2004 of the Dictynidae, Mizaliinae THORELL 1870 of the Oecobiidae, Praetheridiidae WUNDERLICH 2004 (n. stat.), Protheridiidae WUNDERLICH 2004, Pumiliopimoini WUNDERLICH 2008 of the Pumiliopimoidae WUNDERLICH 2008, Sosybiini WUNDERLICH 2004 of the Trochanteriidae, Spatiatoridae PETRUNKEVITCH 1942, and Succinomidae WUNDERLICH 2011 (n. stat.).

- (1) Almost all of these taxa are monogeneric.
- (2) Most of these taxa are rare or extremely rare, reported by a single species only.
- (3) As suggested by me earlier the roots of these taxa should go back at least to the Cretaceous or Jurassic. First results show that this is true (see the paper on Cretaceous spiders in this volume);
  - (a) The Cretaceous Micropalpimanidae are strongly related (and probably even synonymous) to/with the Eocene Spatiatoridae;
  - (b) the Cretaceous genus *Zamilia* shows strong (sister group?) relationships to the Eocene genus *Mizalia* (Oecobiidae: Mizaliinae);
  - (c) the Cretaceous Burmascutidae may be related to the Eocene Protheridiidae.

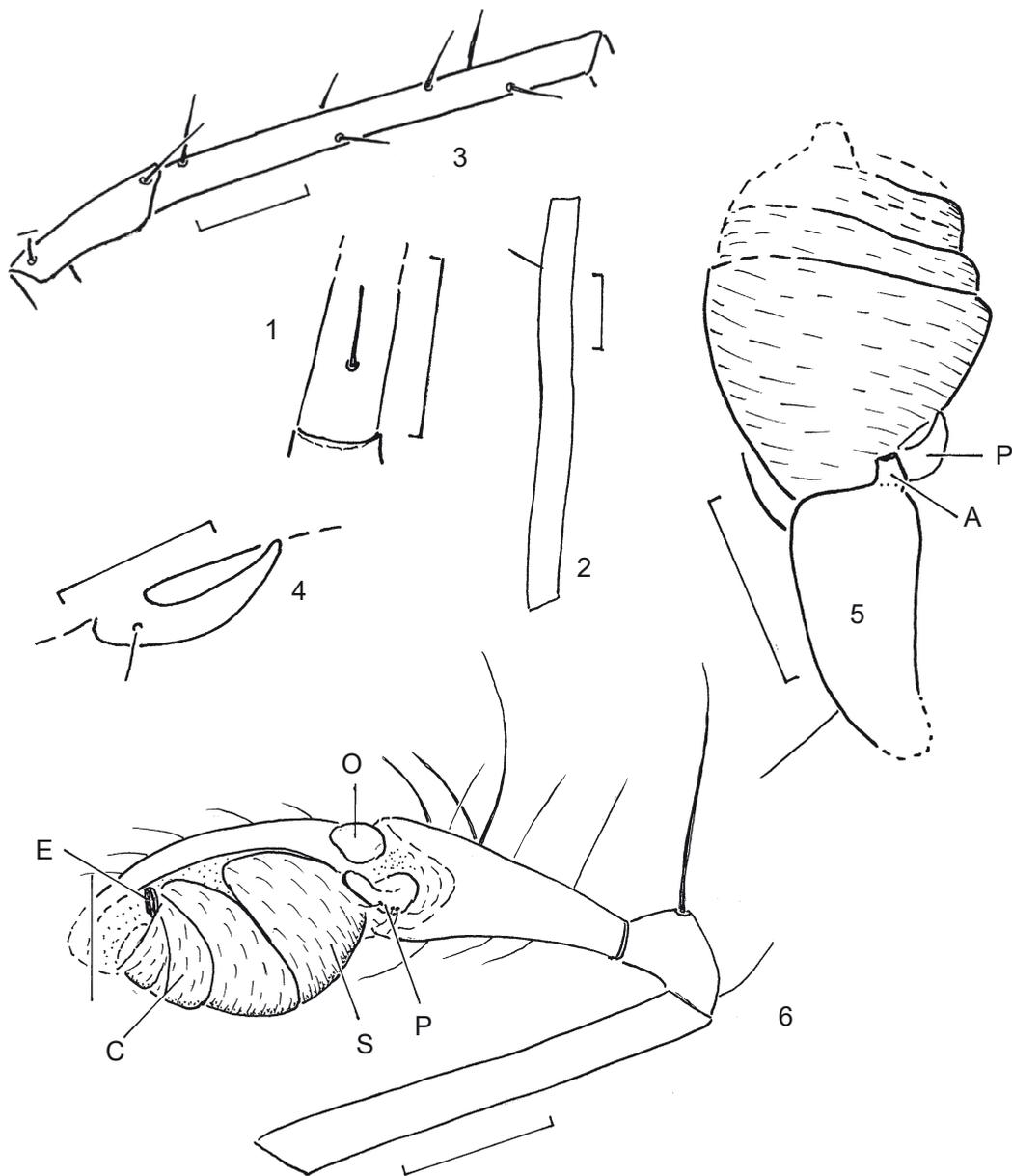
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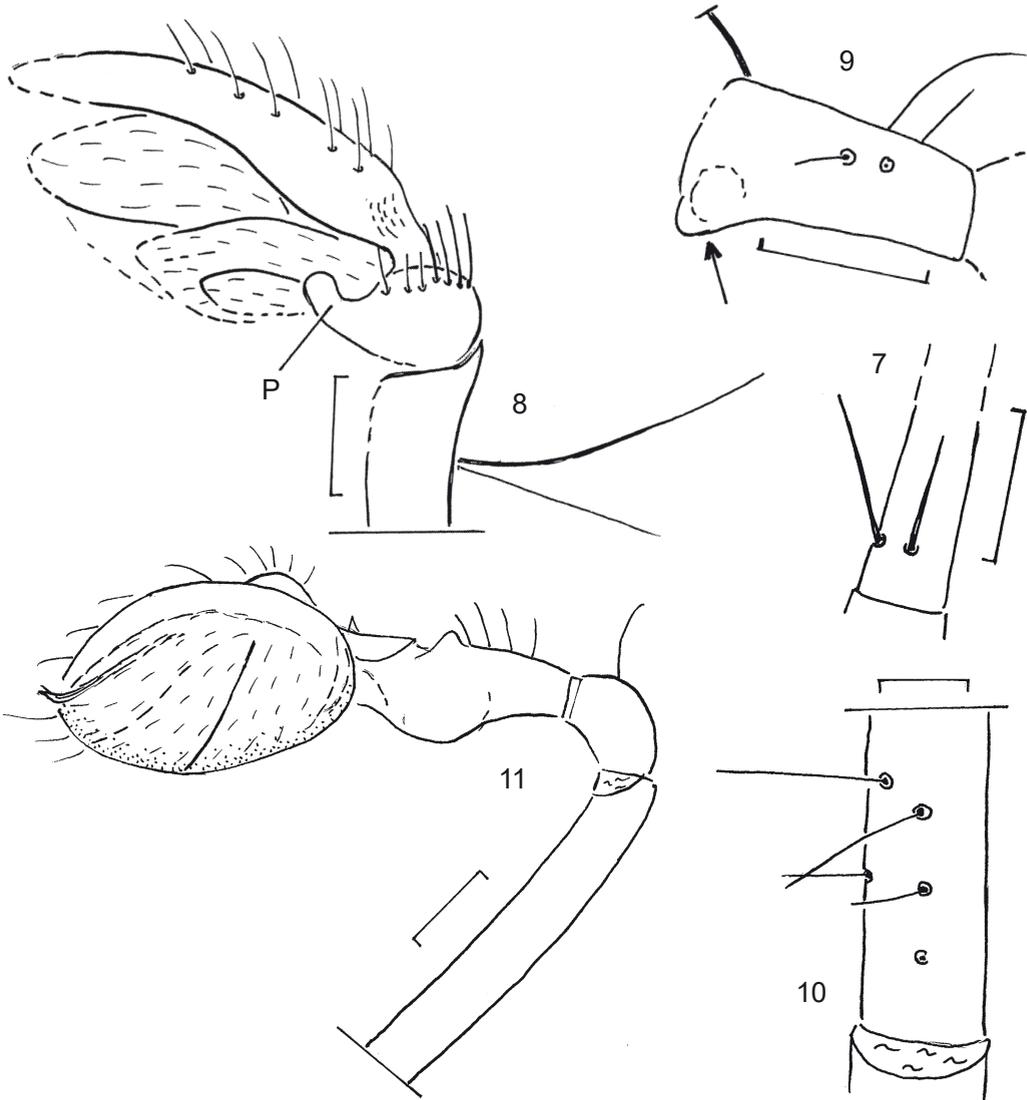
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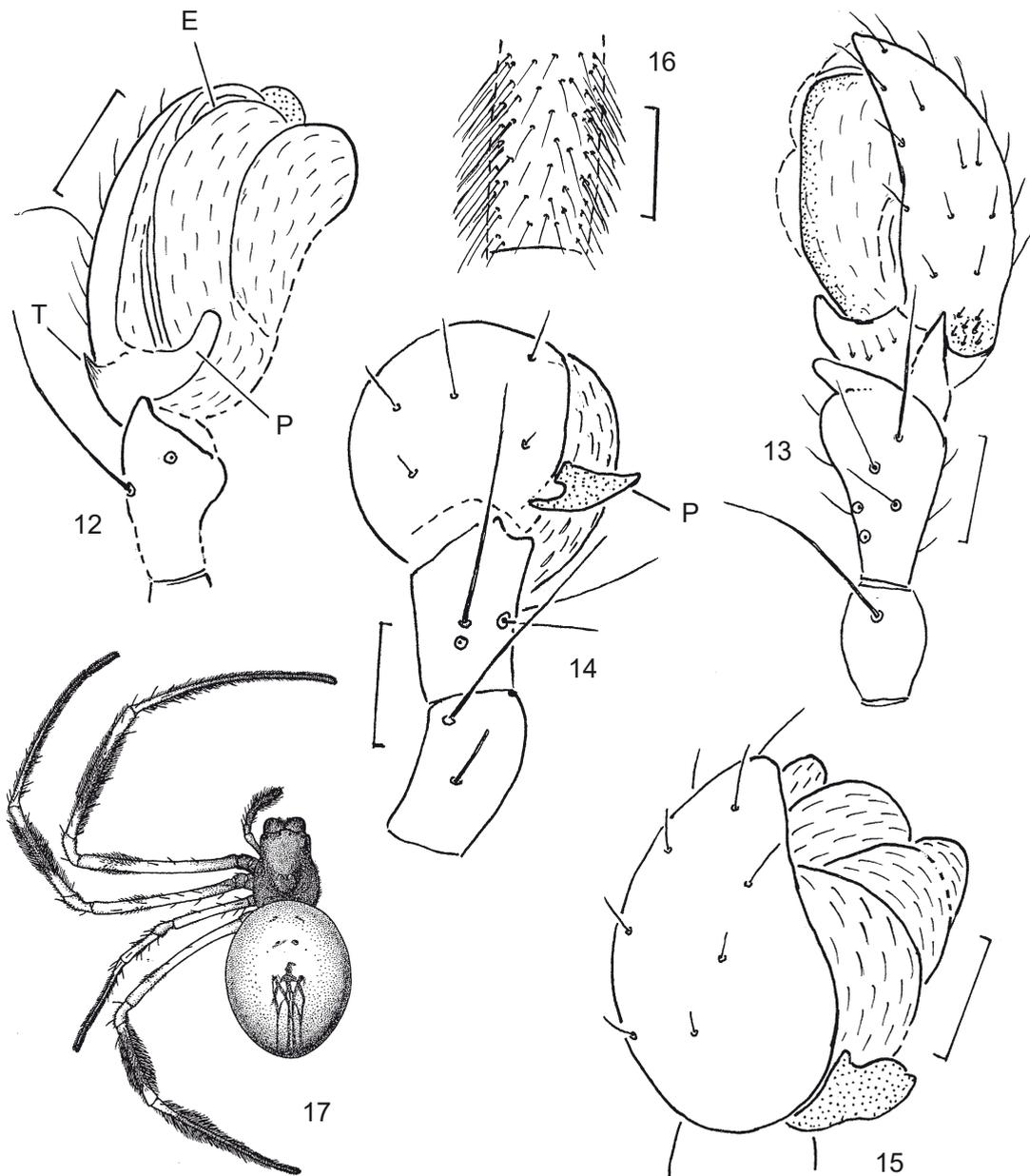
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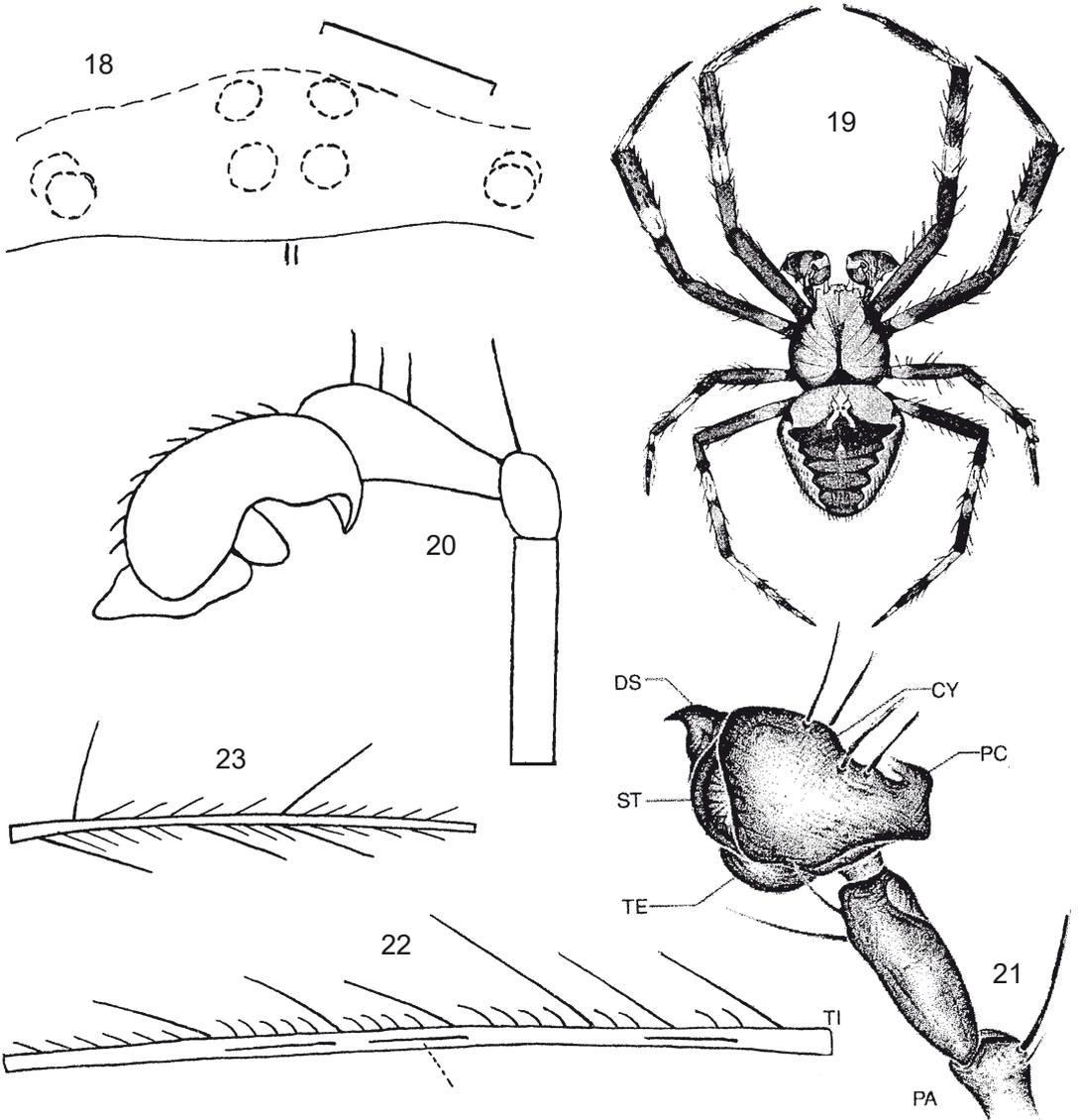
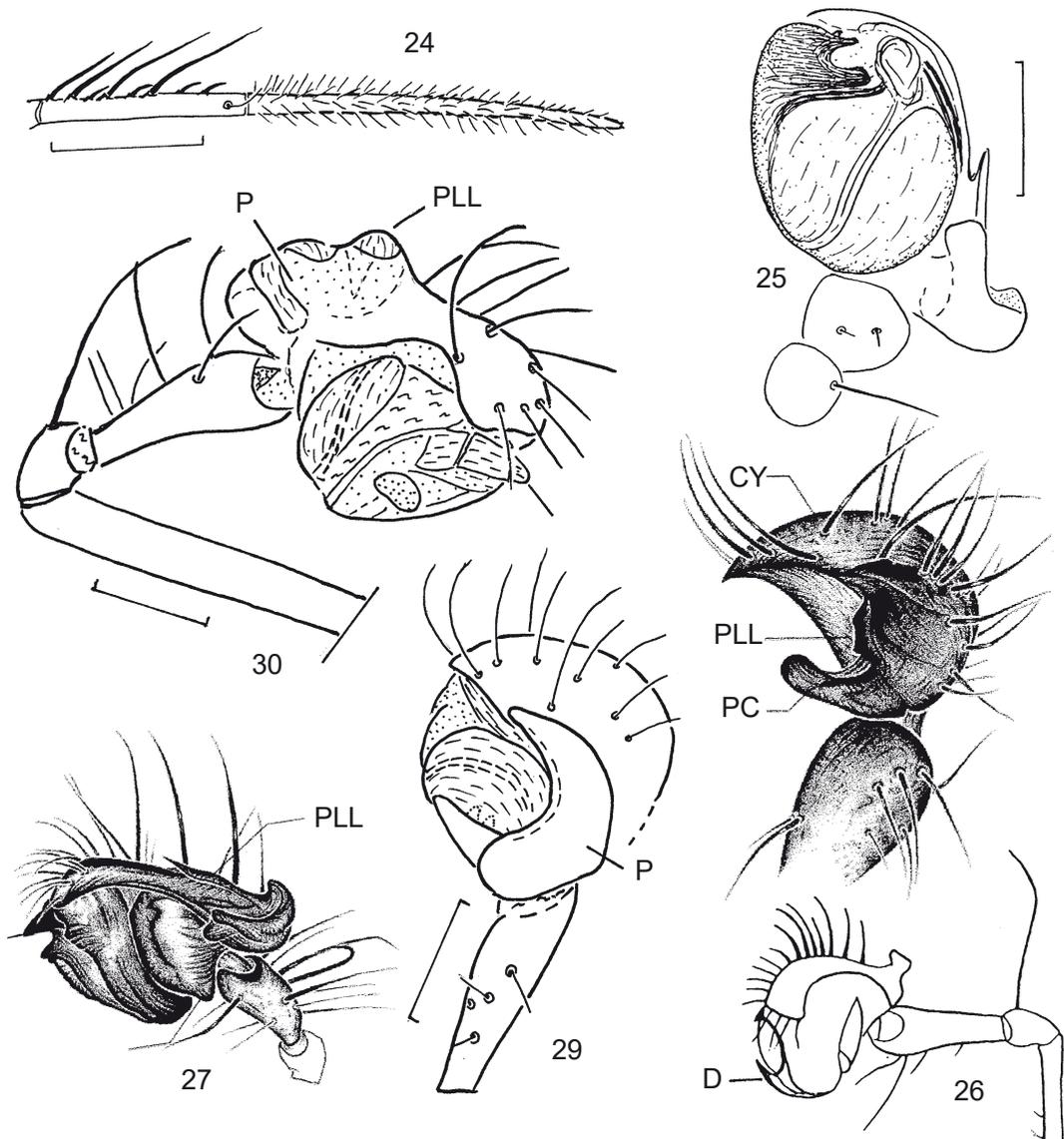


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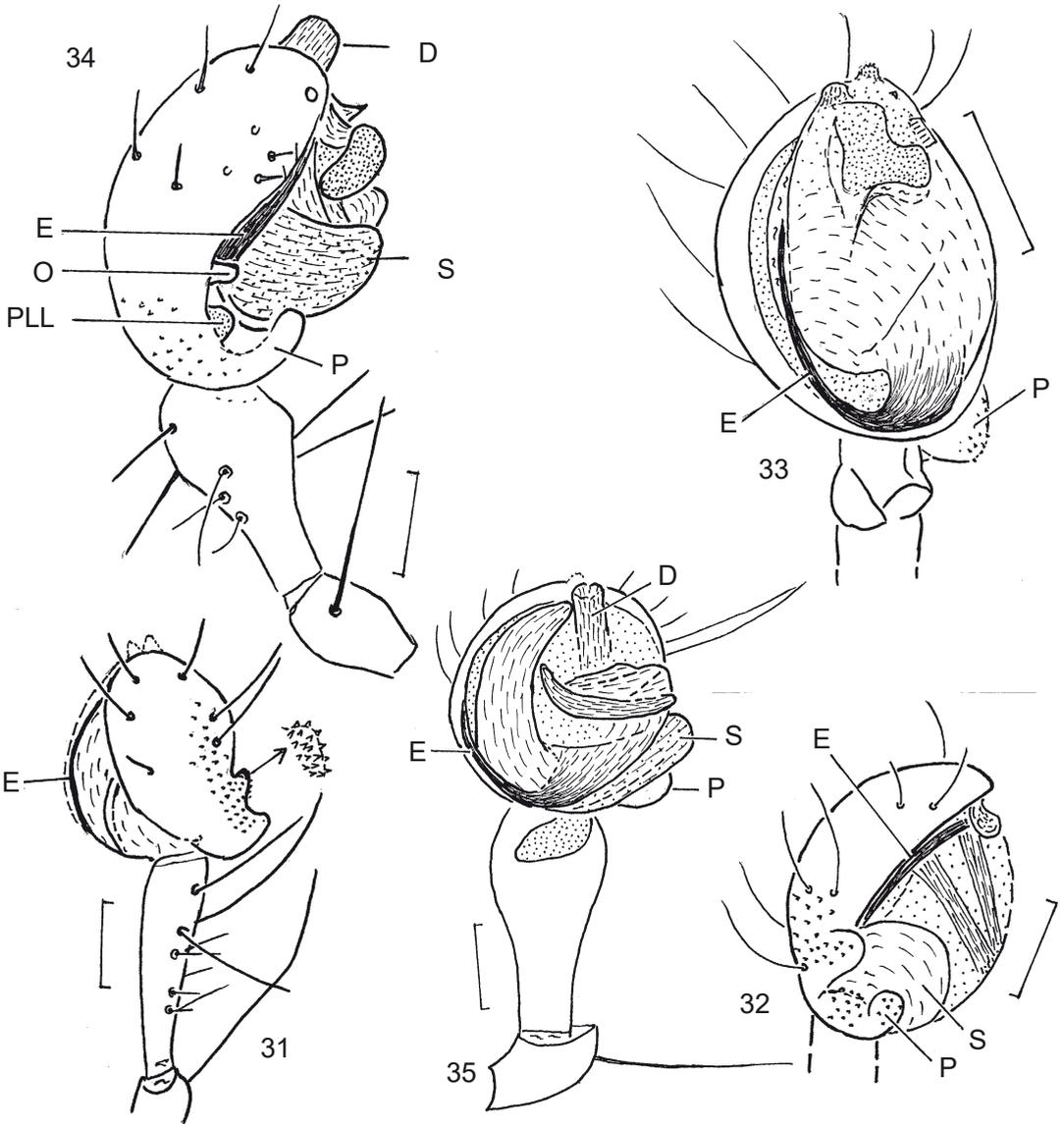


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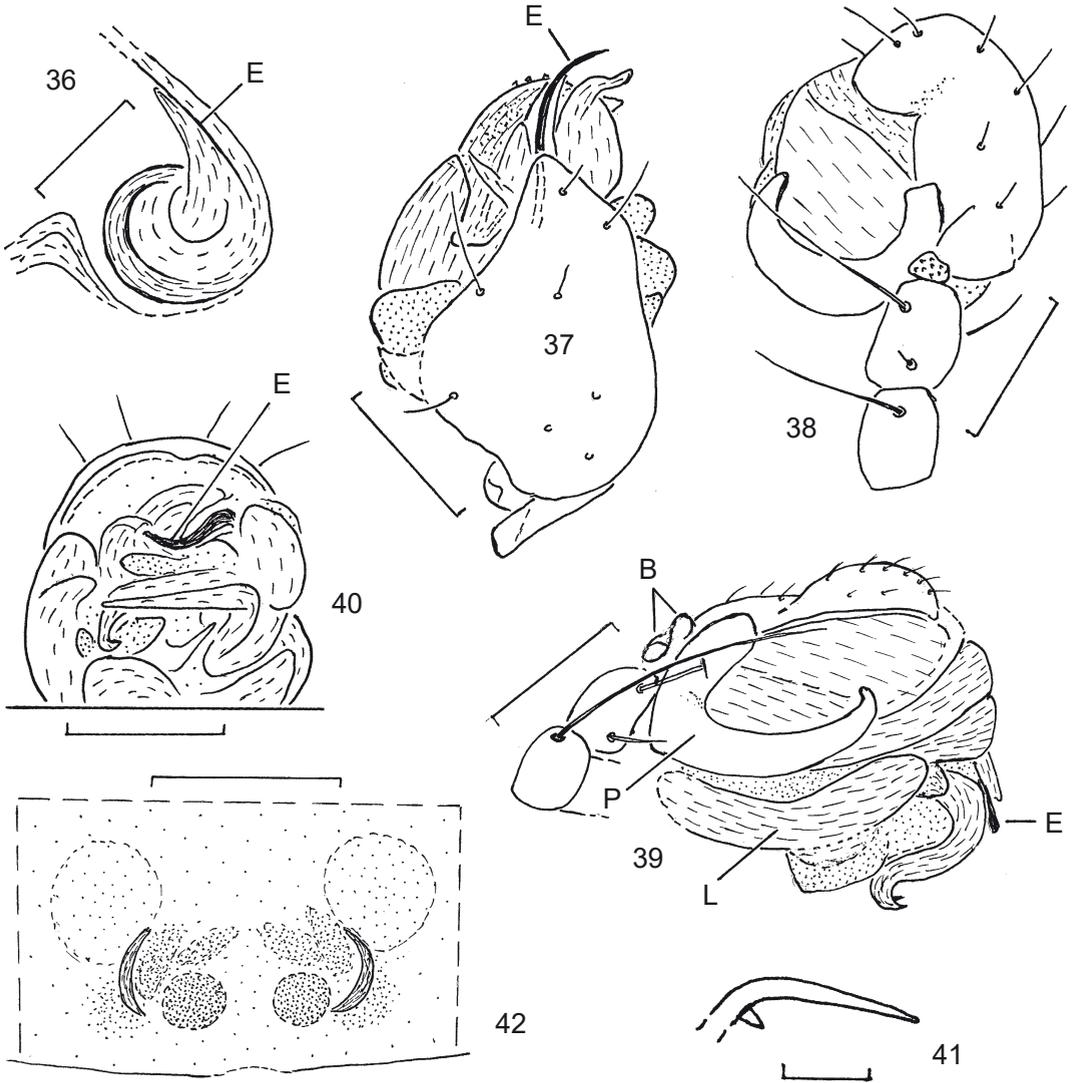
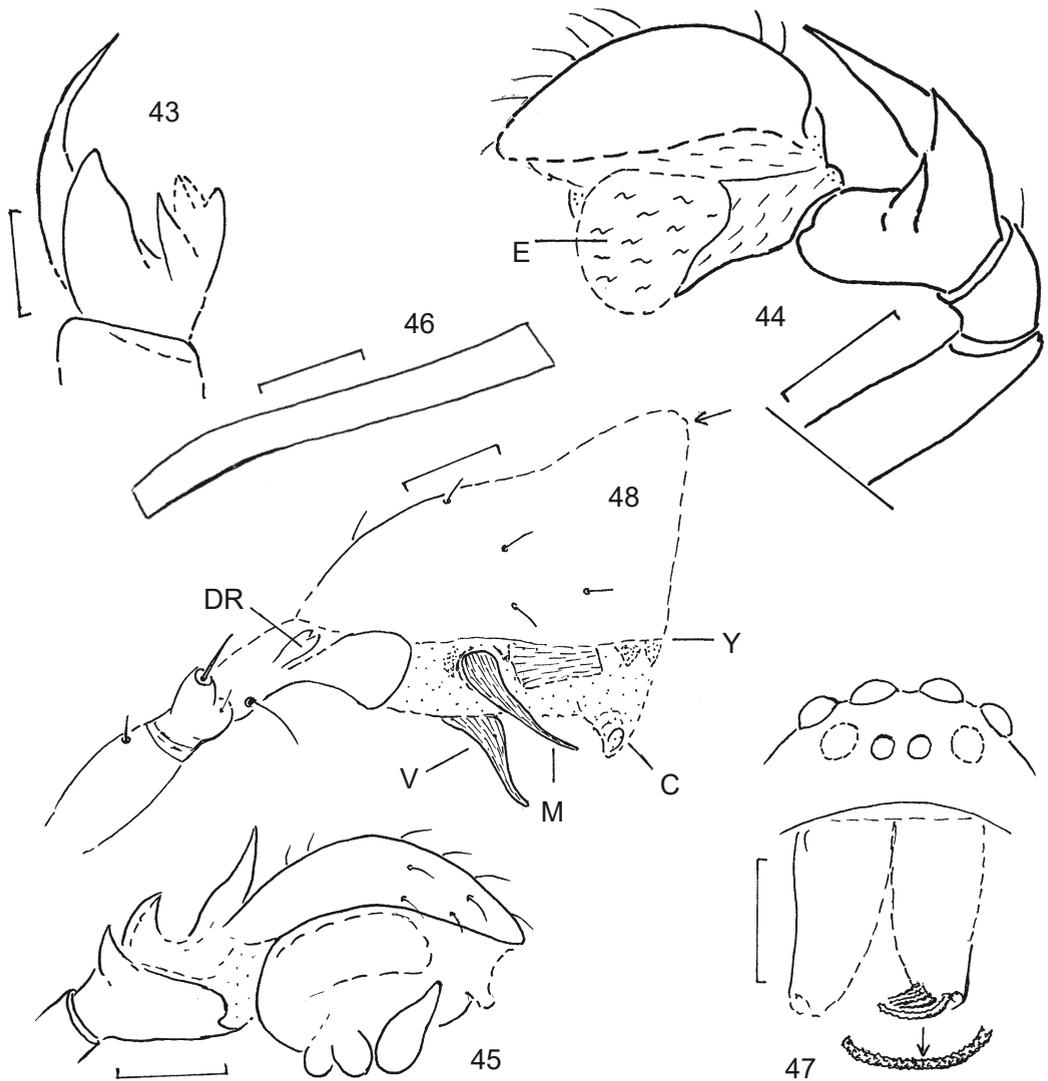


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fig. 41) *Protheridion ?tibiale* WUNDERLICH 2004 (Protheridiidae), ♂ F2274/BB/AR/CJW, retrolateral aspect of the long unpaired claw of the right tarsus I. Scale bar 0.2;

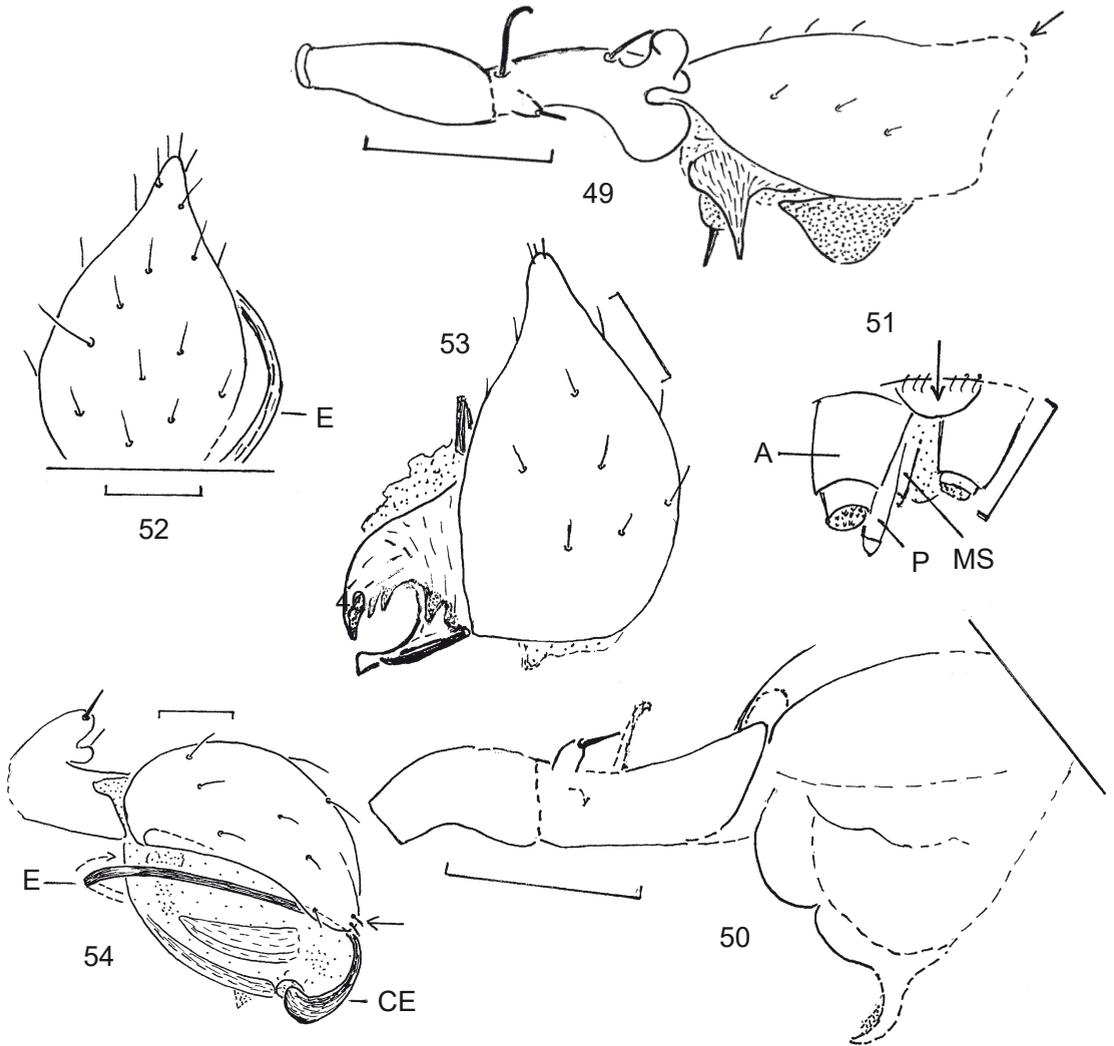
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figs. 43-45: *Succiniropsis runcinata* n. sp. (Zoropsidae), ♂; 43) dorsal aspect of the right padipalpal tibia; 44) retrolateral aspect of the left pedipalpus. Most parts of the bulbus are hidden by a white emulsion; 45) retrolateral aspect of the right pedipalpus. Parts of the bulbus are hidden. E = emulsion. Scale bar 0.2;

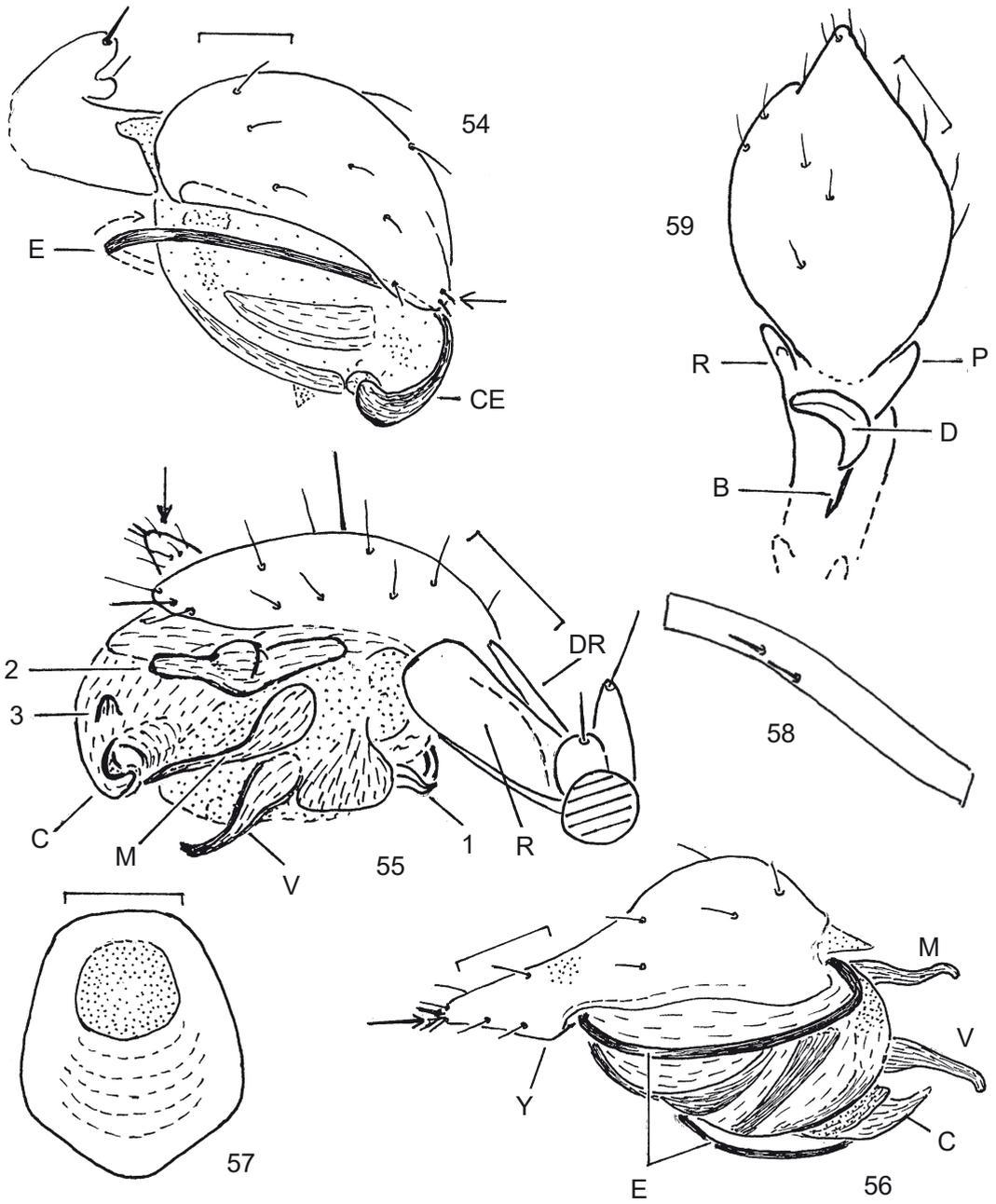
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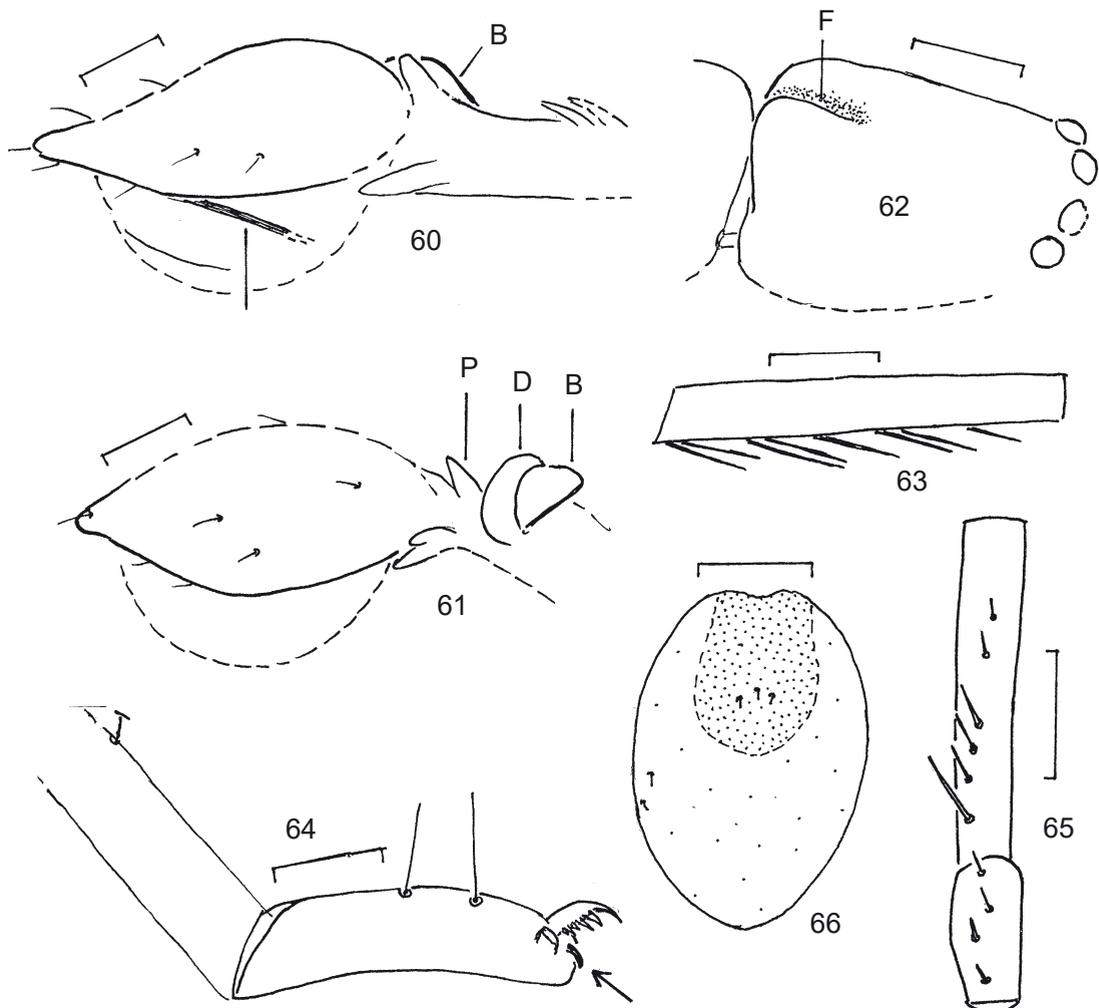


figs. 49-50: *Eohalinobius scutatus* WUNDERLICH 2008 (Succinomidae), ♂ holotype; 49) retrodorsal and slightly basal aspect of the right pedipalpus. The arrow points to the cymbial outgrowth which is covered with a white emulsion; 50) retrolateral aspect of the right pedipalpus. Parts are hidden by a white emulsion. Scale bars 0.2;

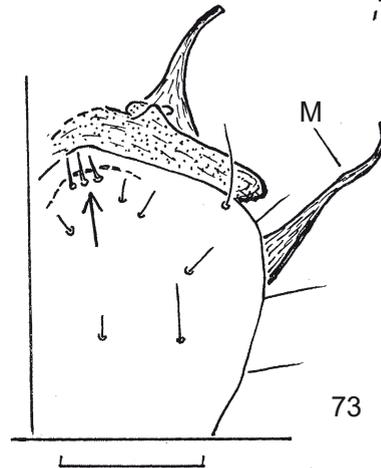
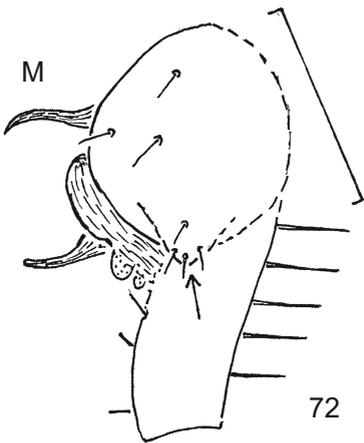
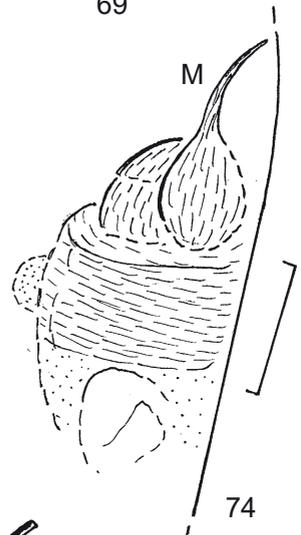
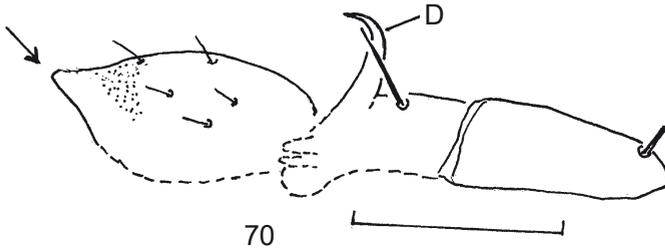
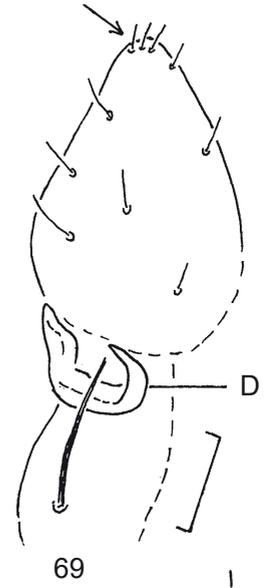
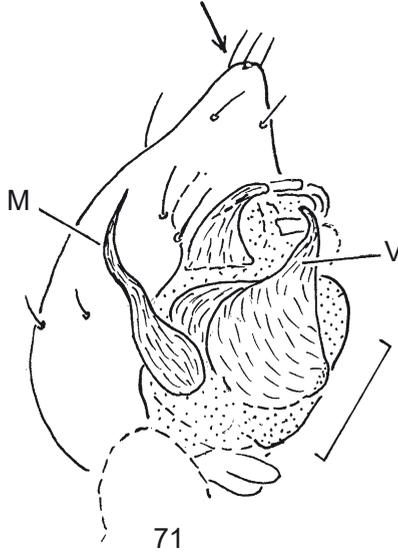
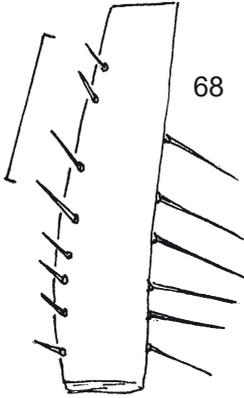
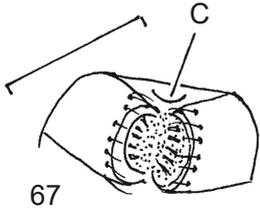
figs. 51-56: *Eohalinobius patina* n. sp. (Succinomidae), ♂; 51) spinnerets. The arrow points to the wide colulus; 52) dorsal aspect of the left cymbium and embolus; 53) retrodorsal-apical aspect of the left pedipalpus; 54) proapical aspect of the left pedipalpus. An emulsion hides parts of the bulbus; 55) retrolateral aspect of the left pedipalpus. The arrow points to the cymbial outgrowth; 56) prodorsal aspect of the right pedipalpus with expanded bulbus. 1 = basal part of the embolus, 2, 3 = tegular apophyses, A = anterior spinneret, C = conductor, CE = conductor/embolus, DR = dorsal branch of the retroventral tibial apophysis, E = embolus, M = median apophysis, MS = right median spinneret, R = retroventral tibial apophysis, P = right posterior spinneret, V = ventral tegular apophysis, Y = tip (apex) of the cymbium. Scale bars 0.2;



figs. 57-61: *Eohalinobius calefactus* n. sp. (Succinomidae), ♂; 57) dorsal aspect of the fairly deformed opisthosoma. The scutum is punctated; 58) prolateral aspect of the right tibia I which length is more than 2 mm; 59) left pedipalpus, dorsal aspect of the cymbium and dorsal-apical aspect of the tibia which basal part is hidden; 60) prodorsal aspect of the right pedipalpus which is partly deformed or hidden; 61) retrodorsal aspect of the left pedipalpus. Some parts are hidden. B = strong dorsal tibial bristle, D = dorsal tibial apophysis, E = embolus, P = prolateral tibial apophysis, R = retroventral tibial apophysis. Scale bars 0.5 in fig. 57, 0.2 in the remaining figs.;



figs. 62-74: ?*Succinomus gibbosus* n. sp. (Succinomidae), ♂; 62) retrodorsal aspect of the prosoma. Note the height thoracic part and the deep thoracic furrow. Parts like the anterior eye row are hidden; 63) prolateral aspect of the left tibia I; 64) prolateral-apical aspect of the left tarsus III. Two long tarsal trichobothria are drawn but no hairs. The right (paired) tarsal proclaw is cut off excepts its stump; the arrow points to the unpaired claw; 65) dorsal aspect of the left patella and tibia III with bristles. Hairs are not drawn; 66) dorsal aspect of the opisthosoma. Only few hairs are drawn; 67) spinnerets; apparently only the anterior spinnerets exist. Only few hairs are drawn; 68) dorsal aspect of the spiny left pedipalpal femur; 69) dorsal aspect of the left pedipalpus. Parts are hidden; 70) retrolateral aspect of the left pedipalpus. The structures of the bulbus are hidden; 71) retroventral aspect of the right pedipalpus; 72) right pedipalpus: Apical aspect of the cymbium and bulbus, ventral aspect of the femur; 73) dorsal-apical aspect of the right pedipalpus which is partly hidden by a white emulsion. The arrow points to the cymbial outgrowth like in previous figs.; 74) ventral aspect of the prolateral part of the left pedipalpus. Parts are hidden. C = colulus, D = dorsal tibial apophysis, F = thoracic furrow, M = median apophysis, V = ventral tegular apophysis. Scale bars 0.5 in figs. 62-66, 68 and 72, 0.2 in the remaining figs.;



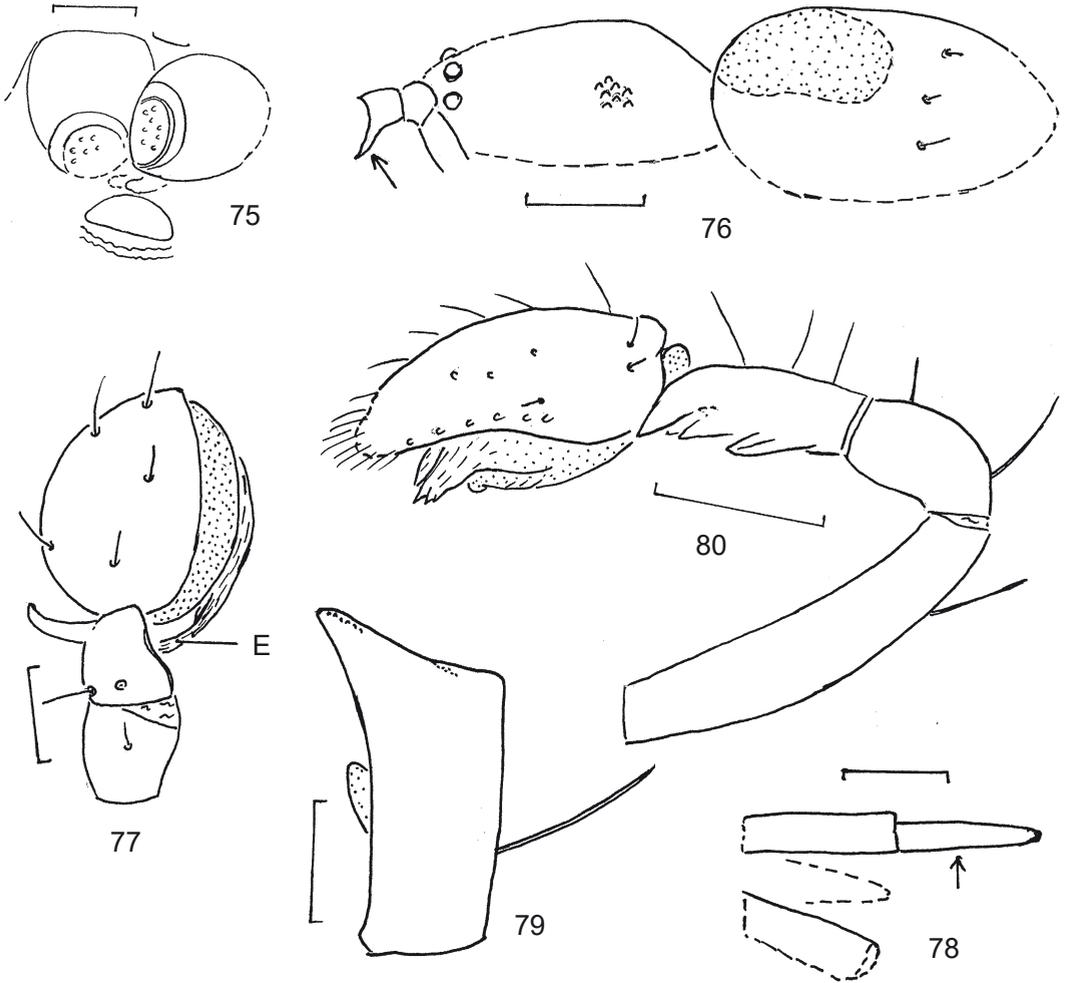
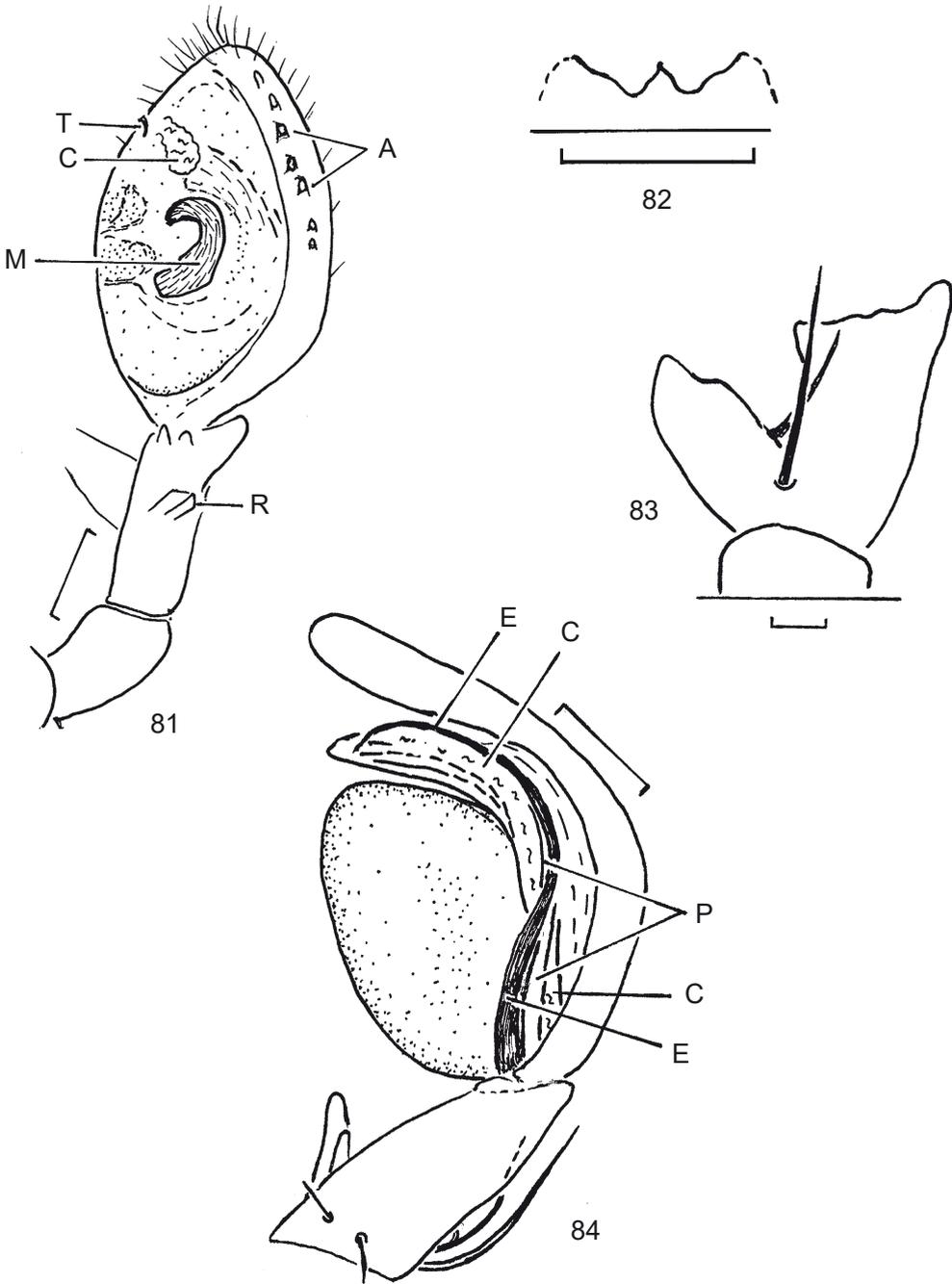


fig. 75) *Succinomus duomammillae* WUNDERLICH 2008 (Succinomidae), ♂, ventral aspect of the spinnerets (only the anterior are well developed), anal tubercle and the small colulus. Hairs are not drawn. Scale bar 0.2. Taken from WUNDERLICH (2008);

figs. 76-77: *Ephalmator tredecim* n. sp. (Ephalmatoridae), ♂; 76) lateral aspect of the body, opisthosoma slightly dorsally. The arrow points to the slender tibia of the left pedipalpus. Parts – e. g. most of the eyes – are hidden by a white emulsion: 77) dorsal aspect of the left pedipalpus. Only few hairs are drawn. E = embolus. Scale bars 0.2 and 0.1;

figs. 78-81: *Eodoter longimammillae* n. sp. (Clubionidae), ♂; 78) lateral aspect of the left spinnerets. The arrow points to the expanded apical article of the posterior spinneret; 79) dorsal aspect of the left pedipalpal tibia; 80-81) retrolateral and retroventral aspect of the left pedipalpus. Most parts of the embolus and other parts of the bulbus are hidden in these positions. A = possible artefacts of the cymbium, C = conductor, M = median apophysis, T = tip of the embolus, R = retroventral tibial apophysis. Scale bars 0.5 in fig. 80, 0.4 in fig. 78, 0.2 in figs. 79 and 81;



figs. 82-84: Gen. indet. (published under *Zachria desiderabilis* (PETRUNKEVITCH 1950) (Sparassidae: ?Heteropodinae), ♂ F2341/BB/AR/CJW; 82) dorsal aspect of the trilobate membrane of the tip of the left metatarsus I (parts are hidden); 83) dorsal aspect of the left pedipalpal tibia; 84) retroventral aspect of the left pedipalpus. C = conductor, E = embolus, P = parembolic apophysis. Scale bars 0.2.

**“FROZEN BEHAVIOUR” IN “VAMPIRES” OF SPIDERS – FOSSIL INSECT LARVAE OF THE FAMILY MANTISPIDAE (NEUROPTERA) AS PARASITES OF SAC SPIDERS (ARANEAE: CLUBIONIDAE) IN EOCENE BALTIC AMBER**

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**Abstract:** Three fossil insect larvae of the family Mantispidae (mantidflies), subfamily Mantispinae (Neuroptera), are described as ectoparasites of a male Sac Spider (Araneae: Clubionidae): The extinct genus *Eodoter* PETRUNKEVITCH, preserved in Eocene Baltic amber. The genus of the larvae is unknown. Behaviour and development of fossil and extant members of the subfamily are discussed. The sure existence of fossil Mantispidae: Mantispinae in Baltic amber is only based on larvae up to now.

Further key words: Egg predator, phoresy.

**Material:** CJW = collection of J. WUNDERLICH.

## INTRODUCTION and remarks on some fossils

Most ectoparasites of fossil spiders in Baltic amber are mite larvae, see WUNDERLICH (2004: 117-119); phoretic mites are also not rare. Fossil larvae of the Neuroptera of the Mantispidae (subfamily Mantispinæ) as spider's ectoparasites in Baltic amber are extremely rare in contrast to Acari; among more than 100 000 fossil spiders I have seen only a single specimen before, see below. In this paper I describe two further mantispid larvae which are carried by a spider (photos). It is remarkable (1) that both fossil spiders which are known to bear mantispid larvae are Sac Spiders of the family Clubionidae, (2) that the mantispid larvae of both spiders represent different taxa, and (3) that within millions of arthropod inclusions in Baltic amber not a single adult member of the Mantispinæ has been found. The single specimen of the Mantispidae which has been found in questionable Baltic amber in British amber (on the coast of Norfolk, *Fera venatrix* WHALLEY (1983), now named *Whalfera venatrix*) is not a member of the subfamily Mantispinæ – and even not of the Mantispidae – but probably of the Rhachiberothidae, see WEDMANN & MAKARKIN (2007). – From the Eocene of the Messel Pit fossil site, Germany, an adult member of the Mantispidae, subfamily Symphrasinæ has been described recently by WEDMANN & MAKARKIN (2007). It is preserved in claystone sediments which are few million years older than Baltic amber. – The larvae described below should be described more closely in the future, and probably named, too.

Which story does the “frozen behaviour” of these animals, the spiders and the insects, tell us?

Mantidflies (family MANTISPIDAE) – which are not flies but members of the order Neuroptera, lacewings – are remarkable insects, and their behaviour is quite striking. In Europe today five species of *Mantispa* occur in Central Europe two. The cosmopolitical family is known since the Jurassic, see WEDMANN & MAKARKIN (2007). Adult members (figs. 1a-b) resemble mantids (Preying Mantids, order Mantodea) in their general appearance, including the existence of raptorial anterior legs, which evolved convergently. In mantids (e. g.) the wings are quite different, the anterior ones are not transparent. The development and the shape of the larvae is also quite different in both orders: In the mantids a pupal stage is absent. Certain mantispids mimik wasps, few wasps (Dryinidae, Gonatopodinae) possess raptorial forelegs, too.

FOOD, BEHAVIOUR and DEVELOPMENT of the subfamily Mantispinæ. Adult Mantispidae feed on arthropods – probably including spiders –, and use their anterior legs for prey capturing (figs. 1a-b). Females lay large clutches of stalked eggs which contain hundreds to thousands of eggs (fig. 2).

The development of the larvae of most if not all species is connected with spiders in an obligatory way including two different strategies:

(a) Probably all *first instar* larvae of one of the subfamilies of the Mantispidae – the Mantispinæ – are parasites of spiders; they are *mobile* (photos 35–36, fig. 3), the youngest are only about 1 mm long or less. All of the major groups of – most often hunting – spi-

ders are attacked by mantispines, cribellates as well as ecribellates, but apparently not spiders which bear an opisthosomal scutum. The egg-sacs even of web-building spiders are entered, too. The ectoparasitic larvae of the first instars are found on various parts of the spider's body, most often anteriorly on the opisthosoma (photo), occasionally as endoparasites within the book-lungs, feeding on their blood (haemolymph). Using special mouth parts the parasites suck through the cuticula of the (soft) opisthosoma or (e. g.) of the intersegmental skin of the legs. A larva may remain aboard a spider for several months, and may even overwinter. The larvae of certain mantispine species locate and penetrate directly spider's eggs/embryos in their sacs (cocoons) which have already been deposited, but others – probably most larvae – first board spiders (see the discussion), and enter the egg sacs during their construction. Three effects in both spider sexes by the parasitising larvae have been reported: (1) An increase in the development, (2) a decrease in the body size, and (3) a delayed development when situated on an overwintering spider – a synchronization of the diapauses of both arthropods.

Mantispinae larvae board juveniles – usually the larvae stand the moultings of the spiders – and adult spiders of both sexes without a preference of a sex. This is surprising because the larvae finally need adult females which build egg-sacs. Therefore the larvae may have to change their host to an adult female. Few cases are reported in which the transfer from spider to spider happens during the mating or preying, including cannibalism. The two fossil spiders which are mentioned or treated more closely in this paper are a juvenile specimen – see OHL (2011) – and an adult male (photos). It is an open question if the larvae are able to detect the sex of a spider.

(b) In contrast to the movable first instar larvae the larvae of the two following stages which live in spider's cocoons are leg-less, *immobile and maggot-shaped* (fig. 4). These larvae are preying on spider's eggs/embryos which they have to find before they pierce and drain the eggs/embryos. Few or even all the eggs within an egg sac are sucked out. The pupation happens within the spiders cocoon.

So in the Mantispinae a “complex developmental strategy ...” (OHL (2011)) exists: The adult Mantispinae are preying on arthropods, the first instar larvae are specialized as ectoparasites or endoparasites of spiders (and are phoretics as well, because they are transported in some cases from spider to spider – see the discussion below –, and finally to the egg sac of a spider). The last two larval instars are always specialized in preying on spider's eggs/embryos of few or numerous species (even 34 species are reported from the Japanese *Mantispa sayi*).

## THE FOSSIL LARVAE (photos 35–36)

**Material:** Three fossil larva, first instars of the family Mantispidae (Neuroptera) – most probably of the subfamily Mantispiniae – are reported from Eocene Baltic amber, two of them are attached to the opisthosoma of a male clubionid spider (one is preserved near to the spider), the holotype of *Eodoter longimammillae* n. sp., private collection of the author no. F2275/BB/AR/CJW. (*Eodoter* is an extinct genus of the family Clubionidae; see the previous paper).

**Preservation and short description:** The body length of the two attached larvae is 9 mm and about 7 mm, their shape is similar to fig. 3. Both specimens are apparently attached (not only appressed) to the spider's opisthosomal surface (an emulsion hides this area), with the tip of their abdomens close together (almost touching) for an unknown reason, bent backwards on the spider's opisthosoma and fairly close to it. A small bubble – blood of the spider? – is preserved just in front of the mouth parts of both larvae. I did not find bite marks on the spider's opisthosoma. The mouth parts of the larvae are well preserved, their abdomen is fairly flattened (more in the larger one) and bears few blunt spines but no long hairs. The legs have thickened femora, the tarsi bear no claw but an apical sensory organ which has an almost circular outline. – A third quite similar larva is preserved almost 1 cm right of the spider's body at the margin of the piece of amber. It has about the same length as the other larvae, the tip of its abdomen is cut off. It appears likely to me that this larva has been removed by the flowing resin from the spider's body or legs.

**Relationships, fossils:** According to the presence of the larvae on the body of a spider and the similarity to extant and fossil larvae of the Mantispiniae which are already published – see fig. 3, BRUSHWEIN et al. (1992), OHL (2011) – it appears likely to me that the taxon in question is a member of the subfamily Mantispiniae whose larvae parasitise spiders today. Several extinct higher taxa of the Mantispidae have been published, but their development, behaviour and relationships are unknown. Therefore it is unknown if one member of these taxa already parasitised spiders like the Mantispiniae. OHL (2011) recently published on a fossil larva of a Mantispiniae which has also been found in Baltic amber, and is also placed on the anterior opisthosomal part of a clubionid spider. Previously it has erroneously been regarded as the larva of a beetle, see JANSEN (2002: Photos 107-108), WUNDERLICH (2004: 119, photo 605). This taxon was not named and is surely not conspecific – and probably even not congeneric – with the larvae which are treated in this paper: Its opisthosoma bears long hairs and is wider anteriorly; furthermore it is not attached to the opisthosoma of its host. A closer comparison of both taxa is needed, and adults in Baltic amber, too.

Two further Eocene taxa, adults of the family Mantispidae – but both not members of the subfamily Mantispiniae – have been reported from the Grube Messel resp. from (Baltic?) amber from Great Britain, see the introduction.

**Distribution:** Eocene Baltic amber forest.

## DISCUSSION

Position of the larvae: The most frequent position of the extant ectoparasitising mantispine larvae is anteriorly on the spider's opisthosoma, the same position as in the fossils which are treated here (photos 35–36), as well as in most fossil Acari, see WUNDERLICH (2004: 117-119, photos 589-600). This is an optimal position for the larvae because spiders can only hardly use their legs to defend themselves or to clean this part of their opisthosoma. Position on a leg article: See BRUSHWEIN et al. (1992: Figs. 1-2).

Transfer of the larvae from spider to spider (see above): Apparently the tip of the opisthosoma of the fossil larvae is attached (fixed) to the opisthosoma of the male (!) spider treated here. For – an obligatory – change of the parasite to a female spider, probably during mating, this attachment has to be detached. The way of this detachment is unknown. The way of the discrimination of the spider sexes through the larvae – through the spider's pheromones? – is also unknown.

Rarity: Not a single adult member of the subfamily Mantisphaeinae has been found up to now in the Eocene Baltic amber (see the introduction), and only a single larva of this subfamily has been reported from this kind of amber before, see above (relationships). What are the reasons for this rarity? There may be several reasons: It is remarkable that both fossil spiders which bear mantispine larvae are members of Sac Spiders (Clubionidae). Clubionidae in Baltic amber are very rare, and if the parasites were specialized on this family they must also be rare in this kind of fossil resin. Extant Clubionidae are frequent outside forests – their rarity in Baltic amber may be explained by their habitat preference. To my knowledge extant European Mantisphaeinae prefer more open biotopes which are mainly covered by bushes but not by a dense forest like the Baltic amber forest. This may be the reasons for the absence of adults and the extreme rarity of larvae in Baltic amber. A further reason may be the more nocturnal activity of Mantisphaeinae; at night the fossil resin was less sticky than at day time, and flying insects were only rarely captured by the resin.

Host specificity: Certain mantispine species parasitise several species and genera of spiders; the two known host specimens in Baltic amber belong to the same family and most probably to the same genus, *Eodoter* PETRUNKEVITCH (Clubionidae). This may well be a hint for a host specificity of these parasites.

Origin/age of the mantispine behaviour: As documented by the present animals the specialized behaviour of the Mantisphaeinae is apparently at least as old as the Eocene, about 45 million years.

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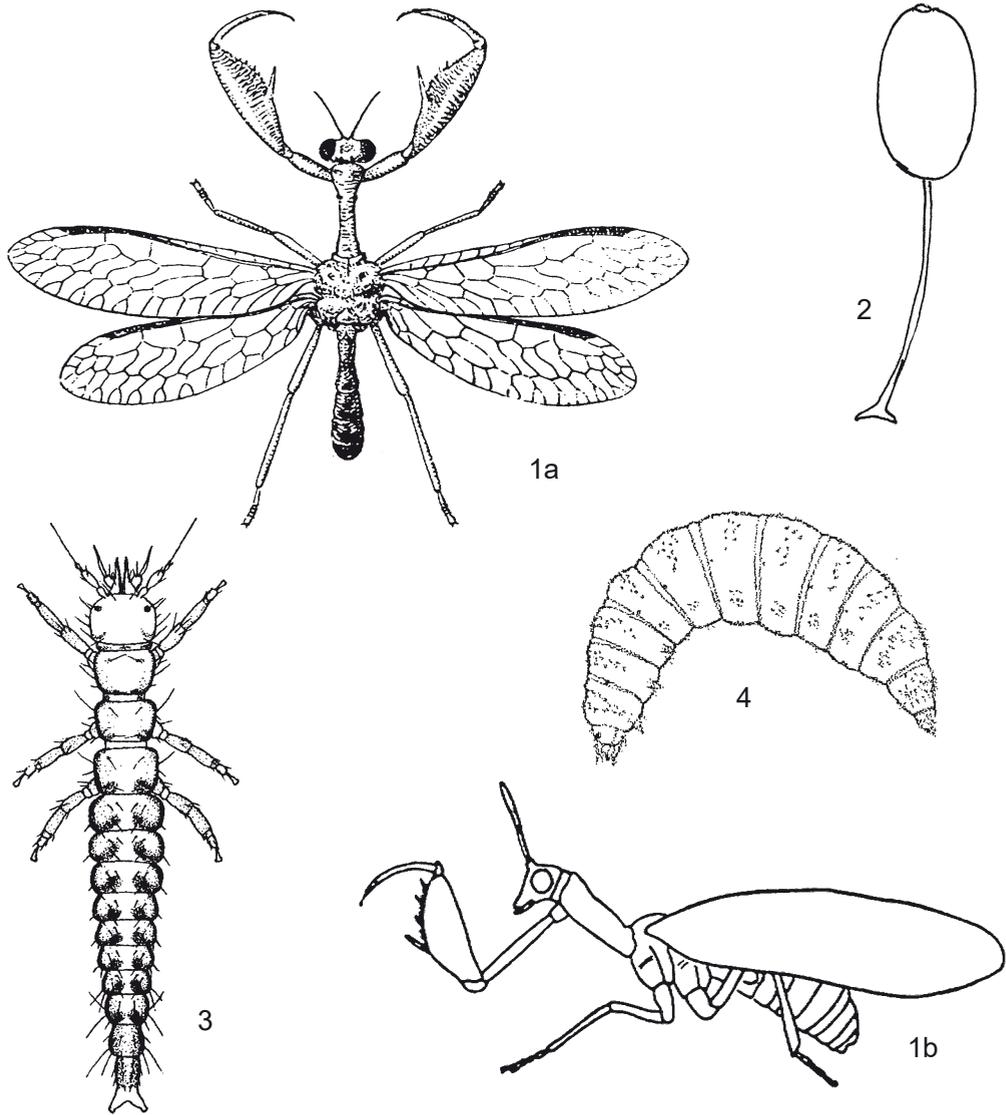


Fig. 1a) Dorsal aspect of an adult member of a European species of the genus *Mantispa*. Its raptorial forelegs and its wings are stretched out. Taken from BRISTOWE (1941);

fig. 1b) Lateral aspect of a European species of the genus *Mantispa*, length 28 mm, outline, forelegs stretched out. Taken from STRESEMANN (1964);

fig. 2) Egg (length 0.5 mm) with stark of a member of the family Mantispidae;

fig. 3) Dorsal aspect of the first instar of a japanese *Mantispa* larva which is about 1 cm long. Taken from KUROKO (1961);

fig. 4) Maggot-shaped third instar larva of a *Mantispa* sp. Taken from OHL (2011). (the last – pupal – stage is not shown here).

**ON THE FOSSIL SPIDER (ARANEAE) FAUNA IN CRETACEOUS  
AMBERS, WITH DESCRIPTIONS OF NEW TAXA FROM MYANMAR  
(BURMA) AND JORDAN, AND ON THE RELATIONSHIPS OF THE  
SUPERFAMILY LEPTONETOIDEA**

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**Key words:** Amber, Araneae, Araneoidea, Archaeoidea, Baltic amber, Burma, Cretaceous, cribellate, orb web, egg sac, Entelegynae, Eocene, evolution, Haplogynae, Leptonetoidea, Mesozoic, Myanmar, new taxa, spiders.

**Abstract:** *?Scytodes hani* **n. sp.** (Scytodidae) is described in Early Cretaceous amber from Jordan, the oldest fossil report of this family. Various spiders (Araneae) in Mid Cretaceous Burmese (Myanmar) amber are treated, new taxa are described, some new synonyms, new combinations, and new ranks are stated. A juvenile Dipluridae and a leg of a Dipluridae indet. with its web are described; *Saetosoma filiembolus* **n. gen. n. sp.** (Tetrablemmidae) is described, *Eogamasomorpha* WUNDERLICH 2008 and *Eoscaphiella* WUNDERLICH 2011 are transferred from the Oonopidae to the Tetrablemmidae, *Eoscaphiellini* **n. trib.** is erected for the taxa of the Tetrablemmidae in Burmese amber, Leptonetidae, Pholcochyroceridae (**n. stat.**), Praeterleptonetidae, and Telemidae are regarded as families of the superfamily Leptonetoidea SIMON 1890 (**n. relat.**), and excluded from the superfamily Pholcoidea (= Scytodoidea). The remarkable convergences of members of the haplogyne family Leptonetidae and the entelegyne family Linyphiidae are discussed. Pholcochyroceridae WUNDERLICH 2004 **n. stat.** and **n. relat.** is upgraded to family rank from the tribe Pholcochyrocerini WUNDERLICH 2004

of the Praeterleptonetidae WUNDERLICH 2004; ?*Pholcochyrocer baculum* **n. sp.** and *P. pecten* **n. sp.** (both Pholcochyroceridae), Palaeoleptonetinae **n. subfam.** (Leptonetidae; first Cretaceous record of the family) with *Palaeoleptoneta calcar* **n. gen. n. sp.**, *Leclercera longissipes* **n. sp.**, *L. spicula* **n. sp.**, and ?*Psilodermes filiformis* **n. sp.** (all Psilodercidae DEELEMANN-REINHOLD 1995; first fossil records of the family) are described. The family Eopsilodercidae WUNDERLICH 2008 (Pholcoidea) = Psilodercidae (**n. syn.**) is splitted: (a) The monotypic nominate tribe Eopsilodercini with its type genus *Eopsilodermes* and type species *Ioxosceloides* (probably a member of the genus *Psilodermes* SIMON 1892) are transferred to the family Psilodercidae (**n. comb./ n. relat.**). (b) The relationships of the second monotypic tribe, Furcembolusini WUNDERLICH 2008, including *Furcembolus andersoni* WUNDERLICH 2008, is unsure; it is regarded as a taxon indet. of the superfamily Pholcoidea, related to the Psilodercidae. *Lagonoburmops plumosus* **n. gen. n. sp.**, and *Myanlagonops gracilipes* **n. gen. n. sp.** (both family Lagonomegopidae, subfamily Lagonomegopinae) are described, the family Grandoculidae PENNEY 2011 is regarded as junior synonym of the Lagonomegopidae: Lagonomegopinae ESKOV & WUNDERLICH 1995 (**n. syn.**), *Archaelagonops salticoides* **n. gen. n. sp.** of the Archaelagonopinae **n. subfam.** (Lagonopidae) are described, a provisional identification key to the genera of the Lagonomegopidae (including three gen. indet.), and a map of their distribution are given. Relationships and rank of the Cretaceous family Micropalpimanidae – they are close to the Spatiatoridae – are discussed. *Ocululoborus curvatus* **n. gen. n. sp.** (Uloboridae) is described together with its possible egg sac and part of a possible cribellate orb web. *Leviunguis bruckschi* **n. gen. n. sp.** and *Hypotheridiosoma paracymbium* **n. gen. n. sp.** (Theridiosomatidae) are described as first members of this family in Cretaceous ambers, from Burma/Myanmar. The Cretaceous as the “era of the Haplogynae” is discussed and confirmed. The spider fauna preserved in Burmese amber may be much less diverse than the spider fauna in the Eocene Baltic amber. The replacement of the orb web by the “irregular” capture web is considered to be an “innovational character” for the strong radiation/diversification of the huge superfamily Araneoidea s. str. during the Palaeocene at latest. Probably hunters related to the family Salticoididae played a specific role in the evolution of derived spiders of the RTA-clade, and also the diverse family Lagonomegopidae. The consequences of erroneous determinations of Cretaceous spiders for conclusions on the phylogeny and biogeography of suprageneric taxa are discussed.

Almost all of the **material** is presently kept in the private Laboratory of Arachnology D-69493 Hirschberg, collection of the author (CJW). Most probably it will be stored later in Senckenberg (SMF).

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*Getting up in the morning without a new hypothesis is not a perfect start of the day!* JW

*Publishing about the relationships of fossil taxa we need far more question marks!* JW

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## INTRODUCTION

The present author treated Cretaceous spiders in amber already in 2008 and 2011; further references are mainly papers by D. PENNEY. An identification key to the spider families in Cretaceous ambers has been given by WUNDERLICH (2008: 564-567). Remarks on this key: The subfamily Gamasomorphinae of the Oonopidae has to be replaced by the family Tetrablemmidae, the extant families Hersiliidae, Leptonetidae, Psilodercidae (but probably not Ochyroceratidae), Scytodidae, and Theridiosomatidae have to be added to this key, as well as the extinct family Pholcochyroceridae WUNDERLICH 2008 because of its new family rank; the family Epsilodercidae WUNDERLICH 2008 (= Psilodercidae DEELEMAN-REINHOLD 1995) is splitted in this paper. Cretaceous proofs of (e. g.) the “symphytognathoids” as well as the family Pholcidae (both are very diverse today), the Dysderidae, the ancient families Hypochilidae and Austrochilidae as well as the advanced members of the RTA-clade are wanting.

New – and partly well preserved – fossil spiders in amber from Burma (Myanmar) allow a revision of several taxa. The quite important – but usually insufficiently preserved or not observable – respiratory system of the fossils is a great problem of sure determinations, and does not allow close conclusions on the relationships of members of several taxa, see below.

I hope that Mesozoic fossils will help in the future to answer two questions regarding the origin of the two most diverse branches of araneomorph spiders:

- (1) Which – extinct? – Cretaceous taxa are surely strongly related to the superfamily Araneoidea s. l. (= Orbiculariae)? See the descriptions of the superfamily Leptoneoidea in this paper;
- (2) which – extinct? – taxa are strongly related to the RTA-clade (\*\*\*) , especially to the families Lycosidae and Salticidae?

### Remarks on inclusions in amber from Burma (Myanmar) and comparison with Baltic amber and its inclusions

- (1) The tiny brownish droplets which are very frequent in many pieces of amber are most probably remains of oil of the resin. See the photos I C.
- (2) Larger grey drops which are elongated a bit pear-shaped may be sap (water-soluble) remains which originate from the resin-producing tree; GORGE POINAR, person. commun.; see e. g. with *Eogamasomorpha nubila* n. gen. n. sp. (Tetrablemmidae). I also found it in Jordan amber, with ?*Scytodes hani* n. sp..
- (3) I observed quite numerous particles of detritus and remains of dissected arthropods in many pieces of Burmese amber, and I do not want to exclude that such pieces have been produced near – or even from – the roots of the amber trees. But remarkably no member of families like the Gnaphosidae – which are typical ground-living spiders – has been found in such pieces of the fossil resin in contrast to remains of ground-living Mygalomorpha, see below.
- (4) I did not find pieces like (1) and (2) in Baltic amber, and much more rarely did I observe pieces quite full of detritus and dissected remains of arthropods (see 3).
- (5) White emulsions on the surface of arthropod inclusions – which are frequent at least on one side of inclusions in Baltic amber – are absent in Burmese (and other Cretaceous) ambers or – in rare cases – of different kind and origin.
- (6) Most arthropod inclusions are deformed by the pressure of millions of years, see the photos. Such deformations are quite rare in Baltic amber arthropods except in pieces which were heated artificially.
- (7) Certain small plant hairs are frequent in Burmese amber but much more diverse – and usually of different shape – than the typical “stellate hairs” in Baltic amber.
- (8) Certain arthropod inclusions – like ants as well as members of advanced spider families as Linyphiidae, Theridiidae and Salticidae – which are all frequent in Baltic amber – are extremely rare in Burmese amber and other Cretaceous ambers (ants) or even even absent (the spider families).
- (9) Finally: The “sweet” smell of the Baltic amber (if it has not been heated strongly) during dry grinding is absent in the Burmese amber.

## Remarks on the Cretaceous spider faunas mainly preserved in amber

The “window to the past” of the Cretaceous spider faunas goes back two or even three times compared to the age of the Eocene European amber forests, and shows quite different faunas than today or the fauna of the Baltic amber (\*). The Cretaceous spider faunas are a mixture of ancient/extinct taxa – e. g. the family Lagonomegopidae which was widely distributed in the Northern Hemisphere – and derived families like the Uloboridae and Theridiosomatidae. The main – and quite surprising – results of my studies are the relatively high frequency in the Cretaceous amber faunas (\*\*) of ...

(a) the more “primitive” (ancient) taxa within the araneomorph spiders of several haplogyne superfamilies in this “era of the Haplogynae” (see below), especially of members of the superfamilies Pholcoidea (= Scytodoidea), Leptonetoidea, and Archaeoidea (= Palpimanoidea): Archaeidae as well as the extinct family Lagonomegopidae – from which seven Cretaceous genera are known, see WUNDERLICH (2008) and below –,

(b) the relatively frequent existence of certain members of the entelegyne superfamily Araneoidea s. l. – like the Uloboridae – which CONSTRUCT ORB WEBS, in contrast ...

(c) to the relative rareness or even absence of advanced entelegyne members of the superfamily Araneoidea s. str., the NON ORB WEAVING taxa: No sure proof of, e. g., Linyphiidae and Theridiidae (which construct “irregular” webs, and which were very diverse already in the Palaeogene of the Baltic amber forest), and

(d) to members of the RTA-clade (\*\*\*) (see (e)), besides some questionable Dictynidae.

(e) Remarkably most (araneomorph) spiders in Cretaceous ambers are web-builders; hunters are surprisingly rare. I miss advanced hunters of the RTA-clade like Clubionidae, Corinnidae, Salticidae and Zodariidae.

These are quite remarkable and HUGE GAPS in the spider faunas of Cretaceous ambers. Apparently the “Big Bangs” of the radiations and diversifications of (a) the non orb-web building taxa of the superfamily Araneoidea and (b) of taxa of the RTA-clade do not go back to the Early or Mid Cretaceous. – See also the following remarks on erroneous determinations, and the paragraph “Evolution, phylogeny ...”.

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(\* ) Although the investigation of the Cretaceous spider amber faunas is still almost at the beginning, and the faunas of the soil may be underrepresented in these kinds of fossil resins.

(\*\* ) See also the report on an ancient member of the order Ricinulei in this volume.

(\*\*\*) Members of the RTA-clade – e. g. Agelenidae, Clubionidae, Corinnidae, Salticidae and Zodariidae) – are entelegyne spiders which possess a retrolateral tibial apophysis of the male pedipalpus as well as usually tarsal trichobothria (which exist also in some members of the ancient haplogyne families Caponiidae and certain extinct Lagonomegopidae).

## Remarks on erroneous and unsure determinations of Cretaceous spider taxa

Recently two Cretaceous spider taxa were reported from rocks from China resp. Korea:

(a) An alleged member of the family Philodromidae by CHENG et al. (2009) as *Cretadromus liaoningensis* n. gen. n. sp. The absence of an unpaired tarsal claw, the position of the eyes, the chaetotaxy, and the trichobothriotaxy of the single described spider are unknown or unclear; according to the shape of the prosoma and the position of the legs – which is not laterigrade but apparently prograde – this taxon is not a member of the family Philodromidae, and most probably even not related to this family. The shape of body and legs is similar to the family Theridiosomatidae which has been reported already from the Cretaceous, see below. Most members of this family are smaller than 3mm, the body length of the Cretaceous *Eocoddingtonia eskovi* SELDEN 2010 is up to 4.52 mm, the body length of the large and – according to the large opisthosoma – apparently egg-bearing female of *Cretadromus liaoningensis* is 5.76 mm.

(b) An alleged probable member of the superfamily Lycosoidea by SELDEN (2012) as *Korearachne jinju* n. gen. n. sp., based on a juvenile or female spider which has a body length of probably about 3 mm or less. The existence of an unpaired tarsal claw, the trichobothriotaxy, the exact chaetotaxy, the area of the eyes as well as most or all parts of the opisthosoma of the spider are unknown. Surprisingly the genus is characterized as “ecribellate” although the area of the spinnerets is not preserved, and although the posterior metatarsus is straight in some cribellate spiders. The existence of very long legs I – compared with the relatively short legs IV – and the relatively weak leg bristles, too, exclude the species in my opinion clearly from the superfamily Lycosoidea (and from other “wandering spiders” like Pisauridae) but long anterior legs do not rarely exist in web building spiders like Araneoidea, Pholcoidea and Leptonetoidea, see below. Therefore relationships of *Korearachne* to the Lycosoidea appear quite unlikely to me, and I would like to exclude it from the superfamily Lycosoidea, and the RTA-clade as well, and transfer it to haplogyne spiders, probably Pholcoidea or Leptonetoidea, which are very frequent in the Cretaceous. A sure proof of a Cretaceous member of the Lycosoidea – and even of the RTA-clade besides questionable Dictynidae – does not exist. – SELDEN (p. 5) again regarded the Cretaceous genus *Palaeohygropoda* PENNEY 2004 in Burmese amber – without hesitation or discussion (!) – as a taxon of the family Pisauridae although I justified its exclusion from this family – and even from the superfamily Lycosoidea, and entelegyne spiders as well –, see WUNDERLICH (2008: 539, 591).

Spiders in Cretaceous amber from Canada were reported as ?Linyphiidae indet. and ?Theridiidae indet. by MCALPINE & MARTIN (1969: 836). These families – the family Ctenidae of the RTA-clade (!) is added without a documentation – are repeated by MC. KELLAR & WOLFE in PENNEY (2010: 148), but remarkably all families are listed in this paper without a question mark.

Such publications and the descriptions of spiders – see above (a, b) – prolong the long list of erroneous or unsure determinations of Cretaceous spiders, see WUNDERLICH (2004: 539-540) (\*). Repetitions of errors do not make them more true. They may seriously harm the reputation of araneology, phylogeography, and palaeontology as well.

Erroneously determined higher (familiar or suprafamiliar) taxa may lead to totally wrong conclusions concerning “ghost lines” within the evolution of spider families. Linyphiidae and its sister group Pimoidae, e. g., are dated back to the Early Cretaceous although not a single sure proof of the Linyphiidae exists from that era, see PENNEY & SELDEN (2011: 73, 97). Mainly for that reason I called some of these lines “lines of phantasy”, see WUNDERLICH (2008: 540). – Removing certain families like Linyphiidae, Pisauridae and Salticidae from the list of Cretaceous spiders would delete two huge taxonomical branches: The “linyphioid branch” of the superfamily Araneoidea, as well as most Trionycha and the Dionycha of the RTA-clade. Such “evolutionary trees” do not reflect the reality. The relationships of various families are unsure but their “ghost lines” are drawn back to their alleged sister groups.

Because of their – erroneous in this case – “gondwanan concept” certain authors have ignored/neglected the well documented proof of the family Cyatholipidae in the Eocene Baltic amber for many years.

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(\* ) It is remarkable that notes on the different/controversial opinions on the determination and relationships of Cretaceous taxa are missing in the Internet Catalog of fossil spiders by DUNLOP et al. within the World Spider Catalog by PLATNICK, as well as in reviews, in which such questionable determinations were never corrected or even noted or discussed. Are these cases of covering up? Why are such erroneous/questionable determinations not corrected or discussed by the original authors? The correction of the misidentification of Cretaceous Salticidae – see PENNEY & SELDEN (2011: 77) – is a rare exception. In the same catalog by PLATNICK – including the part on fossils – the family Mimetidae of the entelegyne superfamily Araneoidea is still listed within the Palpimanoidea, and the haplogyne superfamily Archaeoidea (unter Palpimanoidea) is listed within the Entelegynae, although HUBER (2004: 364) stated – based on male genitalia – that “New evidence is presented against Palpimanidae being representatives of Entelegynae”.

In the case of Tetrablemmidae – Oonopidae: Gamasomorphae – I correct my previous determination on family level, see below.

### Remarks on the ecology and the frequency of spiders which are preserved in Cretaceous ambers

Ancient spiders of the Mesothelae, most Mygalomorpha, the Filistatidae, and the Dysderoidea are ground-dwelling spiders, and therefore quite rare or even absent in Cretaceous ambers. Frequent spiders in Cretaceous ambers are (a) the capture web constructing and usually long-legged haplogyne members of the superfamilies Pholcoidea (= Scytodoidea) (e. g. Psilodercidae), and Leptonetoidea (e. g. Pholcochyroceridae), (b) the non web-building haplogyne members of the superfamily Archaeoidea (e. g. Archaeidae and Lagonomegopidae), and (c) spiders of the entelegyne orb-weaving superfamily Araneoidea s. l. (e. g. Uloboridae and Araneidae). Certain (most?) members of such taxa are/were dwellers of higher strata of the vegetation in contrast, e. g., to the short-legged and rare members of the family Burmascutidae which probably were not capture web builders. See also above “Remarks on the spider faunas...”, and below, “Phylogeny, ...”.

## EVOLUTION, PHYLOGENY, BIOGEOGRAPHY AND FAUNISTIC

See also above.

Extinct members of the superfamily Leptonetoidea – which are revised in this paper – demonstrate the high taxonomical and phylogenetical importance of Cretaceous spider fossils. With regard to the evolution of spiders the oldest – and cribellate – members of the haplogyne family Leptonetidae are one of the most spectacular new discoveries in Burmese amber. Leptonetidae and the extinct Spatiatoridae (compare the Micropalpi-manidae) – also known from the Eocene Baltic amber forest – are families whose roots go back at least to the Cretaceous (e. g. the Burmese amber forest), but surely much further. The conditions in the extinct subfamily Mizaliinae of the Oecobiidae are similar: The genus *Mizalia* KOCH & BERENDT 1854 in Eocene Baltic amber, and the genus *Zamilia* WUNDERLICH 2008 in Cretaceous Burmese amber. Certain haplogyne Cretaceous families like the enigmatic Lagonomegopidae – they were widely distributed in the Northern Hemisphere – and the Pholcochyroceridae – known only from Burmese amber – have not been reported from the Palaeogene, and apparently became extinct at the end of the Cretaceous at latest. Although members of the Lagonomegopidae were frequent and widely distributed during the Cretaceous (see the introduction), they apparently – for unknown reasons – did not survive this era.

In 2008: 559 and 2011: 542 I proposed to call the Cretaceous “THE AGE OF THE HAPLOGYNAE” (1) (see also below, the “long-living” genera which ALL are haplogyne). Now I think that the whole Mesozoicum can be called by this term. Contrarily the Palaeogene and Neogene (= the Cenozoicum) may be called the “AGE OF THE DERIVED ENTELEGYNAE and the RTA-CALDE” (2). It is well documented that Haplogynae – besides orb-weaving entelegyne spiders of the superfamily Araneoidea s. l. (= “Orbiculariae”) (3) – were quite dominant in the Cretaceous, in contrast to NOT capture web building (but hunting) derived entelegyne spiders of the RTA-clade which were extremely rare in that era (the Cretaceous and the whole Mesozoicum). Sure proofs of diverse families of hunting spiders mainly of the two-clawed Dionycha like Jumping Spiders (Salticidae), Sac Spiders (Clubionidae) or Crab Spiders (Thomisidae) – as well as the three-clawed Wolf Spiders (Lycosidae) and Ant Eaters (Zodariidae) – are even totally absent (!) in the Cretaceous proof to my actual knowledge. See above the chapter on “erroneous determinations”.

The identification of mechanisms causing the radiation and diversification of organisms is a main goal of evolutionary biology. We still know little about the forces which drove spider radiation and diversification. Which were the most important steps in the evolution to/of the derived/advanced spiders? Apparently here we have a multicausal event; the evolution of the entelegyne stage may be one of the most important “innovations”, the loss of the cribellum another one. (Cribellate threads are used in capture webs but are not used by mobile hunting spiders).

One of the main ancient characters of spiders is undoubtedly the existence of a capture web, and the orb web is apparently a very old structure. In certain groups the capture web apparently changed its kind, e. g. within the superfamily Araneoidea (a) (3); in others (b) it has been lost: In the Dionycha of the RTA-clade (4) (some reversals exist). So

these alterations happened at least at/within two “high” groups or taxa of spiders which are not closely related – the most diverse spider groups/taxa today! – and thus different questions have to be asked and different answers are expected.

(a) What are the reasons for the – with regard to geological periods – LATE change of the orb web TO AN IRREGULAR web within the Araneoidea, as well as the enormous diversification – and probably also the late radiation – of this branch (3), as well as the replacement of several haplogyne families? Probably the combination of two reasons determined this evolution: The evolution of the entelegyne stage and the coevolution of (mainly) non flying insects, the wingless ant workers, see WUNDERLICH (2008: 550-552). Certain haplogyne families like Praeterleptonetidae and Pholcochyroceridae – which are extinct today, and unknown from the Palaeogene – were probably displaced by advanced entelegyne families of similar/equal life-form types (“Lebensformtypen” in German) like Linyphiidae, Synotaxidae and Theridiidae.

(b) What are the reason(s) for the – with regard to geological periods – LATE and HUGE diversification – and probably also the late radiation – of the numerous hunters (mainly the Dionycha) of the RTA-CLADE (4)?

The evolution of a hunting behaviour and special kinds of prey capturing (pace-makers of the evolution?) – after the loss of the cribellum, the capture web, and most often (not in the Lycosidae and Pisauridae which basal groups are web builders, see, e. g., MURPHY et al. (2006)) of the unpaired tarsal claw (5) – connected frequently with dwelling on the soil, the evolution of large eyes (6), fast running, a jumping behaviour, leg scopulae, claw tufts, strong paired ventral bristles of the tibiae and metatarsi I-II, and a guarding behaviour of the egg sac and/or spiderlings (e. g. in the families Clubionidae, Lycosidae, Pisauridae, and Salticidae) – may have been important steps in the evolution of derived spiders. The evolution of the entelegyne stage, the extension of open biotopes as well as the diversification of ants (with the coevolution of the ant-eating members of the family Zodariidae) – before or within the era about 80 to 50 million years ago – may also have played an essential role in this connection. I do not want to exclude that hunters of the extinct family Salticoididae – they were apparently cribellate, possessed three tarsal claws and feathery hairs (!) – were not too far from the root of the enigmatic extinct taxon of spiders we are searching for (which means the origin of the RTA-clade). – The enigmatic extinct family Lagonomegopidae (they possessed powerful posterior median eyes, figs. 45 and 68, and some species possessed tarsal trichobothria!) may be another candidate in this respect. I am not sure about the haplogyne (more likely to me) or entelegyne stage of this family. – The families Chummidae and Succinomidae – see the paper on Baltic amber spiders in this volume – may be “old” (Jurassic?) relicts which survived up to the Cenozoicum (7).

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(1) PENNEY & SELDEN (2011:76) published a selected list of 7 extant haplogyne families of spiders which are not reported from the Cretaceous; some families like Dysderidae and Palpimanidae – which are haplogyne, too – have to be added. The families Tetrablemmidae, Scytodidae, Leptonetidae and probably Ochyroceratidae (in the case the Psilodercidae are not split off from this family) are reported here for the first time from the Cretaceous and have to remove from the list given by PENNEY & SELDEN (the Plectreuridae are reported even from the the Jurassic), and other haplogyne families will surely follow the removing from this list. Altogether almost 20 – extant + extinct (ca. 5) – haplogyne families are reported from the Cretaceous but only about 10 entelegyne families, which is half of the haplogyne families. Today the number of entelegyne spider families is – the other way round – more than twice the haplogyne families.

So the relation of haplogyne and entelegyne spiders CHANGED BY FOUR TIMES from the Cretaceous (ambers) to today, and so the term “AGE OF THE HAPLOGYNAE” for the Mesozoicum is supported; contra DUNLOP & PENNEY (2012: 118, 123). – The different number of genera of different eras: See WUNDERLICH (2011: 543). Haplogyne stage of the Archaeoidea (= Palpimanoidea): See above: “(\*)” within the paragraph “Erroneous ... determinations”.

(2) Comparable in some respects is the rapid Palaeogene diversification of the Plazentalia among the Mammalia and of derived Formicidae.

(3) Members of the basically orb-weaving superfamily Araneoidea s. l. (= “Orbiculariae”):

(A) The cribellate Deinopidae + Uloboridae (= Deinopoidea), and (B) the remaining ecribellate families (= Araneoidea s. str.) like (a) the orb-weaving Anapidae, Araneidae, Comaromidae, Nephilidae, Mysmenidae, Symphytognathidae, Synsphaeridae, Tetragnathidae, Theridiosomatidae and Zyggiellidae, (b) the families which construct “irregular” capture webs, including (b1) the members of the “spineless femur clade”: Cyatholipidae, Nesticidae, Synotaxidae and Theridiidae, (b2) the members of the “linyphioid branch” like Pimoidae and Linyphiidae, see WUNDERLICH (2008: 117-121), and (c) a family which lost its capture web: The Mimetidae.

(4) Families like Clubionidae, Corinnidae, Salticidae, Sparassidae, and the sit-and-wait predators Thomisidae.

(5) All spiders which construct a capture web possess an unpaired tarsal claw, but not most of all three-clawed spiders build capture webs, e. g. not the advanced members of the Lycosidae and the Pisauridae.

(6) Powerful posterior median eyes (figs. 45, 68) evolved convergently in the extinct family Lagonomegopidae which members may have been “sit-and-wait” predators.

(7) Ancient members of the superfamily Austrochiloidea are restricted to the Southern Hemisphere today. Fossils of its families – Austrochilidae and Gradungulidae – have never been reported up to now.

“Long-living” genera: Only a very small percentage of the genera of the Burmese amber forest – or other Cretaceous forests – survived to my actual knowledge as “living fossils” within the araneomorph spiders. The assignment of some genera appears unsure and may change after revisions in the future, but they are undoubtedly strongly related to the listed genera:

- *Ariadna* AUDOUIN 1826 (Segestriidae) (cosmopolitical),
- *Orchestina* SIMON 1882 (Oonopidae) (cosmopolitical), most probably the diverse genus will be split in the future,
- probably *Scytodes* LATREILLE 1804 (Scytodidae) (cosmopolitical); most probably the diverse genus will be split in the future,
- *Leclercera* DEELEMANN-REINHOLD 1995 (Psilodercidae) (South East Asia),
- probably *Psiloderces* SIMON 1892 (Psilodercidae) (South East Asia) (the determination is not quite sure).

All these genera are members of the relatively basal branch of the haplogyne spiders.

A remarkable assemblage of syninclusions in a piece of amber from Burma (Myanmar), F2272/BU/AR/CJW (size 4.5 x 3.2 x 1.8 cm), which contains numerous taxa:

3 spiders, insects of 5 orders: Two Coleoptera, remains of a Trichoptera, a Hymenop-

tera, a Hemiptera, and a Psocoptera (but not a single Diptera). A thread of a spider's capture web in which small sticky droplets exist, remains of plants including parts of a large leaf are also preserved. Acari are absent. – The spiders within this piece are members of three “primitive” families of the haplogyne superfamilies Dysderoidea: *Burmorchestina pulcher* WUNDERLICH 2008 (Oonopidae), female, body length 1 mm, and Archaeoidea (= Palpimanoidea): *Eomysmauchenius ?septentrionalis* WUNDERLICH 2008 (Archaeidae), ?adult female, body length 2 mm, as well *Burlagonomegops eskovi* PENNEY 2005 (Lagonomegopidae), juvenile, body length 1.4 mm. Members of these three families build no capture web. The existence of these spiders as syninclusions show their similar habitat; at least one of these spiders was probably transported to the resin through a large leaf which is preserved in the same piece of amber.

**TAXONOMY** photos: I C p. 346–351

Note: The relationships of certain of the curious/conspicuous fossil taxa – e. g. of the genus *Pholcochyrocer* – are not sure, even on the family level.

Remark regarding the diagnoses of higher taxa:

In those cases in which I found autapomorphic characters I tried to restrict the diagnosis to such – quite rare or even unique – autapomorphic characters, and to list plesiomorphic characters – as well as synapomorphies with related taxa – separately. Unfortunately clear autapomorphic characters are not very frequent; in such cases a combination of special characters has to use, and synapomorphies with related taxa as well.

### **Determination of the Cretaceous araneomorph spider families:**

An identification key to the spider families in Cretaceous ambers has been given by WUNDERLICH (2008: 564-567). Remarks on this key: The subfamily Gamasomorphinae of the Oonopidae (no. 3 in this key) has to be replaced by the family Tetrablemmidae (see below), the extant families Hersilliidae, Leptonetidae, Psilodercidae (but probably not Ochyroceratidae), Scytodidae, and Theridiosomatidae have to be added to this key, as well as the extinct family Pholcochyroceridae WUNDERLICH 2008 because of

its new family rank; the family Eopsilodercidae WUNDERLICH 2008 (= Psilodercidae DEELEMANN-REINHOLD 1995) is splitted in this paper.

Please add within no. 4 after "... almost sideward": "or in a median position (fig. 68)"; please add to no. 7: "Preening comb usually existing" and to no. 7 -: "Preening comb absent; various ambers";

within no. 8 – "Prolateral spatulate leg hairs exist on metatarsi and tarsi I-II" has to eliminate as well as two lines later the whole line "- Spatulate leg hairs ... 9";

Hersiliidae are easily recognizable by its extremely long posterior spinnerets, the six-eyed Scytodidae by its domed prosoma (fig. 6), the armoured and tiny Tetrablemmidae by its lateral opisthosomal scuta.

## A. MYGALOMORPHA

### Family **DIPLURIDAE**

Dipluridae construct capture webs which contain a part of a sheet web as well as a funnel as retreat, which are placed, e. g., at the base of tree trunks.

Members (or their remains) of this family are not rare in – e. g. Baltic and Dominican – ambers but reports are rare in Cretaceous ambers up to now.

Remains of three mygalomorph spiders – but no complete specimen – in Burmese amber were treated by WUNDERLICH (2008: 68-69). At least two of these remains may be members of the family Dipluridae. Here I add remains of a further specimen of this family, and a complete juvenile, the first published complete diplurid specimen in Cretaceous ambers.

**Dipluridae indet.:** Remains (fig. 1) photos 1–2

**Material** in Cretaceous Burmese amber: A left leg., probably the anterior leg, and a part of a web in contact with the leg and a larger part of a plant. Some parts of leg articles probably of the same spider are preserved in different areas of the piece of amber as well parts of a spiders web, F2278/BU/AR/CJW.

**Preservation and syninclusions:** The leg is completely preserved, broken – most probably by the process of decomposition – in the distal half of the metatarsus and partly broken in the middle of the tibia. Directly above the leg the larger part of an irregular spider's web (of a/the Dipluridae?) is preserved in contact to a larger part of a plant. – Further syninclusions: The – dissected/decomposed holotype of *Oculoborus curvatus* n. gen. n. sp. (Uloboridae) together with a questionable egg sac and part of a (its?) web (see below), Acari, remains of beetles, a cicada and a Blattaria; larvae, excrement ballets of insects, numerous remains of other arthropods and plants, detritus, fungi (hyphae) and bacteria.

**Descriptions:**

(a) The leg (fig. 1, photo 1):

Measurements (in mm): Coxa 2.0, trochanter 0.8, femur 4.2, patella 2.0, tibia 2.8 (height 0.9), metatarsus 4.1, tarsus (the distal part is hidden) probably 2.0.

Colour medium brown. – The hairs are fairly long, a scopula is absent, the coxa (fig. 1) bears short ?stridulatory bristles. Long and slender bristles (some are probably broken off): Femur probably none (parts are hidden), patella none, tibia 1 in an apical-ventral position, metatarsus a ventral pair in the basal half, a ventral pair in the distal half, and 3 apically-ventrally. Club-shaped trichobothria are absent, the tarsal claws are hidden.

(b) The web (photo 2) is irregular and deformed, ca. 1.5 cm long; it consists of fine threads. In my opinion it is only little doubt that it is a part of the web of the spider in question.

**Relationship:** Mainly according to the few and thin leg bristles, the absence of a leg scopula, and the existence of the part of a web close to the spider's anterior leg regard the spider as a member of the family Dipluridae whose remains are not rare in fossil resins.

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

**Dipluridae indet.:** A juvenile (photo 3)

**Material:** 1 juv. in Mid Cretaceous Burmese (Myanmar) amber, coll. ALEX BEIGEL, BU-42/CAB.

The spider is completely and deformed preserved in a clear yellow-orange piece of amber. Spiny remains of a plant are preserved in front of the chelicerae, some bubbles ventrally in contact to the spider.

Measurements (in mm): Body length 1.8, prosoma: Length 1.2, width ca. 1.0, length of the basal cheliceral articles 0.5, of the fangs at least 0.45, femur I 1.05, femur IV 1.15. – Prosoma and legs are brown and darkened, the opisthosoma is grey. – Prosoma almost smooth, bearing a wide transverse furrow in the position of the fovea which may

be an artifact. 8 eyes in a compact group, basal cheliceral articles strongly protruding, at least 4 teeth below the fang, labium wider than long, apparently fused to the sternum, bearing few structures similar to cuspules which I regard as artefacts, gnathocoxae strongly elongated anteriorly, cuspules not observable, sternal sigillae unknown. – Legs fairly long and slender, some of their hairs are quite long, few bristles: all metatarsi bear ventrally apically 3 longer ones. Paired tarsal claws long, bearing numerous long teeth, unpaired claw short and strongly bent. – Opisthosoma oval, 2 pairs of widely spinnerets, the posterior ones as long as the opisthosoma (1.6 mm), its articles subaequal and pointed like the median spinnerets.

Close **relationships** are unknown to me. Extant diplurid genera in SE-Asia are *In-dothele*, *Leptothele*, and *Phyxioschema*.

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

## B. ARANEOMORPHA

### B 1. HAPLOGYNAE

Synonymy and new combinations: See also the abstract.

(1) Superfamily **PHOLCOIDEA** C. L. KOCH 1851 (= Scytodoidea BLACKWALL 1864, the younger name).

This is the branch in which the females carry their egg sac (except the Tetrablemmidae: Tetrablemminae), see WUNDERLICH (2004: 645); Leptonetidae and Telemidae are separated in this paper from this branch, see below, the superfamily Leptonetoidea.

Family **TETRABLEMMIDAE**

Tetrablemminae are tiny and strongly armoured spiders; their legs are bristle-less, prosoma and basal cheliceral articles possess usually (!) modifications/outgrowths; these and the large cheliceral lamina have not been observed by me in the insufficiently preserved fossils. The prosoma of extant spiders is quite high in contrast to the prosoma of the Cretaceous spiders in Burmese amber (fig. 2). In contrast to armoured Oonopidae: Gamasomorphinae LATERAL scuta of the opisthosoma exist, see WUNDERLICH (2008: 659, fig. 10), and an unpaired tarsal claw as well (both may be difficult to observe in the fossils).

Fossils of this pantropical family – of the subfamily Tetrablemminae but not of the Pacullinae – have been reported from Miocene Dominican amber and from Eocene Baltic amber, see WUNDERLICH (2004: 726- 731), but never from the Mesozoicum.

Here I will correct my erroneous determinations, describe a further male of *Eogamasomorpha nubila* WUNDERLICH 2008, the member of a sp. indet., a new tribe (Eoscaphiellini) of the Tetrablemminae, and provide a key to the fossil taxa in Burmese amber.

Corrections: Members of two genera of the Tetrablemmidae have been erroneously described by me as members of the subfamily Gamasomorphinae of the Oonopidae:

- (a) *Eogamasomorpha nubila* WUNDERLICH 2008 (n. gen. n. sp.) (**n. relat.**),
- (b) *Eoscaphiella ohlhoffi* WUNDERLICH 2011 (n. gen. n. sp.) (**n. relat.**).

Based on better preserved fossils I correct herewith my previous erroneous determinations, and transfer these two taxa from the Oonopidae to the Tetrablemmidae. Their prosomal modifications are apparently weak (deformed and difficult to observe), their lateral opisthosomal scuta are frequently hard to observe, and their low prosoma (fig. 2) is extremely rare in extant Tetrablemmidae in contrast to the Oonopidae, see below.

Key to the taxa of the Tetrablemmidae in Burmese amber (♂):

- 1 Posterior half of the prosoma and anterior part of the opisthosoma dorsally covered with long hairs (fig. 2), legs long and slender, prosoma ca 20% shorter than femur I, position of the metatarsal trichobothria unknown, pedipalpal tibia thickened, embolus longer than the bulbus (fig. 3) . . . . . *Saetosoma filiembolus* n. sp.

- No long hairs in this position, prosoma longer than femur I, pedipalpus quite different, its tibia slender. . . . . 2
- 2(1) Prosoma ca. 10% longer than femur I, position of the metatarsal trichobothria in ca. 0.4, see WUNDERLICH (2011: 555, fig. 1): Embolus shorter than the large bulbus which has a diameter of ca. 0.1 mm . . . . . *Eoscaphiella ohlhoffi* WUNDERLICH 2011
- Prosoma ca. ¼ longer than femur I, pedipalpus: Embolus longer than the bulbus, thinner, diameter of the bulbus ca. 0.07 mm . . . . . 3
- 3 (2) Embolus thin, see WUNDERLICH (2008: 659, figs. 712-713), position of the metatarsal trichobothria near the end of the article . . . . .  
. . . . . *Eogamasomorpha nubila* WUNDERLICH 2008
- Embolus thick (figs. 4-5), position of the metatarsal trichobothria unknown . . . . .  
. . . . . Tetrablemminae indet.

**EOSCAPHIELLINI n. trib.**

Type genus: *Eoscaphiella* WUNDERLICH 2011. Further genera: *Eogamasomorpha* WUNDERLICH 2008 and *Saetosoma* n. gen..

**Diagnosis** (♂; ♀ unknown): Prosoma (fig. 2) low, see also WUNDERLICH (2008: 659, fig. 10).

**Further and basic characters:** 6 eyes in a “segestriid position”: A wide anterior row of 4 eyes in a transverse position, and posterior lateral eyes which are widely spaced; prosomal modifications probably weak, body length 0.9-1.1 mm.

**Relationships:** According to the tiny body size Eoscaphiellini should be a member of the subfamily Tetrablemminae, see LEHTINEN (1981). Almost all extant Tetrablemmidae (Pacullinae and Tetrablemminae as well) possess a high/raised prosoma; a FAIRLY low prosoma is only from the extant species *Bacillemma leclerci* DEELEMANN-REINHOLD 1993 from Thailand. – I do not want to exclude that Eoscaphiellini may be a subfamily of its own, and the sister group to all other Tetrablemmidae.

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

## **Saetosoma n. gen.**

The name of the genus points to the long dorsal hairs (lat. setae) of parts of the body (lat. soma). Its gender is neuter.

Type species (by monotypy): *Saetosoma filiembolus* n. sp.

**Diagnosis** (♂; ♀ unknown): Posterior part of the prosoma and anterior part of the opisthosoma dorsally covered with long hairs (fig. 2), six eyes in a “segestriid position”, pedipalpus: Fig. 3, with tibia and cymbium strongly thickened.

**Relationships**: According to the low prosoma a member of the Eoscaphiellini n. trib. I do not know long dorsal body hairs or similar structures of the bulbus in other taxa of the Tetrablemmidae. See the key above.

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

## ***Saetosoma filiembolus* n. gen. n. sp. (figs. 2–3) photo 4**

The name points to the (lat.) filiform (thread-shaped) shape of the embolus.

**Material**: Holotypue (♂) in Mid Cretaceous amber from Burma (Myanmar), F2347/ BU/AR/CJW.

**Preservation and syninclusions**: The spider is completely but distinctly deformed preserved in a clear yellowish piece of amber, bubbles exist at the left tibia III and the left metatarsus IV. Particles of detritus, remains of a Diptera as well as stellate hairs are preserved in the larger piece which was separated.

**Diagnosis** (♂; ♀ unknown): See the genus.

### **Description** (♂):

Measurements (in mm): Body length almost 0.9, prosomal length 0.45, opisthosoma: Length 0.55, width 0.33; leg I: Femur 0.55, patella 0.1, tibia 0.38, metatarsus 0.25, tarsus 0.26, tibia II 0.28, tibia III 0.25, tibia IV 0.3.

Colour mainly redbrown.

Prosoma (fig. 2, photo) deformed, low, distinctly longer than wide; 6 eyes apparently in a “segestriid position”, dorsally in the posterior half with long hairs, anteriorly dorsally probably with a pair of (deformed) outgrowth, clypeus long, bulging and protruding, basal cheliceral articles fairly long, mouth parts hidden, sternum slender, coxae IV weakly separated. – Legs (photo) long and slender, bristleless, order I/IV/II/III, hairs not distinct,

trichobothria unknown, tarsi long, two tarsal claws on an onychium, bearing long teeth, spatulate hairs absent. – Opisthosoma (fig. 2, photo) 1.7 times longer than wide, anteriorly with long dorsal hairs, remaining hairs short, dorsally completely covered with a scutum, a ring exist around the spinnerets, ventrally and laterally scutate, too, lung covers slender, sclerotized. – Pedipalpus (fig. 3, photo; its articles are strongly deformed): Femur and patella slender, tibia and cymbium distinctly thickened, bulbus simple, almost globular, embolus thin, bent, originating almost apically.

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

***Eogamasomorpha nubila*** WUNDERLICH 2008, photos 7–8

Material: 1♂ in Cretaceous Burmese (Myanmar) amber, F2362/BU/CJW.

The spider is only fairly well preserved, partly deformed by pressure (and heating?), parts of the left legs I–IV are cut off, the right leg II is amputated through the tarsus. The prosomal length is 0.5 mm, the position of the metatarsal trichobothria is unknown, the mouth parts are hidden, the large dorsal opisthosomal scutum, the three or four ventral scuta and the three longitudinal opisthosomal scuta are well preserved (photo). The shape of the embolus is as in the holotype, see WUNDERLICH (2008: 659, figs. 712–713).

**Gen. indet.** (Tetrablemminae) (figs. 4–5)

**Material:** 1♂ in Mid Cretaceous Burmese (Myanmar) amber and a large separated piece of amber, F2351/BU/AR/CJW.

**Preservation:** The spider is almost complete (most parts of the opisthosomal ventral surface are lost), distinctly darkened, and strongly deformed preserved in a yellowish piece of amber.

**Description** (♂; ♀ unknown):

Measurements (in mm): Body length 0.9, prosomal length 0.4; leg I: Tibia 0.25, metatarsus ca. 0.17, tarsus 0.2.

Colour dark red brown. Body slender, eyes probably in a “segestriid position”, legs not long, bristleless, opisthosoma dorsally completely covered with a scutum, most parts of the ventral surface are lost. Pedipalpus (figs. 4–5) apparently with slender articles, the deformed embolus is long, fairly thick and bent.

**Relationships:** See the key. The species may well be the member of an undescribed genus.

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

## Family **SCYTODIDAE**

Most members of the six-eyed “Spitting Spiders” are easily recognizable by their domed prosoma (fig. 6, photo); their legs are bristle-less. The family has a cosmopolitan distribution; most species live in the tropics. Fossils were described from Miocene Dominican and Eocene Baltic ambers, see WUNDERLICH (1988: 71–75) and (2004: 706–711). Here I describe the first taxon of this family in Cretaceous amber, in amber from Jordan, as a questionable member of the very diverse genus *Scytodes* LATREILLE 1804 which most probably will be splitted in the future. Jordan amber: See WUNDERLICH (2008: 534 and 643).

?*Scytodes hani* n. sp. (figs. 6–7)

Derivatio nominis: I name the species with pleasure after HANI KADDUMI in Amman (Jordan), who collected the amber piece which includes the holotype.

**Material:** Holotype, a juvenile or adult female in Early Cretaceous amber from Jordan, Zarqa river canyon, F2308/JB/AR/CJW.

**Preservation and syninclusions:** The spider is not well and partly deformed preserved in a small piece of amber, parts are hidden by particles of detritus and fissures in the amber, the opisthosomal hairs are covered with numerous tiny bubbles. The left leg I is apparently lost beyond the coxa, the left leg IV is cut off at the end of the femur. Numerous small and tiny particles of detritus and a half grey drop which may have originated from the amber tree (see above, “Remarks on inclusions...(2)”), are preserved in the same piece of amber.

**Diagnosis** (juvenile or adult ♀): Prosoma (fig. 6) strongly domed and hairy, femur I (fig. 7) distinctly bent; an unpaired tarsal claw is probably absent.

**Description** (juvenile or adult ♀):

Measurements (in mm): Body length ca. 2.2, prosoma: Length 1.0, height ca. 0.5; opisthosoma: Length 1.2, height 0.7; leg I: Femur 0.9, patella 0.23, tibia 0.7, metatarsus 0.8, tarsus 0.45, tibia II 0.68, tibia III 0.58, tibia IV 0.8.

Colour: Prosoma and legs medium grey brown, opisthosoma light grey.

Prosoma (fig. 6) distinctly domed, 1.5 times longer than high, dorsally in the anterior half covered with long hairs, eyes deformed and partly hidden, apparently 6 eyes in a position which is typical in *Scytodes*, chelicerae, mouth parts and sternum hidden. – Legs of medium length, order IV/II/III/III, III distinctly the shortest, hairs not distinct, bristles absent, femur I distinctly bent (fig.7), trichobothria unknown, paired tarsal claws with long teeth, unpaired claw (their area is difficult to observe) probably absent. – Opisthosoma oval, 1.7 times longer than high, hairy, spinnerets hidden.

Close **relationships** are unknown; better preserved and – most important – an adult male are needed for conclusions, e. g., to find out the existence of an unpaired tarsal claw, the position of the eyes, and the teeth of the cheliceral fang furrow. The revision of the supraspecific taxa of the family Scytodidae is in progress, see LEHTINEN (2010: 244) who reported the absence of an unpaired tarsal claw in the genus *Dictis* L. KOCH 1872. The genus *Scytodes* will have to split most probably in the future.

**Distribution:** Early Cretaceous amber from Jordan.

Family **PSILODERCIDAE** DEELEMANN-REINHOLD 1995

(= Eopsilodercidae WUNDERLICH 2008 (**n. syn.**)).

See WUNDERLICH (2008: 585) (upgrading from the subfamilial rank within the Ochyroceratidae), and the possible cladogram below.

In recently studied Cretaceous fossils I recognized a high variability of the structures of the ♂-pedipalpus, and I found no clear limit between the Eopsilodercidae and the Psilodercidae.

Synonymy/combinations within the family **Eopsilodercidae** WUNDERLICH 2008:

The family Eopsilodercidae WUNDERLICH 2008 of the superfamily Pholcoidea included originally two tribes, and is splitted here:

(a) The monotypic tribe Eopsilodercini as well as the genus *Eopsiloderces* are transferred to the family Psilodercidae (**n. comb./relat.**) including *?Psiloderces loxosceloides* WUNDERLICH 2008 (**n. comb.**) which is related to *?Psiloderces filiformis* n. sp.; see the relationships of this species below.

Thus the family Epsilodercidae WUNDERLICH 2008 is regarded as a junior synonym of the family Psilodercidae DEELEMEN-REINHOLD 1995 (**n. syn.**).

(b) The relationships of the second monotypic tribe, Furcembolusini WUNDERLICH 2008, including *Furcembolus anderseni* WUNDERLICH 2008, is unsure; its prosoma is distinctly wrinkled and its clypeus is not protruding. It is regarded as a taxon indet. of the superfamilies Pholcoidea (probably related to the Psilodercidae) or the Leptonetoidea.

Here I describe two Cretaceous species which I regard as members of the extant genera *Leclercera* DEELEMEN-REINHOLD 1995 and probably *Psiloderces* SIMON 1892.

### **Leclercera** DEELEMEN-REINHOLD 1995

*Leclercera* is a genus of South East Asia which is not rare in that region, and which never has been reported from fossils. See DEELEMEN-REINHOLD (1995: 38–51).

#### ***Leclercera longissipes* n. sp.** (fig. 8–11) photos 9–10

The name of the species points to its very long legs.

**Material:** Holotype ♂ in Mid Cretaceous amber from Burma (Myanmar), F2349/AR/CJW.

**Preservation and syninclusions:** The spider is well and almost completely preserved in a yellow piece of amber, distinctly deformed, the thoracal part and some leg articles are distinctly flattened/depressed, the left leg IV is lost beyond the coxa by autotomy, the right leg IV lies inside a large bubble beyond the patella, the ventral side of the spider is hidden by a large grey bubble beyond the sternum. – In the same piece of amber exists more than a dozen of large droplet-shaped grey bubbles (see the introduction) as well as particles of detritus, stellate hairs, and an insect excrement in a long line.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (figs. 9–11) (probably deformed): Femur not spiny, cymbium bearing a long, strong erect and blunt retrolateral bristle which is bent distally, the long bulbous bears some apophyses besides the embolus.

#### **Description** (♂):

Measurements (in mm): Body length 1.55, prosoma (including the clypeus; deformed): Length 0.6, width almost 0.7; opisthosoma: Length 0.9, width 0.45; leg I: Femur 1.8, patella ca. 0.2, tibia ca. 2.15, metatarsus ca. 1.6, tarsus ca. 0.8, tibia II 2.1, tibia III 1.05, tibia IV 2.0.

Colour medium grey brown.

Prosoma (fig. 8, photos) wider than long, eye field strongly deformed, 6 eyes which partly are hidden and covered with an emulsion, anterior row almost straight, clypeus very long and strongly protruding. – Legs very long and thin, order I/II/IV/III, bristle-less although some long and almost bristle-shaped hairs exist, e. g., proventrally on the right metatarsus II, other hairs short, position of the metatarsus II trichobothrium in 0.68, tarsi distinctly pseudosegmented, paired claws large. – Opisthosoma (photo) (ventrally hidden) twice as long as wide, bearing longer hairs, anal tubercle pointed, spinnerets deformed, the medians bear probably a single large spigot. – Pedipalpus (figs. 9–11) (see also the diagnosis), femur slender, patella and tibia fairly thickened, cymbium long, bearing the long bulbus near its end.

**Relationships:** According to the cymbial spine *Leclercera spicula* n. sp. is strongly related, but the spination of the pedipalpal articles is distinctly different, and the long cymbial bristle is stronger bent at its end in *longissipes*.

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

***Leclercera spicula* n. sp.** (figs. 12–14) photos 11–13

The name of the species points to the presence of spines (lat. = spicula) on the pedipalpal articles.

**Material:** Holotype ♂ in Mid Cretaceous Burmese (Myanmar) amber, F2340/BU/CJW.

**Preservation and syninclusions:** The spider is only fairly well and incompletely preserved at the surface of a larger piece of amber, parts are deformed, parts of the left pedipalpus as well as several articles of the legs are cut off, the right leg IV and the left leg III are complete besides the base of the femur. – A longer hairy (plant?) structure which is partly splitted, parts of a long spider leg which bears several bristles, 4 beetles of 2 species, tiny remains of a Diptera, numerous tiny droplets and remains of plants, e. g. stellate hairs as well as insects excrement are preserved in the same piece of amber.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (figs. 13–14, photo 13): Femur with 3 ventral spines and a proapical spine, cymbium bearing a long, strong and blunt retrolateral bristle which is bent apically and has an oblique position, and ventrally with a pair of spines.

**Description** (♂):

Measurements (in mm): Body length 1.9, prosomal length 0.8; opisthosoma: Length 1.1, height 0.45; leg IV: Femur ca. 1.85, patella ca. 0.2, tibia ca. 2.0, metatarsus + tarsus ca. 2.5, left tibia + metatarsus + tarsus III 3.0.

Colour speckled grey brown.

Prosoma (fig. 13–14, photos) probably as long as wide, dorsal hairs short, most eyes hidden, clypeus long and strongly protruding, chelicerae short, teeth hidden, other parts hidden, too. – Legs (photo) only partly preserved, very long and slender, bristles absent, hairs short, III distinctly shorter than IV, position of the metatarsal IV trichobothrium in 0.65, the tarsi bear 3 tiny claws, tarsus IV with pseudosegments, onychium well developed. – Opisthosoma (photo) 2.4 times longer than high, almost cylindrically, bearing few longer hairs, area of the lung covers hidden, spinnerets deformed, anteriors longest, apical article short, median spinnerets probably with a single spigot only. – Pedipalpus (figs. 13–14, photo 13): Femur slender, bearing ventrally three spines and proapically a single spine, patella short, tibia long and fairly thickened, cymbium long, bearing two ventral spines, a long and strong retrolateral bristle (see the diagnosis), and the bulbus in an apical position which bears probably two conductors besides the embolus.

**Relationships:** According to the long and strongly protruding clypeus in combination of the spiny pedipalpal articles and the position of the bulbus I regard *spicula* as a member of the genus *Leclercera* which is strongly related to *longissipes* n. sp. In the extant *L. spinata* DEELEMEN-REINHOLD 1995 from Indonesia: Sulawesi the pedipalpal femur bears spines, too, but cymbium and bulbus are quite different, e. g., the cymbium bears a retrolateral outgrowth.

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

### ***Psilodermes*** SIMON 1892

*Psilodermes* is a genus of South East Asia which is not rare in that region, and which never has been reported under this genus name from fossils. Probably it is not monophyletic in my opinion. See DEELEMEN-REINHOLD (1995: 7–37).

?*Psilodermes filiformis* n. sp. (fig. 15), photos 5–6

The spider is named after its filiform embolus.

**Material:** Holotype ♂ in Mid Cretaceous Burmese (Myanmar) amber, F2267/BU/AR/CJW.

**Preservation and syninclusions:** The spider is fairly well and incompletely preserved just below the surface of a piece of amber which is 2.7 cm long and consists of numerous layers. The deformed inclusions indicate that the piece has been for a long time under strong pressure, its right legs I and IV and its left legs II and III are lost beyond the coxa by autotomy, the left leg I is partly cut off (distally through the femur up to the basal part of the tibia), the right tibia II and the left tibia I are broken through the article within/by the fossil resin, body and legs are fairly deformed, the dorsal side of the prosoma is rugose apparently caused by the preservation, the position of both pedipalpi do not allow to observe the lateral aspect, a small air bubble lies above/in front of the prosoma, a long air bubble lies right on the body. – Syninclusions are 1 Collembola, 3 beetles, ½ Trichoptera, a tiny ?parasitic Acari 7.5 mm below the spider's body, remains of few Diptera, numerous remains of plants and air bubbles.

**Diagnosis** (♂; ♀ unknown): Position of the metatarsal III trichobothrium in 0.5, embolus (fig. 15) long, strongly bent distally, and quite thin.

**Description** (♂):

Measurements (in mm): Body length 1.7, prosomal length 0.7; righth femur III 1.0, left femur IV 1.4, left tibia IV 1.2; pedipalpal tibia: Length 0.2, width 0.09.

Colour light to medium brown.

Prosoma (it is deformed/scrumpled) low, bearing long hairs; eyes and fovea not surely observable, most of the mouth parts are hidden, basal cheliceral articles slender and not diverging, some teeth of the anterior fang furrow are observable as well as a long retroapical spine-shaped “clasping bristle” (quite difficult to observe) like in *Eopsilodermes luxosceloides* WUNDERLICH (2008: 660, fig. 15, arrow). – Legs (photo) prograde, long and slender, IV probably the longest, III distinctly the shortest, metatarsus III 1.8 times longer than tarsus III, covert with distinct long hairs, bristles absent. I did not recognize the position of the metatarsal trichobothria. Onychium well developed, tarsal claws large, paired claws III with at least 5 long teeth, unpaired claw strongly reduced or probably even absent. – Opisthosoma (photo; the dorsal and the inclined right sides are observable) slender, covered with longer hairs, most parts of the area of the – probably existing – lung covers and of most spinnerets hidden, anterior spinnerets apparently short, posterior spinnerets fairly long. – Pedipalpus (fig. 15, photo 6) (only the dorsal aspect is observable): Patella short, tibia long and thick, cymbium relatively long, bulbus oval, originating at the end of the cymbium, embolus long, slender and bent, originating probably at the end of the simple bulbus.

**Relationships:** In the family Psilodermidae exists six eyes, bristle-less legs, as well as a pair of lungs; unfortunately the existence of lung covers is unsure in the present fossils. *Psilodermes* SIMON 1892 is a quite diverse genus in South East Asia, see DEELEMAN-REINHOLD (1995); in most extant species exist similar simple pedipalpi as in the fossil species but cheliceral clasping bristles are unknown. In the only further described fossil and apparently congeneric species – ?*Psilodermes luxosceloides* (WUNDERLICH 2008) (**n. comb.**) in Burmese amber – exists also a long cheliceral clasping bristle but long teeth of the paired tarsal claws are absent, the embolus is less bent and probably shorter.

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

(2) Superfamily **LEPTONETOIDEA** SIMON 1890

“To summarize, the Leptonetidae are not close to any other haplogynes and may belong in their own superfamily.”

BRIGNOLI (1979: 236)

BRIGNOLI was the first to find out that the family Leptonetidae is quite different from other classical “Haplogynae” (see below), possessing, e. g., a bulbus which is well expandable by the basal haematodocha, and having several sclerites in a distal position; he found the vulva also being different. In 2004: 645 I placed the Leptonetidae – following the traditional system and with some hesitation – in the branch in which females usually carry their egg sac (Pholcoidea); but females of the Leptonetidae – like the Telemidae and the Tetrablemmidae, see below – do actually not carry their egg sac, their tibia-patella leg autotomy and shape of the clypeus are quite different, etc. Recently the first cribellate taxon was reported within extant Leptonetidae, see LEDFORD & GRISWOLD (2010). This discovery led these authors to interesting speculations regarding the relationships of the Leptonetidae. The recognition of cribellate as well as ecribellate taxa in Cretaceous Burmese amber, which I regard related to the extant Leptonetidae – certain structures of the fossils are frequently not (well) observable, and I hope my determinations are correct! –, lead me now to further – preliminary – conclusions, see below. Leptonetoids may be an important “key taxon” for the understanding of the evolution of araneomorph spiders.

**Type family:** Leptonetidae SIMON 1890.

Further families: Telemidae (extant), and most probably two extinct families in Cretaceous Burmese/Myanmar amber: Pholcochyroceridae WUNDERLICH 2008 (n. stat.), and Praeterleptonetidae WUNDERLICH 2008, see tab. 2, and the possible cladogram. See also the remark below (under Psilodercidae) on the tribe Furcembolusini WUNDERLICH 2008.

**Diagnosis: Derived characters (apomorphies):**

- slender articles of the male pedipalpus (figs. 20, 33),
- wide/long and ventrally concave cymbium which encloses partly the bulbus (figs. 21, 26, 34),
- well expandable bulbus; well developed basal haematodocha (fig. 35),
- probably tibial glands.

(Autotomy: See the family Leptonetidae below).

**Plesiomorphic characters:**

- a pair of lungs (lost in the Telemidae),
- cribellate (\*),
- free basal articles of the chelicerae without lamella,
- 8 eyes (basically),
- a vertical (not protruding) clypeus,
- 3 tarsal claws,
- absence of tarsal trichobothria,
- a single metatarsal trichobothrium only,
- numerous leg bristles,
- tracheal spiracle close to the spinnerets (\*\*),
- probably at their base widely spaced anterior spinnerets,
- tendency to the evolution of spiny articles of the pedipalpus in both sexes (\*\*\*),
- several distal sclerites of the large bulbus,
- fused tegulum and subtegulum.

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(\* ) *Archoleptoneta* (Leptonetidae: Archoleptonetinae) and Pholcochyroceridae. (No cribellum – in my opinion a loss – in the Leptonetidae: Leptonetinae as well as in *Darkoneta* of the Archoleptonetinae, the Telemidae, and the Praeterleptonetidae). Probably plesiomorphic character: a straight metatarsus IV – even in cribellate taxa – which is not concave dorsally like in most Dictynidae and Uloboridae.

(\*\*) A rare character within the Haplogynae with the exception of the Filistatidae as well as the Psilodercidae of the Pholcoidea which also possesses a pair of lungs, and in which the position of the tracheal spiracle is nearer to the spinnerets than to the epigastral furrow similar to the Leptonetidae. The tracheal position is unknown in the Cretaceous fossils. A tracheal spiracle is absent (lost) in the Pholcidae.

(\*\*\*) In my opinion a convergence of the (a) Leptonetoidea and (b) the Ochyroceridae + Psilodercidae of the superfamily Pholcoidea. In this connection I regard the dorsal outgrowths of the male pedipalpal femur of the Pholcochyroceridae.

**Relationships:** See also the discussion by LEDFORD & GRISWOLD (2010: 8–10), and below (convergences as well as the family Leptonetidae).

Several scenarios are conceivable:

- The present one (this paper): Leptonetoidea as sister taxon to the superfamily Pholcoidea, see the possible cladogram and the discussion below;
- the origin of the – basically cribellate! – superfamily Leptonetoidea goes back much further: Leptonetids as sister to the remaining Haplogynae, see LEDFORD & GRISWOLD (2010: 9),
- the superfamily Leptonetoidea in the present sense is not monophyletic, and the origin of the Pholcochyroceridae may go back much further;
- Leptonetoidea is part of the Pholcoidea, strongly related to Ochyroceratidae and Psilodercidae,
- the Leptonetoidea is the sister taxon to the Araneoidea s. l. (= “Orbiculariae”: Deinopidea + Araneoidea s. str.), and probably even of all Entelegynae. See LEDFORD & GRISWOLD (2010: 9): “leptonetids as proto-entelegynes”, and the end of the next paragraph.

New fossils may support or falsify my present supposition, the first one.

Members of the superfamily Pholcoidea (= Scytodoidea, the younger name) are con-

nected to the Leptonetoidea by plesiomorphies, see the possible cladogram. Pholcoidea possesses usually a cheliceral lamella, a protruding clypeus, a different position of the eyes, a reduced number of leg bristles, thickened articles of the male pedipalpus, the cymbium does not enclose a part of the bulbus, bulbus and vulva are not (well) expandable, frequently exists a larger number of receptacula seminis, and THE FEMALES CARRY THEIR EGG SAC (except the Tetrablemmidae).

### Relationships and convergent evolutions:

Numerous “similarities” (and convergences?) exist between the – relatively derived – haplogyne superfamily Leptonetoidea and the advanced entelegyne ecribellate branch of the Araneoidea (s. l.), e. g.:

- The respiratory system – with a pair of lungs and tracheae near the spinnerets – is basically the same,
- the trichobothriotaxy is most probably identical,
- the clypeus is usually vertically and not protruding in both taxa (with the exception of *?Pholcochyrocer baculum* n. sp. which relationships are unsure),
- in both taxa exist slender but not thickened articles of the ♂–pedipalpus (but a tendency to the existence of spiny pedipalpal articles exists in the Leptonetoidea),
- the cymbium is wide and partly enclosing the bulbus (but a true retrobasal paracymbium is absent in the Leptonetoidea in contrast to the Araneoidea),
- the bulbus is well expandable in both taxa,
- sticky droplets in the capture web exist in almost all Araneoidea and probably in certain extinct taxa of the Leptonetoidea (convergently evolved in the Pholcidae).

Most striking are furthermore – and especially – the similarities between the extant Leptonetidae (Leptonetinae as well as Archoleptonetinae) and the Linyphiidae: Especially the Micronetinae:

- Habitus and chaetotaxy are identical,
- a patella–tibia autotomy exist in all Linyphiidae (the strongly related Pimoidae and the not related Filistatidae as well) (\*) and at least in all extant and Palaeogene Leptonetidae (the kind of autotomy is unknown in Cretaceous fossils),
- retrolateral cheliceral stridulatory files exist in almost all Linyphiidae and at least within three genera of the extant Leptonetidae (a stridulatory pick of the pedipalpal femur may be absent in the Leptonetidae). (Such files are quite frequent in numerous families of spiders),
- an irregular capture web exists in which the spiders are hanging upside down.

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(\*) I found a break between patella and tibia in a male and a juvenile each in the gondwanan, cribellate and basically four-lunged *Austrochilus francke* PLATNICK 1987 of the superfamily Austrochiloidea (family Austrochilidae) from Chile, AMNH. These breaks appear to be old and healed, and are probably cases of autotomy. (To my knowledge autotomy happens usually between coxa and trochanter concerning alcohol material in the case of this “family kind” of autotomy).

Therefore members of fossil Leptonetoidea – especially Leptonetidae, and especially fossils – can easily be mistaken for members of the family Linyphiidae, but – besides differences in the copulatory organs like the existence of an epigynal scape in the basal Linyphiidae and a retrobasal paracymbium, see above – there are certain further dif-

ferences, e. g.: A cribellum or a very large and wide colulus exist in the Leptonetidae in contrast to the ecribellate Linyphiidae in which the colulus is slender and only fairly large, the pattern and the position of the spinnerets is different, the linyphiid labium is rebordered DISTALLY in contrast to the Leptonetidae in which a transverse depression may exist in the basal half, the position of the metatarsal trichobothrium is usually in the basal half in the Micronetinae but in the distal quarter in the Leptonetidae.

The family Linyphiidae is a derived family of the ecribellate branch of the superfamily Araneoidea s. l. It is generally accepted that the capture web of the ancestor of the Linyphiidae has changed from an orb web to an irregular kind. If the Leptonetidae really would be closely related to the Linyphiidae they should possess an orb web like basal Araneoidea. Besides certain similar somatic and behavioural characters several quite important differences between both families (and their superfamilies as well) exist, see above and below. Therefore I regard the similarities of the Leptonetoidea/Leptonetidae and the Araneoidea/Linyphiidae as convergences, and the Leptonetoidea most probably not as a “missing link” from haplogyne to entelegyne (araneoid) taxa.

Leptonetidae and Linyphiidae – the spiders of both families are hanging upside down in their irregular capture webs – are members of the same life form types (“Lebensformtypen” in German), they are members of quite similar niches usually of higher strata of the vegetation, and they therefore evolved similar somatical and behavioural patterns, but the characters of the copulatory organs are quite different (!). In my opinion the root of the entelegyne Araneoidea is more likely close to the entelegyne superfamily Oecobioidea than to the haplogyne Leptonetoidea, see WUNDERLICH (2004: 1119).

According to the expandable bulbus the – basically cribellate! – Leptonetoidea could well be the most advanced haplogyne spiders besides the Archaeoidea/Palpimanoidea.

**Distribution and fossils:** See tab. 1 and 2. Cosmopolitical, mainly pantropical.

## Family **LEPTONETIDAE** SIMON 1890

This haplogyne family has an almost cosmopolitical distribution, most genera are reported from tropic regions, numerous from caves; in Southern France I found members of the subfamily Leptonetinae under stones. Three subfamilies are known, see tab. 2.

The only known fossils of this family were described in Eocene Baltic amber as members of the Leptonetinae, see WUNDERLICH (2004: 712–720). Here I describe the first Cretaceous taxon, a cribellate species of the new and extinct subfamily Palaeoleptonetinae. This oldest known fossil of the family Leptonetidae allows conclusions and speculations on the evolution of taxa within the Leptonetidae, as well on its relatives, and probably the origin of the RTA-clade.

**Diagnostic advanced (apomorphic) characters of the family Leptonetidae;** see BRIGNOLI (1979: 234) and LEDFORD & GRISWOLD (2010: 4):

- Autotomy between tibia and patella (\*),
- existence of iridescence, especially on prosoma and legs,
- existence of tartipores on the anterior lateral spinnerets,
- (– expandable vulva with a single pair of receptacula seminis, known in the extant taxa, according to BRIGNOLI (1979)).

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(\* unique within the Haplogynae besides the convergent evolution in the Filistatidae. It exists to my knowledge at least in the Archoleptonetinae and Leptonetinae of the Leptonetidae but it is unknown from the Palaeoleptonetinae and the related extinct families; different in the Telemidae.

**Plesiomorphic characters:** See below, the subfamily Palaeoleptonetinae and tab. 1. Furthermore (mainly known from extant taxa; most characters exist also in other haplogyne families as synapomorphies or convergences, but they exist not in the present combination):

- A pair of book lungs,
- tracheal spiracle close to the spinnerets,
- clypeus not protruding,
- chelicerae free and lamina absent,
- fangs quite long and slender,
- promargin of the fang furrow bearing several teeth,
- legs long and slender,
- existence of tibial glands (at least in the extant taxa),
- large claw of the female pedipalpus (at least in the extant taxa),
- male pedipalpal articles slender,
- large bulbus,
- no egg-carrying by the female,
- small spiders, body length less than 3 mm.

Furthermore: Feathery and plumose hairs are absent to my knowledge.

**Relationships:** See also above, the superfamily Leptonetoidea. LEDFORD & GRISWOLD (2010: 8–10) discussed the relationships of the Leptonetidae, and presented two “scenarios”, see also above. I agree with these authors that an independent evolution of the leptonetid cribellum (as well as a reversal) appears unlikely. The Leptonetidae are cribellate apparently basically, and the discovery of CRIBELLATE and – in the geolocical sense oldest – member of the family Leptonetidae may underline this supposition. According to the “presence of several entelegyne synapomorphies in the Leptonetidae” this family has been considered (a) as Proto-entelegynes (probably belonging to their own superfamily, see above) or (b) as the sister group to the remaining Haplogynae (or a sister to a certain one of their taxa).

The Telemidae most probably are strongly related to the Leptonetidae according to the presence of tibial glands, a very large colulus, slender articles of the ♂-pedipalpus, the absence of a cheliceral lamina, and the absence of an egg-sac carrying behavior by their females. Certain advanced characters – loss of lungs, the slender cymbium, the existence of a single spermateca – may be the result of the dwarfism of the tiny Telemidae. See tab. 1 and the possible cladogram.

With some hesitation – their respiratory system is unknown – I regard the extinct Cretaceous families Pholcochyroceridae WUNDERLICH 2008 and Praeterleptonetidae WUNDERLICH (in amber from Burma/ Myanmar) as members of the superfamily Leptonetoidea, see tab. 1. In these families exist – in contrast to most members of the Ochyroceratidae –, numerous leg bristles, a short/vertical clypeus (with the exception of *Pholcochyrocer baculum* n. sp.), a wide cymbium, and a well expandable bulbus bearing several tegular sclerites; a cheliceral lamina is apparently absent, but in both extinct families exist 8 eyes – which I regard as a plesiomorphic character –, and in the Praeterleptonetidae a cribellum is absent (lost) like in advanced Leptonetidae: Leptonetinae, as well as in the genus *Darkoneta* of the Archoleptonetinae (and furthermore in the dwarf Telemidae). In these families – Leptonetidae and Telemidae – the anterior median eyes are lost. According to the derived position of the eyes and the lost cribellum the subfamily Leptonetinae is the most advanced subfamily of the Leptonetidae, and of the superfamily Leptoneoidea as well.

Similarities – see above: “Convergences” – exist in the family Psilodercidae DEELEMAN-REINHOLD 1995 (a member of the superfamily Pholcoidea): Lungs are present, too, and the position of the tracheal spiracle is similar, but a cheliceral lamina exists, the clypeus is quite long and protruding (figs. 12, 23), and the structures of the ♂-pedipalpus are different. In the strongly related Ochyroceratidae a cheliceral lamina exists, too, the clypeus is quite long and protruding, too, but lungs are absent, the position of the tracheal opening is halfway between the epigastric fold and the spinnerets, a colulus exists which is twice as long as wide. Both families are ecribellate, and the apomorphic characters of the Leptonetidae – see above – are absent. The extant and Cretaceous family Psilodercidae is restricted to South East Asia.

**Distribution** and fossils: See above and tab. 2.

### **PALAEOLEPTONETINAE n. subfam.**

The name points to the old/extinct taxon (Palaeo-) and the extant genus *Archoleptoneta* GERTSCH 1974 which is cribellate like the new fossil taxon.

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

**Diagnosis** (♂; ♀ unknown):

(a) Apomorphic characters: Unpaired tarsal claw small (reduced), calamistrum absent (lost) (figs. 17–18), existence of a single large cymbial spur (figs. 20–21).

(b) Plesiomorphic characters (see LEDFORD & GRISWOLD (2010: 9) and the characters of the family Leptonetidae above): Cribellate (fig. 19), haplogyne, 6 eyes in a compact group wider than long (fig. 16; a reconstruction only!), probably only few teeth of the promargin of the fang furrow, stridulatory organ absent, unpaired tarsal claw existing, numerous leg bristles (figs. 17–18), cymbium not constricted nor distinctly elongated, bulbus bearing several sclerites besides a long embolus. The respiratory system as well as the existence of tartipores and the autotomy are unknown.

**Relationships** (see tab. 2): According to the existence of a cribellum – in the genus *Archoleptoneta* GERTSCH 1974 but not in *Darkoneta* LEDFORD & GRISWOLD 2010 –, the compact eye group which is wider than long, the not spiny pedipalpal articles, the not constricted cymbium, as well as the long embolus which originates in the basal half of the bulbus the subfamily Archoleptonetinae – a relict taxon of North and Central America – is most related, but Archoleptonetinae lost all leg bristles, a cymbial spur is absent, the cymbium and the bulbus are longer, the embolus is shorter. – In the subfamily Leptonetinae – the most advanced subfamily – the cribellum is replaced by a (large) colulus, a long eye field evolved with a unique position of the posterior median eyes far behind the remaining eyes – see WUNDERLICH (2004: 718, fig. 13c), the pedipalpal articles are usually quite spiny, the cymbium is long and possesses a constriction, the bulbus is long, the embolus is stout and originates in the distal half of the bulbus, see WUNDERLICH (2004: 712–720), (2011: 578).

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

### *Palaeoleptoneta* n. gen.

The name of the genus points to the old/extinct taxon (lat. palaeo-) and the confamiliar genus *Leptoneta*.

Type species (by monotypy): *Palaeoleptoneta calcar* n. sp.

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

*Palaeoleptoneta calcar* n. sp. (figs. 16–21) photos 14-15

**Material:** Holotype ♂ in Mid Cretaceous amber from Burma (Myanmar), F2350/AR/CJW.

**Preservation and syninclusions:** The spider is well and completely preserved in a clear yellow piece of amber, darkened and partly deformed by the pressure for million of years, the right pedipalpus is compressed laterally, a bubble exists directly below the opisthosoma. – The larva of a mite is preserved above the prosoma of the spider, a tiny Collembola and a particle of insects excrement exists right above the body of the spider.

**Diagnosis:** See the new subfamily, ♂-pedipalpus: Figs. 20–21, photo 15

**Description (♂):**

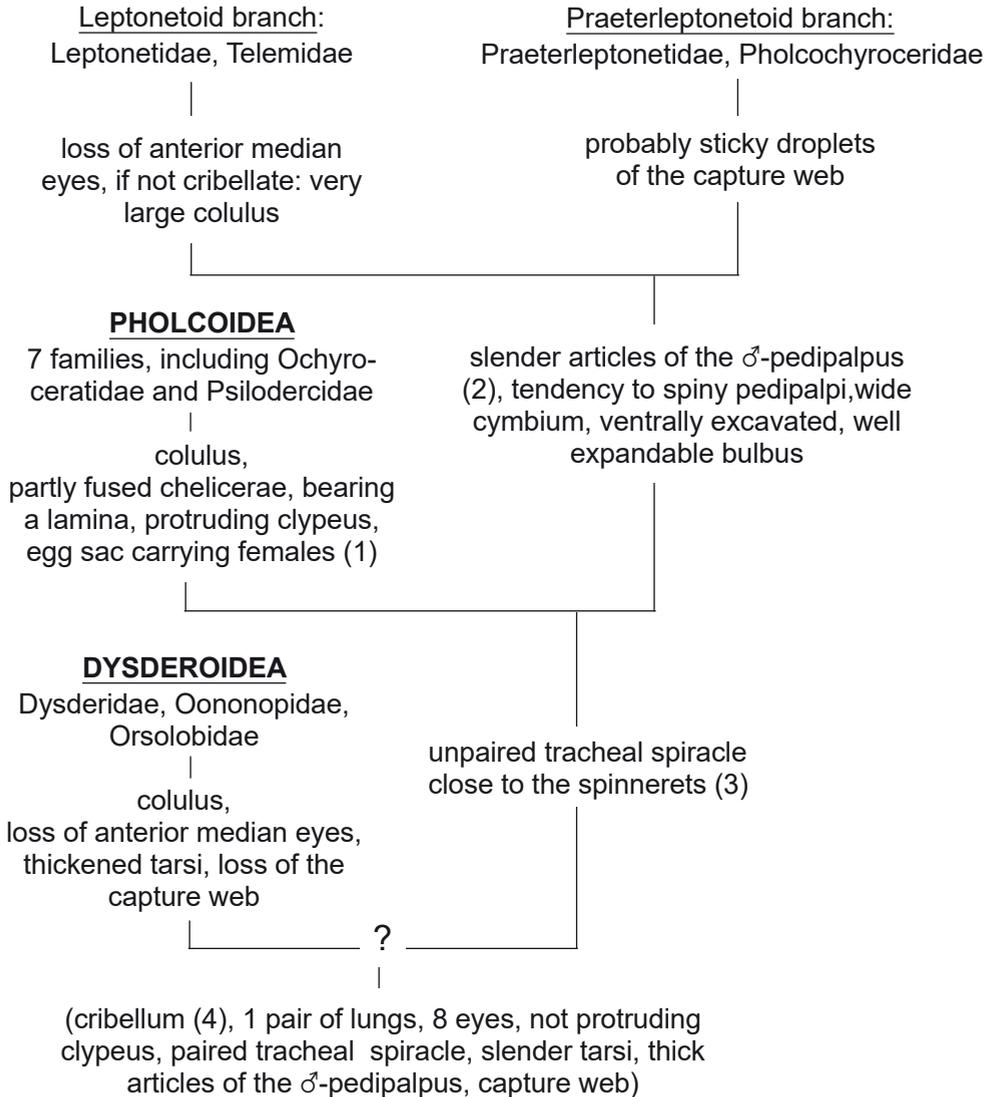
Measurements (in mm): Body length 1.8, prosomal length 0.8; leg I: Femur 1.0, patella 0.23, tibia 0.9, metatarsus 0.8, tarsus 0.47; tibia II 0.73, tibia III 0.65, tibia IV 0.97.

Colour: Prosoma and legs dark brown, with a distinct iridescence, opisthosoma: Left anterior half almost white, the remaining parts dark grey.

Prosoma (fig. 16, a reconstruction only!, photo) longer than wide, bearing some long hairs; eyes strongly deformed, most probably 6 eyes in a compact group of a field wider than long, posterior eyes smallest and close together, clypeus not protruding, basal cheliceral articles fairly large, anterior margin of the fang furrow bearing several small teeth, fangs quite long, in an oblique position, gnathocoxae long and not converging, labium free and wider than long, sternum 1.2 times wider than long, coxae IV separated by less than half of their diameter, stridulatory files absent. – Legs (figs. 17–18, photos) fairly long and slender, order IV/I/II/III, bearing numerous bristles, most femora bear dorsally 1/1, I 1 additionally proventrally and 2 pairs in the distal half, other femora similar (some bristles may be rubbed off), patellae dorsally 1/1 (a long apical and an short/small basal one), no laterals, tibia I dorsally 1/1 and a single ventral one in the middle, metatarsus I a ventral pair in the basal half, metatarsus I bears a very long trichobothrium, position in 0.95, tarsal trichobothria absent, unpaired tarsal claws quite tiny; I did not find tibial glands. Metatarsus IV is straight and bears 2–4 bristles, a calamistrum is apparently absent. – Opisthosoma (photos) 1.7 times longer than wide, bearing not many longer hairs; spinnerets deformed; I regard a transverse structure (fig. 19) in front of the spinnerets as a cribellum because it is very wide, flat, apparently bearing tiny spinules, and situated behind a roll; it may be divided or not (I am not sure). – Pedipalpus (figs. 20–21, photo 15) partly deformed, with slender articles, femur distinctly bent, bearing a small blunt ventral-basal outgrowth, cymbium slender, widened near the middle, with a large retrolateral spur, bulbous with several sclerites including a needle-shaped one, the right embolus is well observable, very long and bent, apparently in an unnatural (expanded?) position.

**Relationships and distribution:** See the new subfamily.

# LEPTONETOIDEA



## Possible cladogram of selected higher haplogyne taxa

- 
- (1) Reversal in the Tetrablemmidae: Tetrablemminae.
  - (2) Convergently evolved, e. g., in several Ochyroceratidae and Psilodercidae (Pholcoidea).
  - (3) Not close to the spinnerets as a reversal in the Telemidae. A tracheal spiracle is absent in the Pholcidae.
  - (4) Lost six times if my suggestion is correct.

Character	Pholcochyroceridae	Praeterleptonetidae	Leptonetidae	Telemidae
Cribellum	+	–	+/- (1)	–
lungs	?	+	+	–
number of eyes	8	8	6	6 or none
leg autotomy (2)	?	?	patella-tibia	coxa-trochanter
genera	<i>Pholcochyrocer</i>	<i>Palaeohygroptoda</i> , <i>Praeterleptoneta</i> (3)	<i>Palaeoleptoneta</i> and numerous extant genera	7 genera ( <i>Telema</i> : extant and Eocene)
special characters	long unpaired tarsal claw, long divided tegular sclerite	retrobasal paracymbial spur (5)	iridescence (4), autotomy (2)	no lungs (6)
distribution, fossils	Cretaceous (Myanmar)	Cretaceous (Myanmar)	Cretaceous (Myanmar) – extant	Eocene (Europe) – extant

- 
- (1) Basically with cribellum: Certain Archoleptonetidae: *Archoleptoneta*.
  - (2) Not found by me in the extinct Cretaceous taxa.
  - (3) Both extinct genera represent a tribe of its own.
  - (4) See the diagnosis of the Leptonetidae. The presence of this character is not sure in the fossils of the three families; in the Telemidae it is absent.
  - (5) At least in Praeterleptoneta. Convergenly evolved in *Althepus* (Pholcoidea: Ochyroceratidae).
  - (6) See above (relationships of the family Leptonetidae). Further characters: Existence of opisthosomal sclerites, advanced position of the posterior tracheal spiracle, presence of spermatophores.

**Tab. 1. Main differences of the families of the superfamily Leptonetoidea including their genera and their distribution (the tibial glands are not treated).**

Character	Leptonetinae	Archoleptonetinae	Paleoleptonetinae
cribellum/colulus	large colulus, ca. as long as wide	wide cribellum (*) or large colulus	wide cribellum, fig. 19
eye field	longer than wide, backward position of the posterior eyes	wider than long, compact, similar to fig. 16	wider than long, compact, fig. 16
leg bristles (**)	few	none	numerous, figs. 17–18
very spiny pedipalpal articles	+	–	– figs. 20–21
cymbium	long, constricted, usually with spur	long, not constricted, no spur	relatively short, not constricted, large spur, fig. 21
embolus	stout, originating in the distal half of the bulbus	long, originating in the basal half of the bulbus	long, originating in the basal half of the bulbus, fig. 21
distribution	extant, mainly tropical; Eocene Baltic amber forest	extant, North America	Mid Cretaceous amber forest of Burma (Myanmar)

(\*) *Archoleptoneta*.

(\*\*) "Spines" sensu LEDFORD & GRISWOLD (2010).

Tab. 2. Main characters of the subfamilies of the Leptonetidae

Family **PHOLCOCHYROCERIDAE** WUNDERLICH 2008 (n. stat.)

(= Pholcochyrocerini WUNDERLICH 2008 of the family Praeterleptonetidae WUNDERLICH 2008).

Type genus (by monotypy): *Pholcochyrocer* WUNDERLICH 2008, extinct, in Mid Cretaceous Burmese (Myanmar) amber.

**Diagnosis of the family Pholcochyroceridae** (♂; ♀ unknown): Tarsi IV with long auxiliary hairs and a long unpaired claw (fig. 31). Pedipalpus (figs. 25–26, 32–37): Femur dorsally modified by outgrowths (unknown in *Pholcochyrocer guttulaeque*), tibia with several apophyses but no retrolateral one, the bulbus bears branches of extremely long conductors which stand widely out, one of these branches guides the thin embolus; a large regular apophysis exists which may be sciny.

Further important characters: 8 eyes in two rows of a wide field with the lateral eyes widely spaced from each other (fig. 27), basal cheliceral articles not fused, leg bristles rather numerous (figs. 24, 28–31), absent on patellae and tarsi, no paired ventral tibial and metatarsal bristles nor femoral trichobothria, prosomal cuticula (magnification 150x) apparently smooth (not furrowed); pedipalpus (figs. 25–26, 32–37): cymbium wide (figs. 24–34–36), paracymbium absent. I did not find feathery or plumose hairs on body and legs. The structures of the tip of tarsus IV (fig. 31) – as well as the existence of parts of a capture web in the same piece of amber as the holotype of *P. pecten* – indicate a web building behaviour (kind and structure of the web are unknown).

Basic characters: Existence of lungs unknown, cribellate (calamistrum fig. 30, structures of the cribellum unknown), 3 tarsal claws, tarsal trichobothria most apparently absent (I did not recognize leg trichobothria in the three known specimens of *Pholcochyrocer*).

**Relationships:** The single male of the generotype (and type of the tribe Pholcochyrocerini as well), *Pholcochyrocer guttulaeque* WUNDERLICH 2008, is preserved in a quite muddy and intransparent piece of amber, most structures are not or only hardly observable. I did not recognize that this spider is cribellate like the strongly related *P. pecten* n. sp. although I supposed that the spiderlings near the male may be cribellate (but probably not conspecific), and spider threads bearing sticky droplets in the same piece of amber may originate from quite another taxon. In 2008 I mistook a structure as a questionable outgrowth of the cymbium which I now regard as an outgrowth of the bulbus, a conductor. – The absence of tarsal trichobothria and the presence of only a single metatarsal trichobothrium restrict the relationships of the family (and of the Praeterleptonetidae as well). According to the existence of a cribellum, the structures of the chelicerae, the slender articles of the male pedipalpus, and the well expandable bulbus the family is not a member of the superfamily Pholcoidea. In contrast to the Araneoidea s. l. – in which “auxiliary hairs” of tarsus IV usually exist, too – a retrobasal paracymbium is absent and the spiders are cribellate, in contrast to the Uloboridae femoral trichobothria are absent, and metatarsus IV is straight. A membership of the superfamily Leptonetoidea – in which cribellate taxa already are known – appears most likely to me. – Pholcochyroceridae possesses 8 eyes like the Praeterleptonetidae but the Praeterleptonetidae are ecribellate, the unpaired tarsal claw is not elongated, a retrobasal tibial spur of the male pedipalpus exists at least in *Praeterleptoneta*, and the structures of the bulbus are different. – Because of the listed differences I exclude the genus *Pholcochyrocer* and the tribe Pholcochyrocerini from the family Praeterleptonetidae WUNDERLICH 2008, and elevate the tribe to family rank, Pholcochyroceridae WUNDERLICH 2008 (n. stat.).

See the possible cladogram above.

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

?*Pholcochyrocer baculum* n. sp. (figs. 22–26) photos 19–21

The name of the species points to the long dorsal outgrowth of the pedipalpal femur which is staff = baculum (latin).

**Material:** Holotype ♂ in a piece of Mid Cretaceous Burmese (Myanmar) amber which has been separated from two larger pieces of amber, F2339/BU/CJW.

**Preservation and syninclusions:** The spider is completely and fairly well but deformed preserved in a muddy piece of amber which contains numerous tiny dark brown bubbles hindering the view on the spider; larger bubbles cover parts of the right side of the spider, a movable gas bubble exists within a fluid in the anterior part of the opisthosoma. A thin emulsion covers parts of the legs. Both pedipalpi (figs. 25–26) are expanded; small parts of detritus exist in the same piece of amber, larger and small parts in the other two pieces. A small Diptera is preserved in one of the separated pieces.

**Diagnosis** (♂; ♀ unknown): Cephalic part fairly elevated and clypeus protruding (figs. 22–23). Pedipalpus (figs. 25–26): Femur basally with a slender, pointed and erect apophysis (it is similar in certain Anapidae), cymbium large/wide, a remarkable “lamella” (tegular apophysis) exists which is not skinny, free part of the embolus short.

**Description** (♂):

Measurements (in mm): Body length 2.5, prosoma: Length 1.0, height 0.4, opisthosoma: Length 1.7, height 0.4 (diameter of the enclosed gas bubble 0.39); leg I: Femur 1.0, patella 0.3, tibia 1.1, metatarsus 1.05, tarsus 0.4, tibia II 0.55, tibia III ca. 0.2, tibia IV 0.53.

Colour: Prosoma dark brown, legs and opisthosoma grey brown.

Prosoma (figs. 22–23, photos) distinctly longer than wide, hairs indistinct, cephalic part fairly raised, clypeus long and protruding, most eyes are hidden, field wide, posterior median eyes large, basal cheliceral articles short, its teeth and remaining mouth parts hidden. – Legs (fig. 24, photos) long and slender, order I/II/IV/III, III distinctly the shortest, anterior metatarsi bent. Bristles frequent and fairly long, probably partly rubbed off; most femora with a single dorsal one, but the left femur II bears 1/1 bristles, most patellae bear 1 dorsal-distal one, metatarsus I 1 dorsally in the basal half and an apical pair, metatarsus II dorsally 1/1/1, metatarsus IV straight, calamistrum(?) indistinct, three small tarsal claws, metatarsi apparently with a single trichobothrium, tarsal trichobothria absent. – Opisthosoma (photos) slender, 2.4 times longer than high, soft, hairs short, existence of lungs (lung covers) unknown, epigaster not protruding, three pairs of spinnerets which are deformed and fairly short, area of the – probably existing – cribellum hidden. – Pedipalpus (figs. 25–26, photos), both are expanded, (see the diagnosis): Femur quite long and slender, bulbus oval.

**Relationships:** Remark: The exact position of the eyes and the (the really existence of a) cribellum of more conspecific fossils are needed for a more close determination. – According to the structures of the bulbus – especially the long and bent embolus/conductor – and the chaetotaxy *baculum* apparently is a member of the genus *Pholcochyrocer*. Because of the very long and distinctly protruding clypeus I am quite unsure about the relationships of this species. The shape of the clypeus is similar to most members of the superfamily Pholcoidea in which a cribellum is absent (its existence in *baculum* is unknown!), and usually a low number of leg bristles exist. In the remaining congeneric species a long and erect stalk of the pedipalpal femur is absent.

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

***Pholcochyrocer pecten* n. sp.** (figs. 27–36) photos 16–18

The species is named after the comb- (pecten-) shaped structure dorsally on the femur of the male pedipalpus.

**Material:** Holotype ♂ in Mid Cretaceous Burmese (Myanmar) amber and 5 separated pieces of amber which contain spider's threads, F2268/BU/AR/CJW.

**Preservation and syninclusions:** The spider is completely and fairly well preserved (several parts of the body are deformed by pressing for a long time in the earth) in an orange and only fairly muddy small piece of amber. This and further five pieces have been taken apart by me from a larger piece which has been worked as a piece of decoration – an ant-shaped “spider” which had four pairs of legs but three body parts, see the photo. – Remains of spider's threads are preserved at/near the tip of the left tarsus III, and – together with remains of a questionable Psocoptera – near the left tarsus IV. In three of the separated pieces of amber remains of spider's threads are preserved (see the photos) which may have been produced by the holotype. Some of these threads are branched, some may be cribellate, others are clearly ecribellate. Few “stellate” plant hairs and larger remains of a plant are also preserved and are in contact with some of the threads.

**Diagnosis** (♂; ♀ unknown): Pedipalpus (figs. 32–37): Free part of the embolus beyond the tip of the conductor (dorsal aspect, fig. 33) shorter than half of the length of the conductor's branch 1.

**Description** (♂):

Measurements (in mm): Body length 3.0, prosoma: Length 1.5, width 1.05; leg I: Femur 1.85, patella 0.6, tibia 1.5, metatarsus 1.5, tarsus 0.85, tibia II 1.05, tibia III 0.55, tibia IV 0.9.

Colour: Prosoma and legs light brown, legs not annulated, opisthosoma light grey, teeth of the comb of the pedipalpal femur black.

Prosoma (it is distinctly deformed) 1.42 times longer than wide, widest near the middle, low, bearing hairs which are partly longer, fovea well developed, 8 small eyes in 2 rows of a wide field (see the reconstruction, fig. 27), area of the anterior median eyes apparently protruding, lateral eyes widely spaced from each other. Basal cheliceral articles only fairly large, free, not diverging, existence of lateral files unknown, teeth of the fang furrow hidden, fangs fairly long, labium wider than long, gnathocoxae not strongly diverging, coxae IV close together.- Legs (figs.28–31) slender, order I/IV/II/III, I distinctly the largest but not strongly elongated, hairs fairly short and not dense, bristles rather numerous, all femora 1 dorsal in the basal half and several apical/distal ones, I additionally 2 prolaterally, patellae and tarsi none, no paired ventral tibial or metatarsal bristles, tibia I bears 10 bristles, the metatarsi bear usually 6 apical bristles, additional ones exist, 3 in the basal half on I. Metatarsus IV almost straight and not compressed, calamistrum well developed in a single row in the basal half, a regular row of slightly bent hairs in a retrolateral position. “Preening comb” and ventral bristles of metatarsus III and IV absent. Paired tarsal claws long and toothed, unpaired claw strongly bent, IV longer than the paired claws. “Auxiliary hairs” long. – Opisthosoma 1.63 times longer than wide, deformed, covered with numerous short hairs, spinnerets short, cribellum hidden, lung covers probably absent. – Pedipalpus (figs. 32–36; see also the diagnosis): Femur slender and bent, bearing a retrodorsal-distal comb of 5 strong teeth. Its function is unknown, apparently it is a sexually dimorphic structure, and it may have played a role during the mating. This comb is similar to a retrofrontal comb on the male chelicerae in certain members of the family Pholcidae, see WUNDERLICH (1988: 268, figs. 138, 140, 141); its function is unknown, too. Patella long (partly deformed), tibia complicated, bearing few dorsal bristles (the distal one is the strongest); it bears additionally a retrodistal and a divided retrolateral-ventral apophysis; cymbium wide, not elongated, apically with long hairs but without bristles, bulbus extraordinary complicated, its basal part small, bearing a sciny flat apophysis, a strongly sclerotized ?median apophysis (A), and a conductor which possesses 3 branches, one of these guides (and hides partly) the embolus which is thin, bent, and free observable in its distal part.

**Relationships:** In the strongly related *P. guttulaeque* WUNDERLICH 2008 a comb-shaped structure of the pedipalpal femur may be absent (or it is very small so far it is observable in the muddy piece of amber which includes the holotype), and the free part of the embolus beyond the tip of the conductor (dorsal aspect, fig. 30) is longer, at least half as long as the branch of conductor 1, compare fig. 36 to fig. 37. In *?P. baculum* n. sp. the clypeus is very long and protruding, and the pedipalpal femur bears a single long erect outgrowth.

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

Family **PRAETERLEPTONETIDAE** WUNDERLICH 2008

(= Praeterleptini WUNDERLICH 2008).

Relationships of this ecribellate family: See tab. 1, the possible cladogram above, and WUNDERLICH (2011: 548). – The absence of a (retrobasal) tibial apophysis of the male pedipalpus (a spur may exist, at least in *Praeterleptoneta*) and the conformation of the structures of the bulbus exclude the Praeterleptonetidae in my opinion most probably from the superfamily Araneoidea s. str.. The large cymbium and the relatively large and free bulbus of the Praeterleptonetidae – two tribes: Praeterleptonetini and the Palaeohygropodini – indicate relationships of this family to the haplogyne superfamily Leptonetoidea, and to the cribellate family Pholcochyroceridae (see above and tab. 1) in which also 8 eyes exist, the same kind of trichobothriotaxy, and slender articles of the male pedipalpus.

Remark: In the original description of *Praeterleptoneta tibialis* WUNDERLICH 2011 I did not report lung covers but they are existing, and I erroneously reported the presence of feathery hairs, but such hairs are absent.

(3) Superfamily **ARCHAEOIDEA** s. l. (= Palpimanoidea s. l.)

Family **LAGONOMEGOPIDAE** ESKOV & WUNDERLICH 1995 photos 22–25

The extinct, diverse, and – according to its eyes – quite unusual family Lagonomegopidae is only known from Cretaceous ambers, it has been widely distributed in the Northern Hemisphere. Only very few Cretaceous lagerstätten are known from the Southern Hemisphere up to now, and therefore fossil Lagonomegopidae may well be discovered in the Southern Hemisphere in the future. Seven genera are named now; additionally one genus each from Spain, from Burma, and from New Jersey will probably be named/described in the future, see the key and the map. Members of the family existed at least for 60 million years, from the Lowest Cretaceous (Jordanian amber) to the Upper Cretaceous (Canadian amber). No member has been found in the Cretaceous African or in the Eocene Baltic or Indian ambers; so the family probably became extinct at the end of the Cretaceous like numerous other taxa, but I suppose that it will be discovered in the Jurassic in the future. In Burmese amber and in other Cretaceous ambers the fam-

ily Lagonomegopidae is – on the generic level – the most diverse spider family besides certain Haplogynae like the Archaeidae and the Uloboridae. According to the long and slender legs in combination with the metatarsal preening comb – and its apparently related Archaeidae – the Lagonomegopidae may well have been “sit- and- wait predators” and probably spider eaters. Juveniles of this family in amber are relatively frequent, but – for unknown reasons – adults are very rare (did they prefer different habitats/strata? The first adult males are described in this paper. Especially lagonomegopid males from different kinds of amber and from other than known taxa are needed for more sure conclusions on the relationships of its genera and even of the whole family. The existence of tarsal trichobothria in certain genera of the Lagonomegopidae is of great taxonomical and phylogenetical value, but is still not well studied/understand.

The Burmese (Myanmar) amber forest contained a diverse lagonomegopid fauna, I know members of four monotypic genera: *Archaelagonops* n. gen., *Burlagonomegops* PENNEY 2005, *Lagonoburmops* n. gen., *Myanlagonops* n. gen., and taxa indet.

Revised **diagnosis** of the family Lagonomegopidae; see WUNDERLICH (2008: 613): The family is best diagnosed by its unique powerful posterior median eyes in a more anterior position which are directed obliquely laterally (in the Lagonomegopinae, figs. 38, 45–46) or anteriorly (in the Archaelagonopinae, figs. 67–68), and a very wide and long eye field. At least one – but most probably two – small/tiny pairs of eyes exist in addition to the large eyes in all taxa; they are also widely spaced (\*). The ♂-pedipalpus is only – and insufficiently – known from the genera *Myanlagonops* (figs. 49–50) and *Archaelagonops* (figs. 67–68); it has long and slender articles and a very long cymbium which includes/hides parts of the small and not protruding bulbous. – Tarsal trichobothria exist at least in some genera, e. g., in the Spanish taxon, in the Burmese genera *Lagonoburmops* n. gen. (fig. 41) and *Archaelagonops* n. gen. (fig. 69), probably even in two rows.

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(\* ) The anterior median eyes are probably absent in almost all Lagonomegopidae like in numerous other spider families; the taxon from Spain may be an exception (E. SAUPE, person. commun.). The lateral eyes are small to tiny, and are easily overlooked or mistaken for tiny bubbles. The position of the posterior lateral eyes is distinctly behind the posterior median eyes (figs. 45–46) (these eyes are probably absent in the genus *Grandoculus* but – more likely in my opinion – cut off or hidden in its single known specimen. See also *Archaelagonops salticoides*). The position of the anterior lateral eyes (figs. 38, 45–46) is slightly medially in front of the large posterior median eyes.

Further important and basic characters: Ecribellate, 3 pairs of spinnerets, unpaired tarsal claw existing (figs. 42, 71), respiratory organs unknown (most probably a pair of lungs), metatarsi with a single trichobothrium or few ones, tarsi with few trichobothria or a single one or – probably in certain taxa – without trichobothria (figs. 39, 44, 69). Cheliceral promarginal “peg teeth” exist (figs. 40, 68), lateral stridulatory files are absent. Feathery and plumose hairs are absent. The colulus is large. Legs: Patellae not elongated, bristles (not spines!) are quite rare and most often very thin. Scopulae are absent, prolateral scale-shaped flattened hairs exist in *Archaelagonops* (fig. 70), prolateral hairs in *Grandoculus* and dense LONG hairs in *Lagonoburmops* (photos, fig. 44), a “preening comb” of stiff hairs/bristles exist on metatarsus III–IV at least in adult spiders

of *Lagonoburmops* (fig. 43), *Myanlagonops* (figs. 47), and *Archaelagonops* (fig. 69), the paired tarsal claws bear several long teeth (figs. 48, 70) or a single large tooth (fig. 41–42). Pedipalpal tibial apophysis absent. Autotomy apparently absent. Up to now no report exists that Lagonomegopidae were spider eaters. Ecology. See below, the genus *Archaelagonops* n. gen..

**Relationships:** Mainly according to the cheliceral “peg teeth” (\*), the reduced or absent leg bristles (not spines), and the raised cephalic part (in certain genera only!) I regard the diverse Lagonomegopidae as a family of the superfamily Archaeoidea (= Palpimanoidea). In most members of the Archaeoidea prolateral spatulate or scale-shaped leg hairs exist (not in the Archaeidae s. l.: Mecysmaucheniinae and in most Lagonomegopidae), cheliceral stridulatory files (absent in the Lagonomegopidae), a long eye field (it is short e. g. in the Huttoniidae and Spatiatoridae) as well as 8 eyes (six eyes in some members of the Mecysmaucheniinae in which eyes and chelicerae are quite different from six-eyed Lagonomegopidae). A low prosoma exists in the family Huttoniidae (extant), a flat bulbous in the Spatiatoridae (known from Baltic amber) in which the position of the eyes is quite different to the Lagonomegopidae. – Because of the existence of tarsal trichobothria (\*\*), the absence of cheliceral files – besides the unique eye position – I regard the family Lagonomegopidae as a branch of its own besides the Archaeidae s. l. and the palpimanoid branch, see WUNDERLICH (2004: 761, cladogram). In contrast to the trichotomy in that cladogram I now regard the Lagonomegopidae as the sister group to the Archaeidae s. l. (it possesses a prosomal foramen) + the palpimanoid branch (it possesses long patellae); both possess cheliceral files but no tarsal trichobothria. – If Lagonomegopidae really is a member of the Archaeoidea s. l. it should be a haplogyne family.

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(\* ) “Peg teeth” are not direct outgrowths of the cuticula = teeth, but stiff, straight and blunt modified HAIRS which possess a “ring” around their base like normal hairs. Such structures are quite rare in spiders and are known besides the Archaeoidea only from the family Mimetidae as well as from certain members of the families Theridiidae and Thomisidae.

(\*\*) Is the existence of tarsal trichobothria – which is unique within the Archaeoidea – a reversal in the family Lagonomegopidae? Within another haplogyne superfamily – the Dysderoidea s. l. – exists a similar case: Only in the Caponiidae exist such sensory hairs on the tarsi in contrast to all related families, see WUNDERLICH (2004: 644).

**Distribution:** Known from Lowest to Upper Cretaceous of the Northern Hemisphere: Burma (= Myanmar), Canada, Russia (Siberia), Spain (Alava) and USA (New Jersey), see the map below.

**Synonymy:** The monotypic Cretaceous family Grandoculidae PENNEY 2011 was based on a single incomplete juvenile or female spider of the genus *Grandoculus* PENNEY 2004 from Canada, and was split off from the family Lagonomegopidae. In *Grandoculus* the main diagnostic character of the family Lagonomegopidae exists (it is unique in spiders!): Powerful and widely spaced posterior median eyes as well as tiny and widely spaced anterior lateral eyes. Posterior lateral eyes were not reported but may exist, see above. Bulging parts of the long clypeus exist as a further typical lagonomegopid character but exceptions exist. (\*). One of the typical archaeoid characters – spatulate/scale-shaped prolateral leg hairs (see above) – is absent in *Grandoculus*,

such hairs are absent in several members of the Lagonomegopidae. – As main diagnostic characters (apomorphies) of the family Grandoculidae PENNEY regards “The enlarged first leg with a dense scopular brush of hook-shaped setae on metatarsus I.” Surprisingly the first leg pair is called enlarged although the legs are quite incompletely preserved, and tibia II is not much shorter than tibia I (1.3 : 1.6). As known to araneologists scopula hairs exist on the pro- and retro-VENTRAL side of (distal) leg articles. The position of the special hairs of leg I is identical to the spatulate/scale-shaped hairs in most Archaeoidea; I regard these slender hairs as an apomorphic character of the genus *Grandoculus*. Another apomorphic character of the legs are the dense hairs of the genus *Lagonoburmops* which exist AROUND the leg articles (fig. 44). (\*\*). – In my opinion a splitting of the family Lagonomegopidae is not justified, and I regard the Grandoculidae PENNEY 2011 as a junior synonym of the Lagonomegopidae ESKOV & WUNDERLICH 1995 (n. syn.).

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(\* Other characters of *Grandoculus* – like the existence of “peg teeth” (not surely reported), absence or rareness of leg bristles, a raised part of the cephalic part – are typical patterns of the Archaeoidea, see above.

(\*\*) Although PENNEY (2004: Figs. 2A, B) explicitly figures and calls some bristles “spines”, the same author says on p. 582 “All legs lack spines and are covered with fine, feathery setae;”. Feathery hairs are not figured in this paper. I found neither leg spines nor feathery hairs in members of the family Lagonomegopidae. (Several authors mistook feathery hairs; shape of a true feathery hair: See WUNDERLICH (2008: 670: Fig. 113). See also the remark directly below.

Remark (see also the remarks above regarding the number of eyes): Most lagonomegopid taxa (specimens and species as well) are known from juveniles. In juveniles the proportions of body and legs may be different from adults – e. g. stouter leg articles may exist, and relatively longer tarsi –, and a slightly higher number of leg bristles may exist, too. Leg bristles are completely absent in the three adult Lagonomegopidae described in this paper.

**Subfamilies:** Lagonomegopinae ESKOV & WUNDERLICH 1995 and Archaelagonopinae n. subfam.

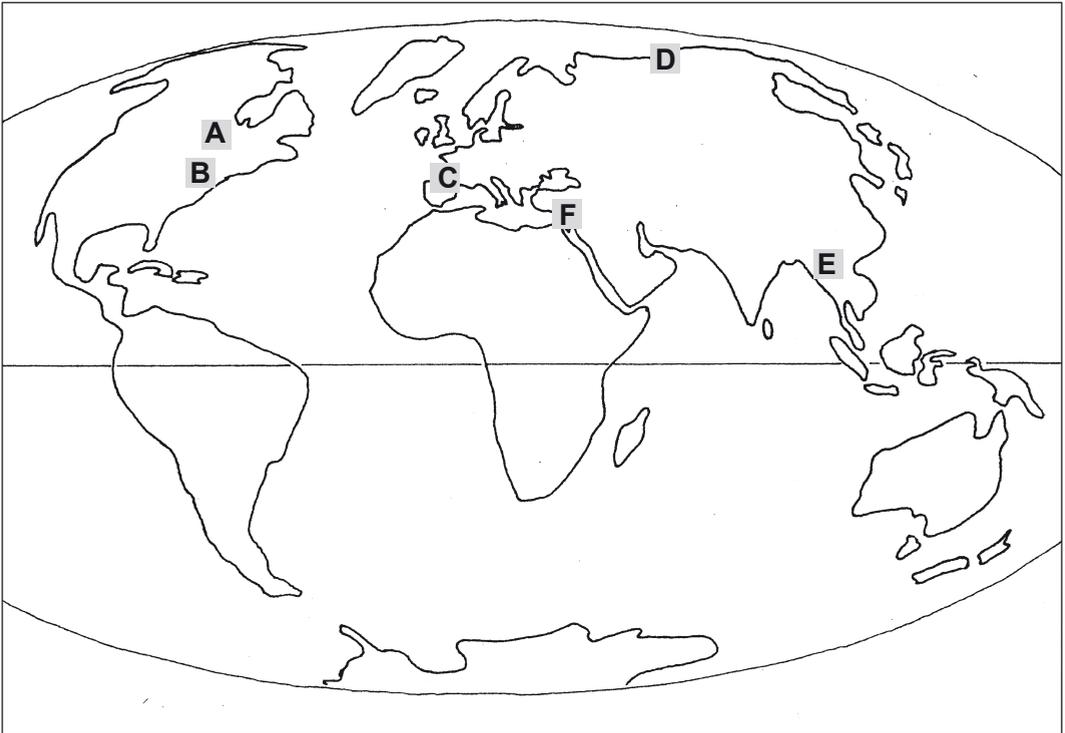
Subfamily **LAGONOMEGOPINAE** ESKOV & WUNDERLICH 1995

Type genus: *Lagonomegops* ESKOV & WUNDERLICH 1995. Further genera: *Burlagonomegops* PENNEY 2005, *Grandoculus* PENNEY 2004, *Lagonoburmops* n. gen., *Maynlagonops* n. gen., and *Zarqagonomegops* KADDUMI 2007.

**Diagnosis** (♀; ♂ unknown): The subfamily is best diagnosed by its unique powerful posterior median eyes in a more anterior position which are directed **OBLIQUELY LATERALLY** (figs. 38, 45–46). The long and usually bulging clypeus bears a pair of low humps, see **ESKOV & WUNDERLICH (1995: Fig. 1)**, **WUNDERLICH (2008:667: Fig. 73)**, the cephalic part is raised in some genera like *Lagonomegops* or low like in *Myanlagonops* (fig. 45).

**Relationships:** See the *Archaelagonopinae* n. subfam.

**Distribution:** Lower and Mid Cretaceous of the Northern Hemisphere, see the map below.



Genera:

- Archaelagonops* (E)
- Burlagonomegops* (E)
- Gen. indet./indescr.? 1 (B)
- Gen. indet./indescr.? 2 (C)
- Gen. indet. 3 (E)
- Grandoculus* (A)
- Lagonoburmops* (E)
- Lagonomegops* (D)
- Myanlagonops* (E)
- Zarqagonomegops* (F)

Deposits:

- A: Canada
- B: New Jersey (USA)
- C: Spain (Alava)
- D: Siberia (Taimyr)
- E: Burma (Myanmar)
- F: Jordan

Map: **Distribution** of the genera of the Cretaceous spider family Lagonomegopidae.

Provisional key to the genera of the family Lagonomegopinae:

Notes:

(1) Because of the lack of characters it was impossible to me to include the genus *Zaragonomegops* KADDUMI 2007 – based on a single juvenile specimen of *Z. wunderlich* – from Lowest Cretaceous amber of Jordan, see WUNDERLICH (2008: 615). Its cephalic part is high, its legs are fairly slender. – Gen. indet. 3: See below.

(2) The determination of the Lagonomegopinae from Spain (under *Burlagonomegops*) and USA: New Jersey (under *Lagonomegops*, too), appear quite unsure to me, see the key nos. 2 and 3. The descriptions of both taxa are based on juvenile spiders.

(3) The existence of tarsal trichobothria and their exact number have not been closely studied, see figs. 41, 69).

1 Body and legs (fig. 44, photos) densely covered with long hairs. Paired tarsal claws with a single large tooth (fig. 42). Body length (♀) ca. 8 mm, ♂ and juveniles unknown. Mid Cretaceous Burmese (Myanmar) amber. Only *L. plumosus* n. gen. n. sp. . . . . . *Lagonoburmops*

- Hairs of body and legs not unusually dense and/or shorter (photos), a brush exists in *Grandoculus*. Paired tarsal claws with several long teeth as in fig. 48 or otherwise. Inclusions in amber from different countries including Burma (Myanmar). . . . . 2

2(1) Prosoma low (cephalic part not raised). Legs long and slender, tarsi distinctly shorter than metatarsi (photos) . . . . . 3

- Shape of the cephalic part unknown, legs fairly slender, tarsi clearly shorter than metatarsi. Upper Cretaceous amber from the USA (New Jersey). Only "*Lagonomegops*" *americanus* PENNEY 2005 . . . . . Gen. indet./indescr.? 1

- Cephalic part raised, see WUNDERLICH (2008: 666, fig. 71), legs stouter, tarsi frequently as long as metatarsi, but see the remark (1) above. Adults unknown . . . . . 4

3(2) ♂: Pedipalpus (figs. 49–50) with long and slender articles. Mid Cretaceous Burmese amber. Only *M. gracilipes* . . . . . *Myanlagonops*

- ♂ unknown. Lower Cretaceous amber from Spain (Alava). Only "*Burlagonomegops*" *alavensis* PENNEY 2005 (juv.) . . . . . Gen. indet./indescr.? 2

4(2) Metatarsus and tarsus I bear a distinct prolateral brush/line of thin hairs which are strongly bent distally on the metatarsus (as a result of the preservation?). Leg I

distinctly the largest. Upper Cretaceous from Canada. Only *G. chemahawinensis* PENNEY 2004 ..... Grandoculus

- No such hairs ..... 5

5(4) Prosoma 1.6 times longer than wide. Labium longer than wide. Burmese amber. Only *B. escovi* PENNEY 2005. .... Burlagonomegops

- Prosoma 1.25 times longer than wide. Labium wider than long. Siberian amber. Only *L. sukatchevae* ESKOV & WUNDERLICH 1995. .... Lagonomegops

### Lagonoburmops n. gen.

The name is composed by the terra typica Burma (= Myanmar) and the name of the genus *Lagonomegops*. Its gender is masculine.

Type species (by monotypy): *Lagonoburmops plumosus* n. sp.

**Diagnosis** (♀; ♂ unknown): Tarsi with several long trichobothria (fig. 41), body and legs densely covered with long hairs (photo 23, fig. 44). Tarsi distinctly shorter than metatarsi, the paired tarsal claws bear a single long tooth (fig. 42).

**Relationships**: See the key. Close relationships are unknown. Numerous long hairs on body and legs are different, and unknown from all other lagonomegopid spiders.

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

***Lagonoburmops plumosus* n. gen. n. sp.** (figs. 40–44) photos 22–23

**Material**: Holotype (♀) in Mid Cretaceous Burmese (Myanmar) amber, F2270/BU/AR/CJW. – Remark: According to the body size as well as the proportions of prosoma, opisthosoma and legs I regard the female as most probably adult.

**Preservation and syninclusions**: The spider is completely but badly preserved in a mainly yellowish piece of amber, body and legs are strongly flattened (depressed dorso-ventrally) apparently by strong pressure during millions of years, the original eye position is not observable. Tiny bubbles cover mainly the ventral part of the opisthosoma. – Syninclusions: Some spider's threads are preserved, e.g. a thread running to

the right tarsus III; it may be a part of a dragline; a tiny pseudoscorpion below and in front of the chelicerae, two insect's larvae (one of a beetle, the other one probably from a Diptera), the leg of a beetle, and some ballets of insect's excrement.

**Diagnosis** (♀; ♂ unknown): See the genus.

**Description** (♀):

Measurements (in mm): Body length about 8.0, prosoma: Length 3.0, width unknown (probably about 2.5); leg I: Femur 3.5, patella 1.6, tibia 3.2, metatarsus 2.2, tarsus 1.1, tibia II 3.2, tibia III 2.0, tibia IV 2.3; diameter of a posterior median eye 0.35.

Colour light brown.

Prosoma (fig. 40, photo) strongly deformed/depressed, longer than wide, densely covered with longer hairs, fovea unknown, lense of the left posterior median eye is fairly well preserved (the right one less well), at least 7 long cheliceral "peg teeth", further teeth unknown (probably absent), lateral stridulatory files absent, fangs long and apparently slender. Gnathocoxae (they are turned under the left side of the spider) long and not converging (so far observable), labium hidden, sternum strongly deformed. Plumose and feathery hairs absent. Pedipalpus hairy, tarsal claw absent. – Legs (figs. 41–44, photo 23) fairly long, tarsi relatively short, order I/II/IV/III, III distinctly the shortest, I not elongated, densely covered with longer hairs around the articles (no scopula), depressed by the preservation with the exception of the distal articles of the right leg III. Bristles absent, position of one metatarsal I–II trichobothrium in ca. 0.8, tarsi with several long trichobothria (fig. 41). The (all?) paired tarsal claws bear a single large tooth in the basal half, unpaired claw well developed, bent in a right angle. – Opisthosoma (photo) about twice as long as wide, densely covered with longer hairs. The ventral side is additionally covered with numerous tiny gas bubbles which may be the result of decomposition; therefore the lung covers, the tracheal spiracle, and most parts of the short spinnerets are hidden.

**Relationships:** See the genus.

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

**Myanlagonops n. gen.**

The name is composed by the terra typica Myanmar (Burma) as well as the name of the genus *Lagonomegops*. Its gender is masculine.

Type species (by monotypy): *Myanlagonops gracilipes* n. sp.

**Diagnosis** (♂; ♀ unknown): Tarsal trichobothria probably existing, legs slender (photo 24), fovea distinct; pedipalpus (figs. 49–50) with long and slender articles, cymbium long, bulbus not protruding, partly covered by the cymbium, structures of the bulbus only partly and insufficiently observable.

**Relationships:** See the key. Probably a taxon (juv.) in Lower Cretaceous amber from Spain is related.

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

***Myanlagonops gracilipes* n. gen. n. sp.** (figs. 45–50) photo 24

**Material** in Mid Cretaceous Burmese (Myanmar) amber, holotype ♂, F2269/BU/AR/CJW.

**Preservation and syninclusions:** The spider is fairly well but incompletely preserved at the margin of an orange piece of amber which has apparently been under strong pressure. About 20 layers build the piece and demonstrate a rapid frequency of flows of the fossil resin. Cut off are the opisthosoma of the spider and several leg articles: Both legs IV basally through the femora (distal parts of tarsi, metatarsi and parts of the tibia are preserved), few dorsal parts of the right tibia and patella I, and distal or apical parts of all tarsi except the left legs II and III. The prosoma is deformed anteriorly. – Syninclusions: Some thin spider's threads are preserved, e.g. below the right legs I–III, more than a dozen Acari of several taxa, remains of 2 Diptera, a question larva of an insect with parts of large anterior legs, and remains of plants like “stellate hairs”.

**Diagnosis** (♂; ♀ unknown): See the genus.

**Description:**

Measurements (in mm): Body length about 4.0, prosoma: Length 2.0, width ca. 1.4; leg I: Femur 2.4, patella 0.8, tibia 2.5, metatarsus 1.9, tarsus ca. 1.5, tibia II 2.4, tibia III 2.0.

Colour dark brown.

Prosoma (figs. 45–46, photo) 1.54 times wider than long, low (cephalic part not raised), bearing numerous thickened appressed hairs, fovea well developed, 3 pairs of eyes which all are widely spaced, anterior median eyes absent, the powerful posterior median eyes are directed anteriorly-laterally, anterior and posterior lateral eyes tiny, clypeus long, vertical and bulging with a pair of humps, basal cheliceral articles long, not diverging, lateral files apparently absent, “peg teeth” most probably existing, fangs long, gnathocoxae apparently not distinctly converging, labium almost triangular, sternum hidden. – Legs (figs. 47–48, photo) long and slender, femur I 13.5 times longer than wide, order I/II/III (IV is lost), I not strongly elongated, III not very much shorter than II, hairs short and dense, bristles absent, metatarsal preening comb (fig. 10) consisting of ca. 5 apical bristles, tarsal trichobothria probably existing, position of a metatarsal I–II trichobothrium in 0.8 (further trichobothria may exist), paired tarsal claws (fig. 11) with several very long teeth, unpaired claw shorter. – Opisthosoma cut off. – Pedipalpus (figs. 49–50): Coxa and trochanter short, remaining articles long and slender, femur, patella and tibia with longer dorsal-distal hairs, tibia with long ventral hairs, without an apophysis, cymbium long and slender, enclosing parts of the bulbus which is not protruding, darkened and partly hidden, several sclerites are insufficiently observable.

**Relationships:** See the genus.

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

Gen. indet. 3: 1 juv. in Burmese amber, F2376/BU/AR/CJW. Measurements (in mm): Body length 4.0, prosoma (dorsal parts are cut off): Length 2.0, width 1.5; leg I: Femur 1.3, patella 0.65, tibia 1.3, metatarsus 0.9, tarsus 0.6. Prosoma high and wide anteriorly, “peg teeth” very long and slightly bent, pedipalpal tarsal claw absent, legs bristleless, fairly stout, tarsus I bears about half a dozen trichobotria (some are long), paired tarsal claws with several long teeth, tarsi, metatarsi and tibiae bear dense THIN hairs, which are shorter than in *Lagonoburmops*. Large part of a spider web is preserved above the spider.

Subfamily **ARCHAELAGONOPINAE n. subfam.**

The name of the subfamily is composed by a part of the name of the related family Archaeidae and a part of the name of the family name Lagonomegopidae.

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

**Diagnosis** (♂; ♀ unknown): Prosoma (figs. 67–68, photo 25): Posterior median eyes very large and directed ANTERIORLY on a high clypeus which is sloping vertically. Most probably six eyes. Basal cheliceral articles very long, slender and not diverging. Scale-shaped appressed leg hairs existing (fig. 70). Tarsal trichobotria existing (fig. 69).

Further and basic characters: Ecribellate, probably haplogyne, three-clawed (fig. 71), cheliceral peg teeth probably existing (fig. 68), metatarsal III–IV preening comb existing (fig. 69), legs long and slender (fig. 69, photos), bristles absent, tarsi I–II with long hairs (fig. 70), cheliceral foramen and feathery hairs absent.

**Relationships:** According to the combined absence of leg bristles, the existence of scale-shaped appressed leg hairs, and (most probably) cheliceral peg teeth Archaelagonopinae is a member of the superfamily Archaeoidea (= Palpimanoidea). In the Archaelagonopinae exist characters of the Archaeidae – appressed scaly hairs – as well of the Lagonomegopidae: powerful posterior median eyes and tarsal trichobotria. Tarsal trichobotria are absent in the Archaeidae, and a cheliceral foramen exists in contrast to the Lagonomegopidae. The position of the posterior median eyes (fig. 68) is quite different from the Lagonomegopinae (figs. 38, 45). – Remarkably the Deinopidae of the superfamily Araneoidea evolved also powerful posterior median eyes which are

directed anteriorly similar to the Archaelagonopinae but the Deinopidae are entelegyne cribellate spiders which possess a capture web, feathery hairs, no metatarsal preening comb, and the position of the eyes besides the median ones is quite different. Powerful median eyes which are directed anteriorly exist also in the extinct Salticoididae and in the extant Salticidae but the large eyes are ANTERIOR median eyes in these families.

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

### **Archaelagonops n. gen.**

Etymology: See the subfamily. The gender is neuter.

Type species (by monotypy): *Archaelagonops salticoides* n. sp.

**Diagnosis and distribution:** See the subfamily.

### ***Archaelagonops salticoides* n. gen. n. sp.** (figs. 67–72) photo 25

The name of the species points to certain similarities of the family Salticidae.

**Material:** Holotype ♂ in Mid Cretaceous Burmese (Myanmar) amber, F2364/BU/AR/CJW.

**Preservation and syninclusions:** The spider is only fairly well and incompletely preserved in a yellow (partly orange) piece of amber; tiny bubbles exist on the body and within the piece of amber, the opisthosoma is deformed and transparent, parts of both anterior legs and of the left pedipalpus are cut off. – A larger leaf (probably of the “amber tree”, Araucariaceae), detritus and remains of insects and spiders legs are preserved in the same piece of amber.

**Diagnosis** (♂; ♀ unknown): prosoma (figs. 67–68) long and high, pedipalpus (fig. 72) with an elongated cymbium and a long bulbous.

#### **Description** (♂):

Measurements (in mm): Body length 4.0, prosoma: Length 2.0, width ca. 1.3; femur I 2.3, leg II: Femur ca. 2.2, patella 0.8, tibia 2.75, metatarsus 2.0, tarsus 0.65, tibia III 1.5, tibia IV 1.9, femur IV ca. 2.2, length of a basal cheliceral article 0.8.

Colour grey brown.

Prosoma (figs. 67–68, photo 25) (it is covered with tiny bubbles) high, distinctly longer than wide, fovea well developed; most eyes are hidden, only the powerful median eyes are well observable (I regard these eyes as the posterior median eyes which changed in the anterior position of the lost anterior median eyes); apparently 3 pairs of eyes like in (all?) other Lagonomegopidae. The large posterior median eyes are directed anteriorly on a high and sloping clypeus. The cephalic part has a dorsal depression and bears apparently tiny dorsal spines. The basal cheliceral articles are very long and slender, not diverging, the lateral sides are hidden, few “peg teeth” are apparently existing, the fangs are of medium length, other mouth parts are hidden, a foramen is absent. – Legs (figs. 69–71, photos) long and slender, order probably II/IV/III, bristles absent, 3 tarsal claws, paired claws with few long teeth, scopulae and claw tufts absent, the legs I–II bear flat scaly hairs (fig. 69). – Opisthosoma (fig. 67, photos) oval, hairs and spinnerets short. – Pedipalpus (fig. 72): Femur slender, patella and tibia fairly thickened (deformed), tibia longer than the patella, cymbium long, slender and hairy, bulbus long and slender, most structures hidden or cut off.

**Ecology and behaviour:** Numerous members of the superfamily Archaeoidea (= Palpimanoidea) are spider eaters, and powerful basal cheliceral articles are typical for most araneophagous spiders, including the Mimetidae of the superfamily Araneoidea. Most of such long-legged and slowly moving spiders like Archaeidae are “sit-and-wait” predators, and the life style of the Lagonomegopidae was apparently the same. The existence of a metatarsal preening comb exclude a web-building behaviour.

**Relationships and distribution:** See above.

#### Family **MICROPALPIMANIDAE** WUNDERLICH 2004

Only a single genus and species of this extinct Cretaceous family has been described: *Micropalpimanus poinari* WUNDERLICH 2004, the male holotype and a probably conspecific male. In this paper I describe a female – the first female of this family – of a species which I consider as congeneric and probably even conspecific.

**Relationships of the family Micropalpimanidae:** Mainly according to the raised cephalic part and the wide cymbium I now regard the – also monotypic and extinct – Eocene (Baltic amber) family Spatiatoridae PETRUNKEVITCH 1942 as closely related, but not synonymous, see PENNEY & SELDEN (2011: 103), and separate from the Huttoniidae. Spatiatoridae may be the sister group to the Micropalpimanidae. In the Spatiatoridae the cephalic part is almost smooth, and the articles of the male pedipalpus are more slender than in the Micropalpimanidae. More Cretaceous fossils are needed for more thorough conclusions.

***Micropalpimanus* sp. indet.** (figs. 51–53) photo 26

**Material:** A female in Mid Cretaceous Burmese (Myanmar) amber, and a larger separated piece of amber, F2285/BU/AR/CJW.

**Preservation and syninclusions:** The spider is completely but deformed preserved in a muddy, 3 cm long piece of amber, from which it has been separated in a small piece of amber. The spider's opisthosoma is removed from the prosoma within the amber by 0.3 mm. – Remains of two insects as well as stellate hairs exist in the same piece. A small Diptera, a tiny beetle (body length 0.55 mm), cerci of a larger insect, and remains of plants are preserved in the separated piece.

**Description** (♀):

Measurements (in mm): Body length 2.0, prosoma: Length 1.0, width ca. 0.5, tibia I 0.45, leg II: Femur ca. 0.9, patella ca. 0.35, tibia 0.55, metatarsus 0.35, tarsus ca. 0.28, tibia III 0.35, tibia IV 0.55.

Colour: Prosoma and legs medium to dark brown, opisthosoma light grey, genital area darker.

Prosoma (fig. 51) about twice as long as wide, cuticula rugose, cephalic part raised (less strongly and more anteriorly than in the male of *M. poinari*), 8 eyes in two rows (partly hidden), anterior median eyes largest, thoracal fissure well developed and long. Clypeus slightly longer than the large anterior median eyes, basal cheliceral articles stout, lateral files strongly developed, "peg teeth" hidden, fangs stout, labium long and pointed, gnathocoxae long and converging, coxae IV spaced by the sternum by less than their diameter. – Legs (figs. 52–53) fairly long, order IV/I/II/III, spatulate hairs on legs I–II indistinct through the preservation or absent, true bristles absent, all metatarsi with a long trichobothrium in the distal half, tarsi with a long erect prolateral sensory hair near the middle, metatarsi III–IV with an apical "preening comb" of bristle-shaped hairs, 3 tarsal claws, the paired claws are toothed. – Pedipalpus shorter than the prosoma, tarsal claw absent. – Opisthosoma 1.75 times longer than wide, soft, covered with short hairs, lung covers distinct, three pairs of spinnerets which are deformed like the genital area.

**Relationships:** In the male generotype, *M. poinari* WUNDERLICH 2004, and in *M. sp.* sensu WUNDERLICH (2004) I did not find a long tarsal sensory hair but a similar rugose prosomal cuticula and well developed lateral cheliceral stridulatory files like in the present female. Therefore I do not want to exclude that this female may be conspecific with *M. poinari*.

**Distribution:** Mid Cretaceous Burmese amber forest.

## B 2. ENTELEGYNÆ

(1) Unsure superfamily (really Entelegynae?):

Family **BURMASCUTIDAE** WUNDERLICH 2008

Only a single species of this extinct enigmatic family has been described: A male and a female of the genus *Burmascutum* WUNDERLICH 2008 in Cretaceous Burmese amber, see Beitr. Araneol., 5 (2008: 624–627).

Remark:

The type genus has been published correctly under *Burmascutum*, see Beitr. Araneol., 5 (2008: 624) but the type species *aenigma* has erroneously been listed p. 625 under *Burmarachne* instead of *Burmascutum*.

The key of the spider families in Cretaceous ambers – see Beitr. Araneol., 5 (2008: 565) (\*) – has to modify in no. 3 (to the family Burmascutidae):

no. 7: Please add: Metatarsus III bears a ventral-apical “preening comb”.

no. 7 -: Please add: “Preening comb absent”.

no. 8 -: Please delate “Prolateral spatulate hairs exist on metatarsi and tarsi I–II”.

(This character is already listed previously, in no. 7).

no. 8 – -: This line has to delate completely.

(2) Superfamily **ARANEOIDEA s. l. (= Orbiculariae) (incl. Deinopoidea)**

(a) The CRIBELLATE BRANCH (= “Deinopoidea”: Deinopidae and Uloboridae):

## Family **ULOBORIDAE**

Three monotypic Cretaceous genera of this family have been described by WUNDERLICH (2004) from Burmese amber. One of these genera – *Burmoloborus* – may be related to the family Pholcochyroceridae, see below. The family Uloboridae was diverse in the Cretaceous. Here I describe a further genus based on a female, a part of (its?) cribellate orb web and remains of (its?) questionable egg sac.

### **Ocululoborus n. gen.**

The name is a combination of oculus (latin, eye) and the family name Uloboridae.

Type species (by monotypy): *Ocululoborus curvatus* n. sp.

**Diagnosis** (♀; ♂ unknown): Posterior lateral eyes (fig. 54) very large, prosoma long and slender, 1.57 times longer than wide, metatarsus IV (fig. 55) strongly curved. Femoral trichobothria have not been found, probably they are lost by the preservation.

**Relationships:** The lenses of the posterior lateral eyes (if they really are the lenses and not only the humps of the eyes) are larger than in other fossil and extant uloborid genera, the shape of the long prosoma is also different to other genera, metatarsus IV is stronger bent than in other taxa in Burmese amber, see WUNDERLICH (2004).

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

***Ocululoborus curvatus* n. gen. n. sp.** (figs. 54–55) photos 27–29

**Material:** Holotype ♀ and a part of (its?) capture web and (its?) egg sac in Mid Cretaceous Burmese (Myanmar) amber, F2278/BU/AR/CJW.

**Preservation and syninclusions:** The spider is decomposed and dissected, loose legs, pedipalpi, the peltidium and mouth parts are preserved on a single layer within the amber. – 3 ½ mms below the spider a decomposed and depressed and probably con-specific egg sac is preserved, and just below the surface of the piece of amber some spiders threads are preserved. Further syninclusions: See above: Dipluridae.

**Description** (♀):

Measurements (in mm): Body length (the opisthosoma is lost) probably about 2.2 prosoma: Length 1.1, width 0.7; leg I: Femur ca. 1.0, patella 0.45, tibia 1.0, metatarsus ca. 1.15, tarsus ca. 0.75; leg IV: Femur 1.0, patella 0.35, tibia 0.65, metatarsus 0.8, tarsus ca. 0.45, tarsus of the pedipalpus 0.4.

Colour medium grey brown.

Prosoma (photo 27, fig. 54; only the peltidium is fairly well preserved) 1.57 times longer than wide, not distinctly widened posteriorly, flat, without humps, fovea, mouth parts and sternum unknown or not closely observable. Probably 8 eyes (most eyes are hidden), lenses of the posterior lateral eyes (or their humps) very large. Pedipalpus slender, tarsal claw large. – The loose legs are fairly long and slender, their order probably I/II/IV/III, I not distinctly elongated, trichobothria – including the femoral ones – unknown (probably absent or not observable due to the decomposition), metatarsus IV strongly bent (fig. 55), calamistrum long, bristles long (some bristles may be lost), patellae and tibiae bear two dorsally. The tarsal claws are hidden. – The opisthosoma is not preserved.

Threads (photo 28) which originate probably from the holotype: Some more or less parallel lines of threads – partly consisting of several lines and partly cribellate? Remains of a questionable orb web, very few sticky droplets, and remains of prey like a beetle are preserved in a layer near the surface of the piece of amber on the opposite side to the spider's position.

Questionable egg "sac" (photo 29) which originates probably from the holotype. It is depressed, ca. 3 mm in diameter, connected with a furcate spider's thread but not within a cocoon of dense hairs. About a dozen questionable eggs/embryos and exuviae (?) are preserved within a transparent medium (probably remains of a kind of a gelatine-like secretion), some of these are preserved outside nearby the "lump".

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

(b) The ECRIBELLATE BRANCH (= Araneoidea s. str.):

Fossils of this ecribellate entelegyne branch may be recognizable by its rosette-shaped position of the relatively short spinnerets in which the anterior ones are stout and weakly spaced, and – with the exception of the family Theridiidae – the existence of a retrobasal paracymbium. Up to now only orb weavers are surely known from the Cretaceous, no weavers of irregular webs like Linyphiidae or Theridiidae. Below two of the quite rare Cretaceous araneoid males are described, the first araneoid adult males in Burmese amber, members of two genera of the family Theridiosomatidae which are orb weavers.

## Family THERIDIOSOMATIDAE

The eight-eyed family Theridiosomatidae is best diagnosed by its unique paired sternal pits which are not observable in the present fossils. Furthermore the VERY LONG AND THIN leg bristles (figs. 57, 64) as well as the very long trichobothria (fig. 57) – especially on tibia III – are typical characters of the family. Basically femoral and lateral tibial bristles exist in the Theridiosomatidae – e. g. in the Cretaceous taxa – but they are lost in several extant taxa. Unfortunately CODDINGTON (1986) did not treat the chaetotaxy in his revision of the family. He (p. 8) only mentioned “robust setae”. Setae are bristle-shaped hairs but in Theridiosomatidae thin but true (and long) bristles exist (figs. 57, 64); their position on the tibiae is exactly the same as (e. g.) in the related symphytognathoids or in the Linyphiidae. Quite thin leg bristles exist in other araneoid families, too, e. g., in the Theridiidae. The same author mistook spines for spurs. – Most extant, Miocene and Eocene males possess voluminous bulbi (*Chthonos* is an exception) in contrast to the small bulbi of the basal extant Luangnaminae – see WUNDERLICH (2011: 439) – and of the genus *Hypotheridiosoma* n. gen. in Cretaceous Burmese amber. A claw of the female pedipalpal tarsus is absent like in the related symphytognathoids. The orb web in several Theridiosomatidae is usually strongly modified, absent in *Chthonos*.

Fossil Theridiosomatidae have been described from Miocene Dominican amber, see WUNDERLICH (1988: 113–117), from Eocene Baltic amber, see WUNDERLICH (2004: 998–1019) (2011: 436–437), and recently from the Cretaceous of Russia, preserved in about 130 million year old clayrock, see SELDEN (2010) and WUNDERLICH (2011: 430). The present taxa are the second ones described from the Cretaceous, the first known ones in Burmese amber, and in Cretaceous ambers as well. See also above, the remarks on erroneous determinations, the alleged philodromid genus *Cretadromus*.

### **Leviunguis n. gen.**

Etymology: The name points to the smooth or almost smooth tarsal claws in this genus (and probably the family as well): *Levis* = smooth, *unguis* = claws. – The gender of the name is masculine.

Type species (by monotypy): *Leviunguis bruckschi* n. sp.

**Diagnosis** (♂; ♀ unknown): Femur I bears a single prolateral bristle (fig. 56); ♂-pedipalpus (figs. 59–62): Tibia I (see below) with a long prolateral outgrowth which is bent distally, cymbium very wide (fig. 59), bulbous with a long embolus and a long parembolic apophysis which is partly guided by the cymbial margin.

Further character: “Thoracic shoulders” absent, metatarsus IV bears a trichobothrium in its distal half.

**Relationships:** A long parembolic apophysis exists (e. g.) also in *Chthonopes* WUNDERLICH 2011 from South East Asia in which strong prolateral leg hairs exist, femoral bristles are absent, the male pedipalpal tibia is not elongated, the cymbium is more slender, and the parembolic apophysis is shorter. In the Early Cretaceous genus *Eocoddingtonia* SELDEN 2010 from Russia – which may be most related – exist several bristles in rows on all femora, a trichobothrium on metatarsus IV is probably absent, the structures of the male pedipalpus are unknown, and the receptacula seminis are not connected. – According to the existence of a long parembolic apophysis I do not want to exclude that *Leviunguis* is a member of the Chthonopini of the South East Asian subfamily Luangnaminae WUNDERLICH 2011 – which is diagnosed by its plesiomorphic not connected receptacula seminis which are unknown in *Leviunguis*, but its bulbus is fairly large. – According to the quite different structures of the male pedipalpus the genus *Hypotheridiosoma* n. gen. is not strongly related: A large paracymbium exists, the bulbus is small, the embolus is hidden (small?), the legs are relatively longer, tibia I bears a proapical bristle, and the position of the metatarsal trichobothrium is more basally.

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

***Leviunguis bruckschi* n. gen. n. sp.** (figs. 56–62) photos 30–31

**Derivatio nominis:** The species is dedicated to KLAUS-PETER BRUCKSCH, the previous owner of the piece of amber which included the holotype; he discovered this interesting spider within the collection of a dealer.

**Material:** Holotype ♂ in Mid Cretaceous amber from Burma (Myanmar), F2266/BU/AR/CJW.

**Preservation and syninclusions:** The small piece of amber which include the holotype and spider's threads as well has been separated by the present author from a larger piece of the collection of ALEX BEIGEL no. BU-20, which include several organic inclusions like parts of plants, 1 Aphidina, 5 Diptera and 3 Coleoptera. The colour of the amber piece is yellowish orange, partly brownish by heating and pressure. About two mms behind the spider few branched, deformed and partly brownish spider's threads without droplets are preserved. – The spider is completely preserved, body, legs and pedipalpi are strongly deformed, the prosoma (laterally) and the pedipalpi are compressed. A slightly crumpled light bubble – probably a digestive secretion – is lying below the mouth, a further similar bubble is preserved between the coxae IV, the anterior median eye lenses are set forward on stalks, the opisthosoma is crumpled.

**Diagnosis** (♂; ♀ unknown): See the genus. *L. bruckschi* is one of the smallest members of the family Theridiosomatidae.

**Description** (♂):

Measurements (in mm): Body length 1.0, prosomal length 0.6; leg I: Femur 0.6, patella 0.2, tibia 0.4, metatarsus 0.37, tarsus 0.3, tibia II 0.32, tibia III 0.2, tibia IV 0.28.

Colour: Prosoma and legs light brown, legs not annulated, opisthosoma light greyish. Prosoma (photo 30; it is strongly deformed) distinctly longer than wide, 8 eyes in two rows, probably similar to *Burmascutum aenigma*, see Beitr. Araneol., 5 (2008: 669, fig. 101). Clypeus long, longer than the field of the median eyes, chelicerae slender and long, not diverging, other mouth parts hidden, area of the sternal pits hidden, the coxae IV are distinctly spaced. – Legs (deformed, figs. 56–58) only fairly long and stout, order I/II/IV/III, tarsi shorter than metatarsi, bristles very long, thin; femora: Only I bears a single prodistal one, patellae and tibiae bear 2 dorsal bristles, tibia I bears an additional prolateral one, metatarsi and tarsi none. Trichobothria very long: Tarsi none, all metatarsi bear a single one, position on I/II in 0.63/0.8, the tibiae bear several ones which are hard to recognize. Three tarsal claws which are long, slender and probably smooth (tiny teeth may exist), unpaired claw long and bent in a right angle. – Opisthosoma (strongly deformed) almost globular, covered with long hairs, colulus and tracheal spiracle not observable, spinnerets short and close together, three pairs. – Pedipalpus (strongly deformed, its structures are difficult to identify, figs. 59–62, photo 31) fairly large, with slender articles, patella short, tibia – if correctly identified – strongly elongated prodorsally up to the tip of the wide cymbium, bent distally and widened retrolaterally in the middle. Cymbium (fig. 59) very wide, the questionable paracymbium is short and divided. Embolus long; the long parembolic apophysis is partly guided by the cymbial margin. The remaining structures of the bulbus are difficult to recognize, a median apophysis may exist, a conductor exists.

**Relationships, life style and distribution:** See above.

**Hypotheridiosoma n. gen.**

Etymology: Hypo- (latin) = below, points to the apparently basal position of the genus within the family Theridiosomatidae.

The gender of the name is neuter.

Type species (by monotypy): *Hypotheridiosoma paracymbium* n. sp.

**Diagnosis** (♂; ♀ unknown): Tibia I bears a proapical bristle (fig. 64), pedipalpus (figs. 65–66): Bulbus small and simple, paracymbium very long, pointing and standing out, embolus hidden, probably short.

Further characters: “Thoracal shoulders” absent, metatarsus IV bears a trichobothrium in a position of 0.45.

**Relationships:** See *Leviunguis* n. gen. I do not know a closely related genus. In most taxa of the Theridiosomatidae the paracymbium is reduced. The long paracymbium of *Hypotheridiosoma* may be a plesiomorphic character of the family.

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

***Hypotheridiosoma paracymbium* n. gen. n. sp.** (figs. 63–66) photos 32–33

**Etymology:** The name of the species points to its large paracymbium.

**Material:** Holotype ♂ in Mid Cretaceous amber from Burma (Myanmar) and two separated pieces of amber, F2348/BU/AR/CJW.

**Preservation and syninclusions:** The spider is completely and well preserved in a clear yellow piece of amber which has been separated from a larger piece, a bubble covers parts of the left side of the prosoma. – Few stellate hairs and numerous tiny bubbles are preserved in the same piece of amber. In the larger piece are preserved few Coleoptera, a Hymenoptera, Diptera, insects excrements, particles of detritus including a plants “brush”, and stellate hairs.

**Diagnosis** (♂; ♀ unknown): See the diagnosis of the genus. *H. paracymbium* is one of the smallest members of the family Theridiosomatidae.

**Description** (♂):

Measurements (in mm): Body length 0.9, prosoma: Length 0.5, width at least 0.35, opisthosoma: Length 0.5, width 0.35; leg I: Femur 0.55, patella 0.16, tibia 0.35, metatarsus ca. 0.4, tarsus ca. 0.25, tibia II 0.27, tibia III 0.2, tibia IV ca. 0.25.

Colour: Prosoma and legs light brown, opisthosoma light grey.

Prosoma (fig. 63, photos 32–33) ca. 1.43 times longer than wide, low, “thoracal shoulders” absent, thoracal fissure unknown, eyes large, clypeus short, basal cheliceral articles large, few teeth on the cheliceral promarginal furrow, fangs only fairly long, mouth parts and parts of the sternum hidden, area of the sternal pits not well observable. – Legs (fig. 64, photos) fairly long and slender, order I/IV/II/III, hairs short, trichobothria long, bristles very long and thin, femur I with a single prolateral one near the middle, their sequence on patellae and tibiae 2/2/2/2, tibia I with an additional prolateral bristle near the middle and a further proapical one, position of the metatarsal IV trichobothrium in 0.45, three long and slender tarsal claws. – Opisthosoma (photos) 1.43 times longer than wide, higher than long, hairs fairly short, spinnerets stout, colulus well developed. – Pedipalpus (figs. 65–66) (see the diagnosis) (most parts are hidden) with stout articles, cymbium large and hairy, bulbus relatively small, most sclerites are hidden.

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

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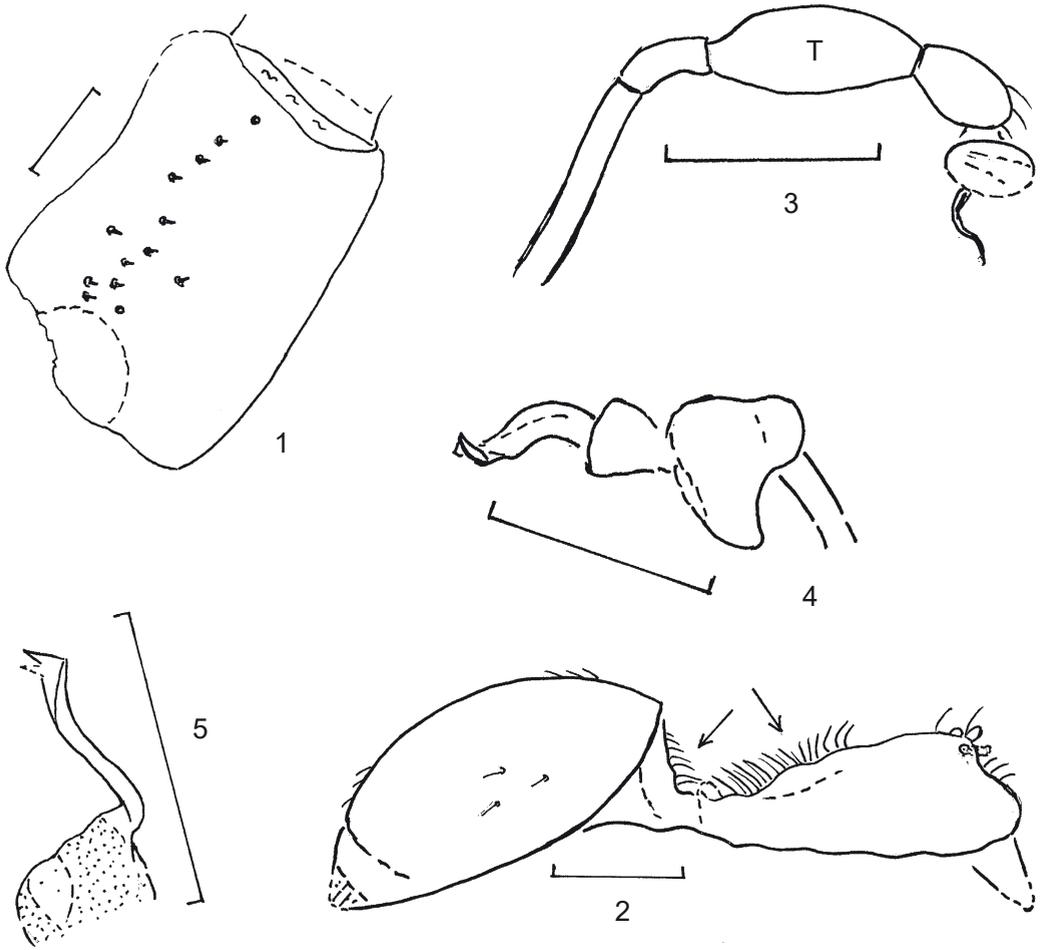
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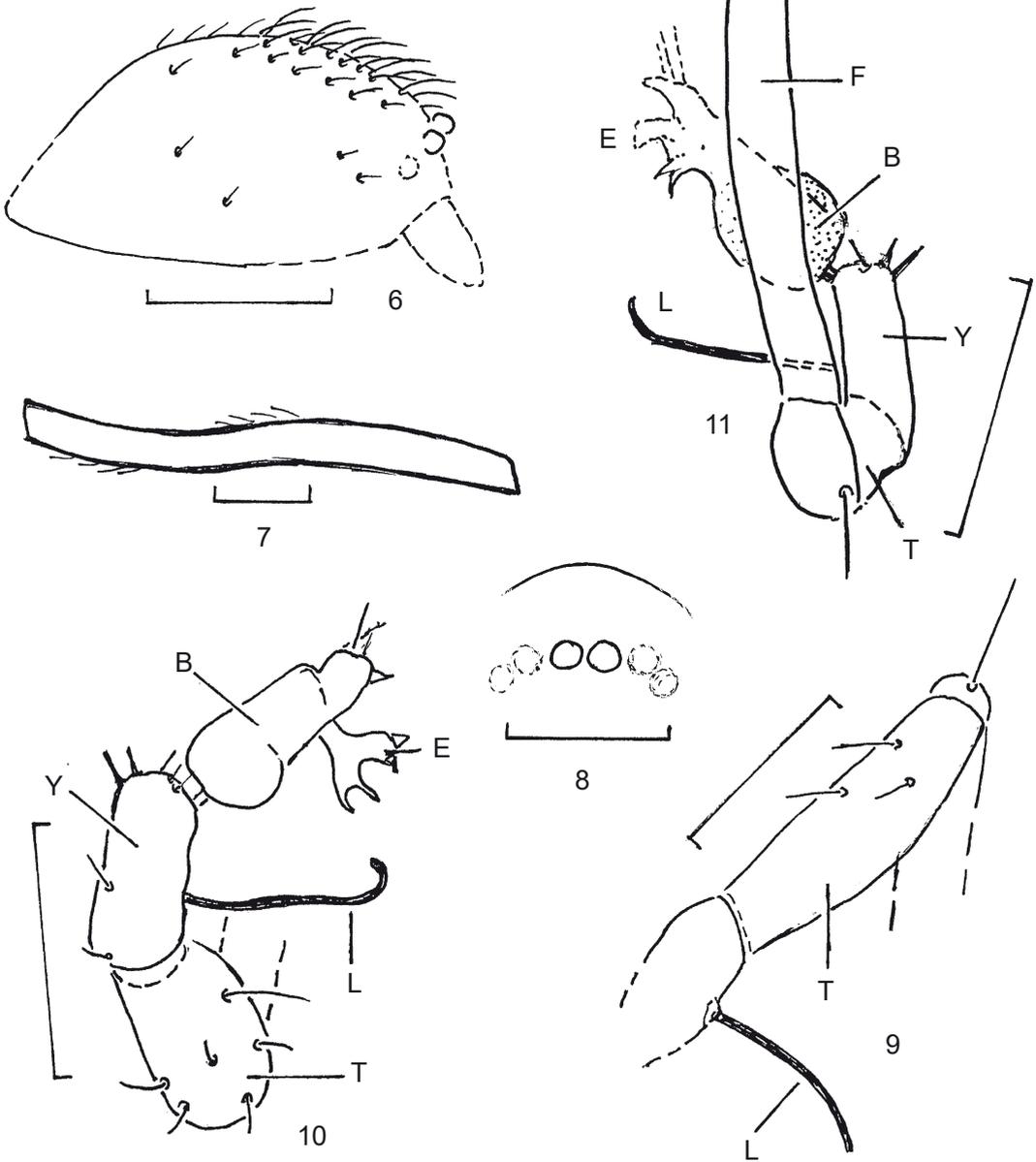


**Note** on the figures: Most species are preserved in Burmese amber, only *Scytodes hani* (Scytodidae, figs. 6-7) is preserved in amber from Jordan.

Fig. 1) *Dipluridae* indet., posterior aspect of the probably left anterior? coxa with questionable stridulatory bristles. Hairs – including the long ventral ones – are not drawn. Scale bar 0.5;

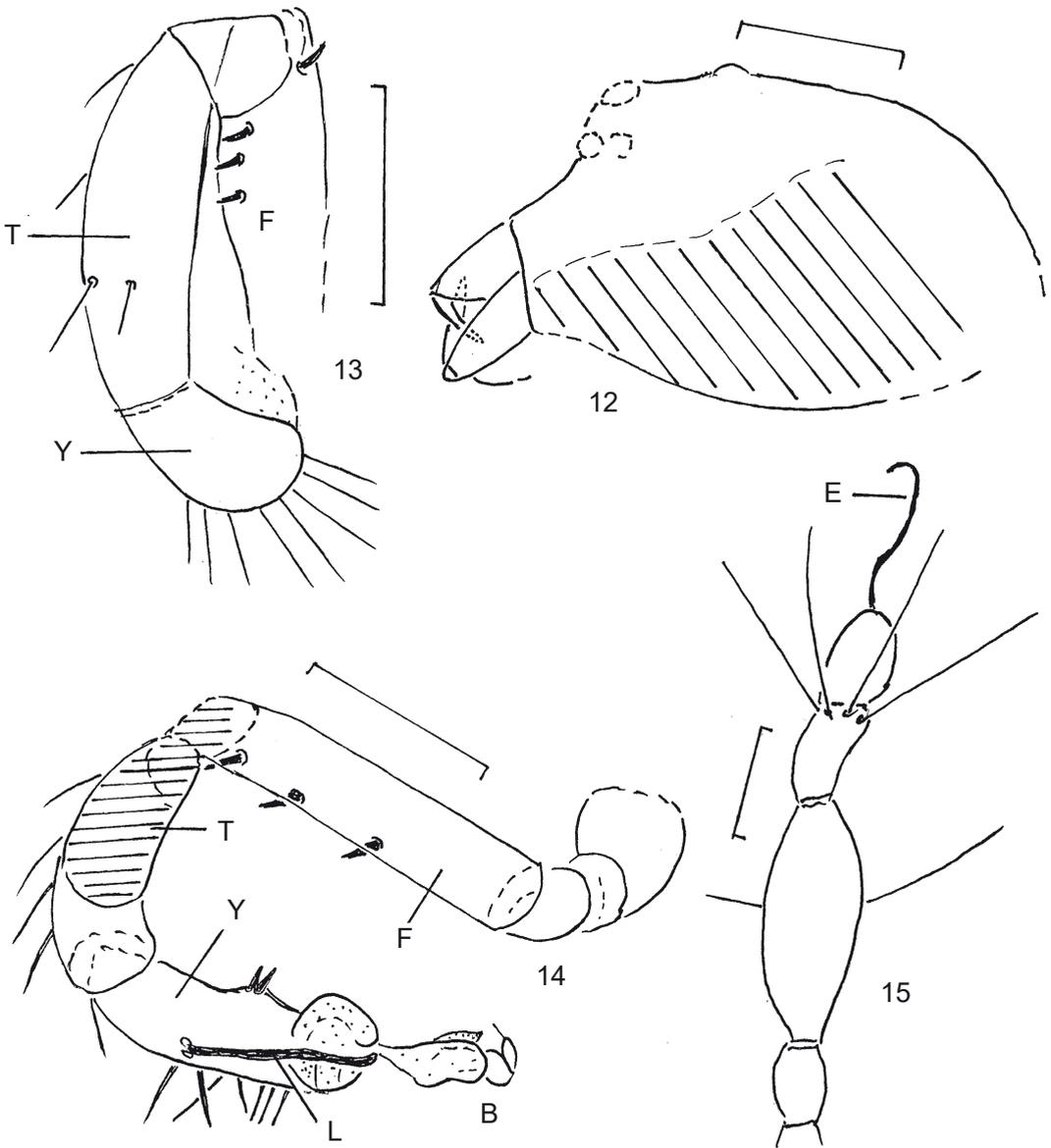
figs. 2-3: *Saetosoma filiembolus* n. gen. n. sp. (Tetrablemmidae), ♂; 2) lateral aspect of the body. Note the long dorsal hairs (arrows). Some areas – e. g. of the eyes, the clypeus and the petiolus – are strongly deformed; 3) attempt of a reconstruction of the right pedipalpus, retrolateral aspect. Compare the deformed pedipalpi in the photos. T = tibia. Scale bars 0.2 and 0.1 mm;

figs. 4-5: *Tetrablemmidae* indet., ♂, retrolateral and anterior aspect of the deformed left pedipalpus (in fig. 5 only embolus and distal part of the bulbus are shown). Scale bar 0.1;



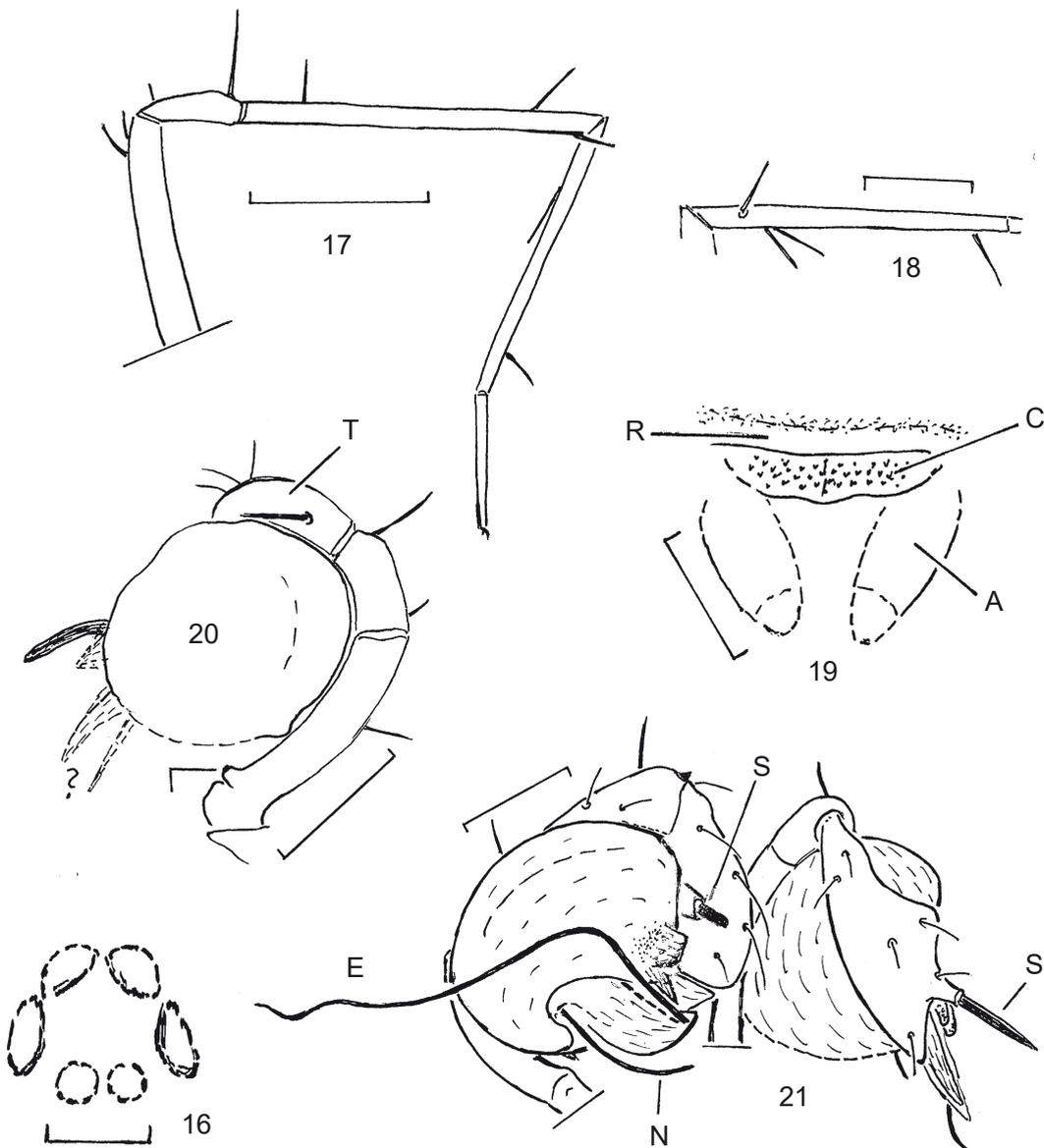
figs. 6-7: ?*Scytodes hani* n. sp. (Scytodidae), juv. in amber from Jordan; 6) lateral aspect of the prosoma. 7) Prolateral aspect of the right femur I, fairly thicker drawn than the real shape. Only few hairs are drawn. Some parts – like the deformed eyes – are only insufficiently observable. Scale bar 0.2;

figs. 8-11: *Leclercera longissipes* n. sp. (Psilodercidae), ♂; 8) dorsal aspect of clypeus and eyes, reconstruction; 9) dorsal aspect of the tibia and basal part of the cymbium of the left pedipalpus; 10) dorsal aspect of the right pedipalpus; 11) right pedipalpus: Dorsal aspect of the femur, ventral aspect of tibia, cymbium and bulbus. B = bulbus, E = embolus, F = femur, L = long cymbial bristle, T = tibia, Y = cymbium. Scale bars 0.2;

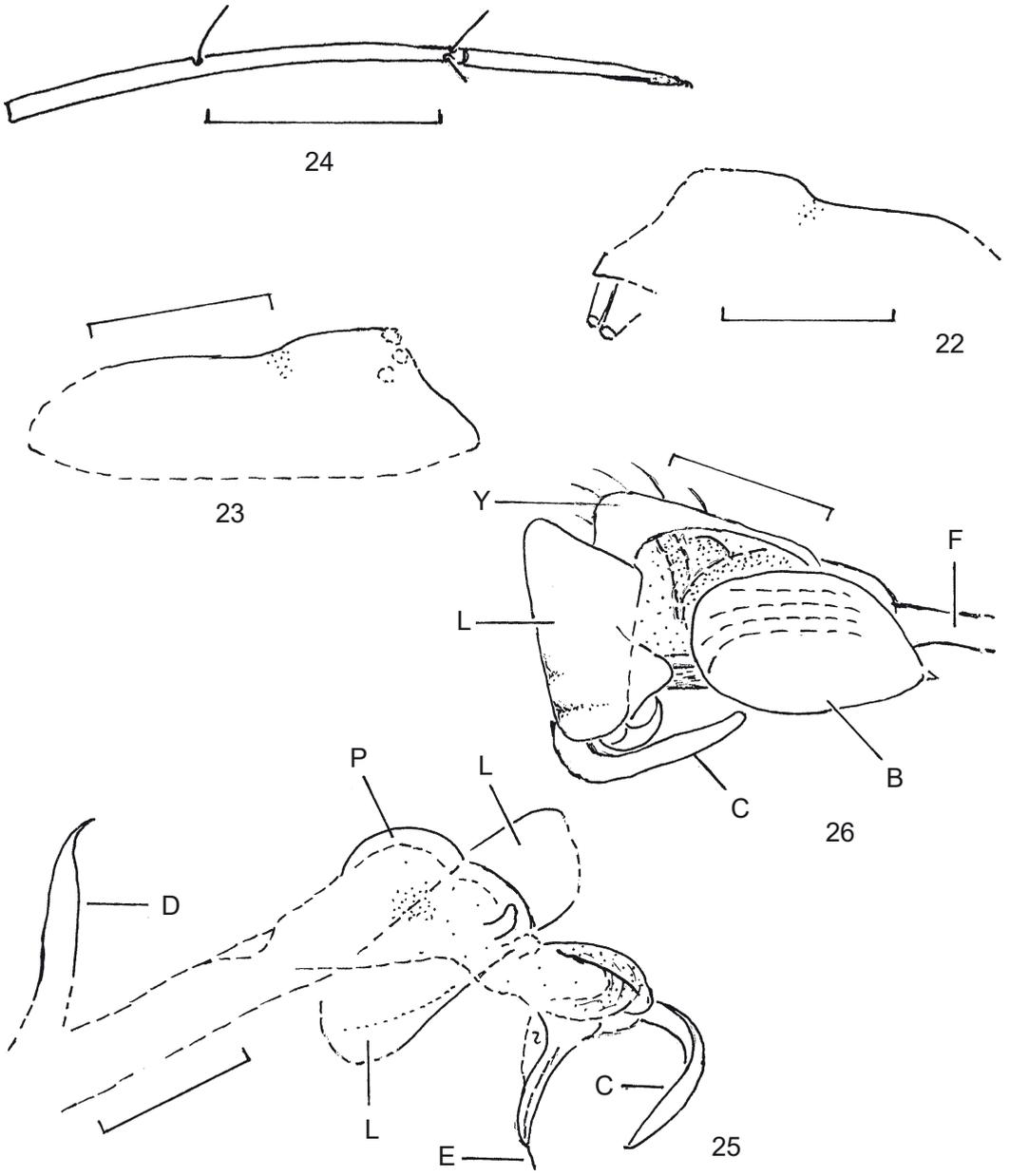


figs. 12-14: *Leclercera spicula* n. sp. (Psilodercidae), ♂; 12) lateral aspect of the prosoma. Parts are cut off, some of the six eyes are hidden; 13) proteral (femur provenventral) aspect of the right pedipalpus. The structures of the bulbus are hidden in this position. Only few hairs are drawn; 14) retrolateral (distal articles ventral) aspect of the left pedipalpus. Parts (hatched) are cut off, others are deformed. Only few hairs are drawn. B = bulbus with embolus, F = femur, L = long cymbial bristle, T = tibia, Y = cymbium. Scale bars 0.2;

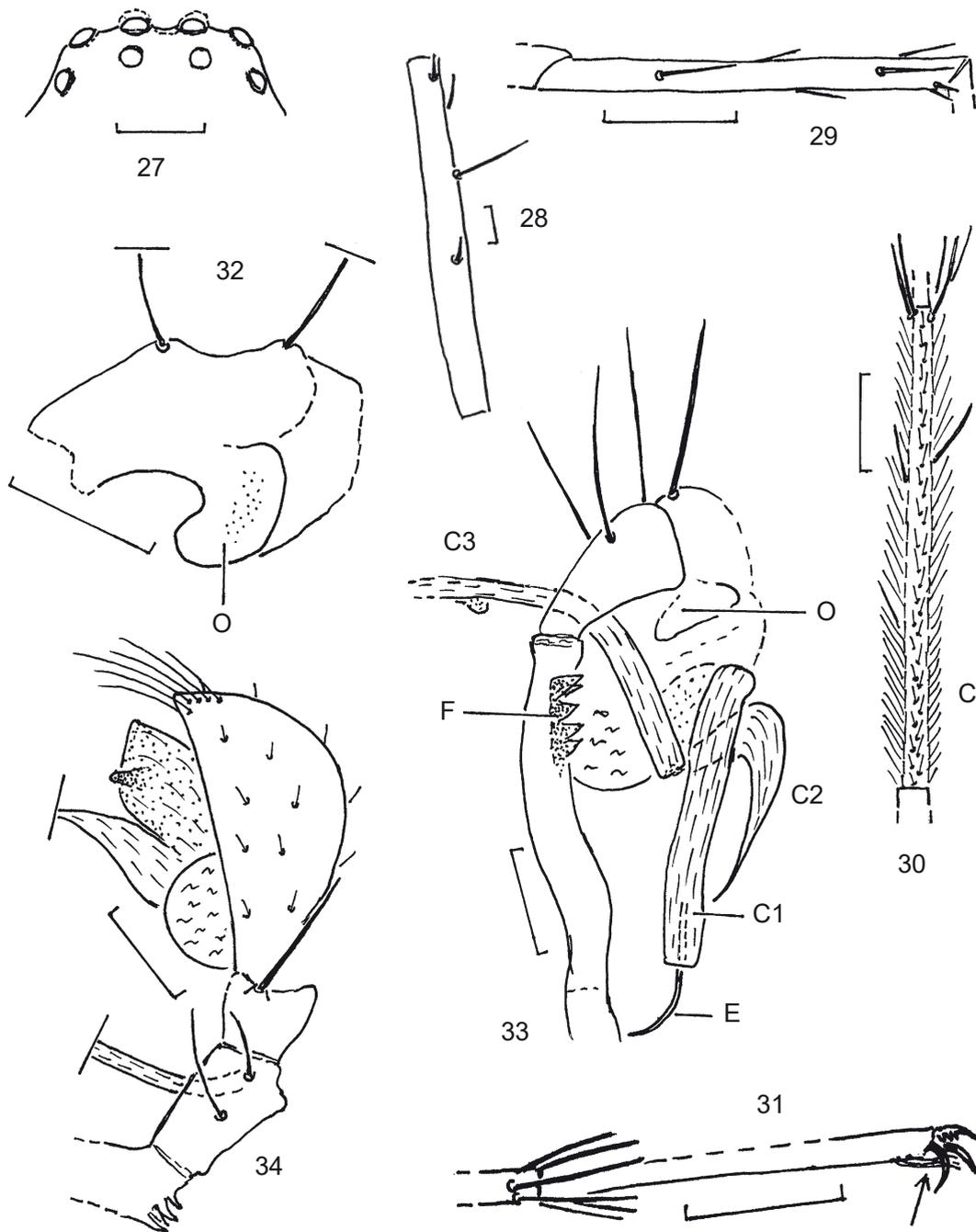
fig. 15) *?Psilodermes filiformis* n. sp. (Psilodercidae), ♂, dorsal aspect of the left pedipalpus. Only few hairs are drawn. E = embolus. Scale bar 0.1 mm;



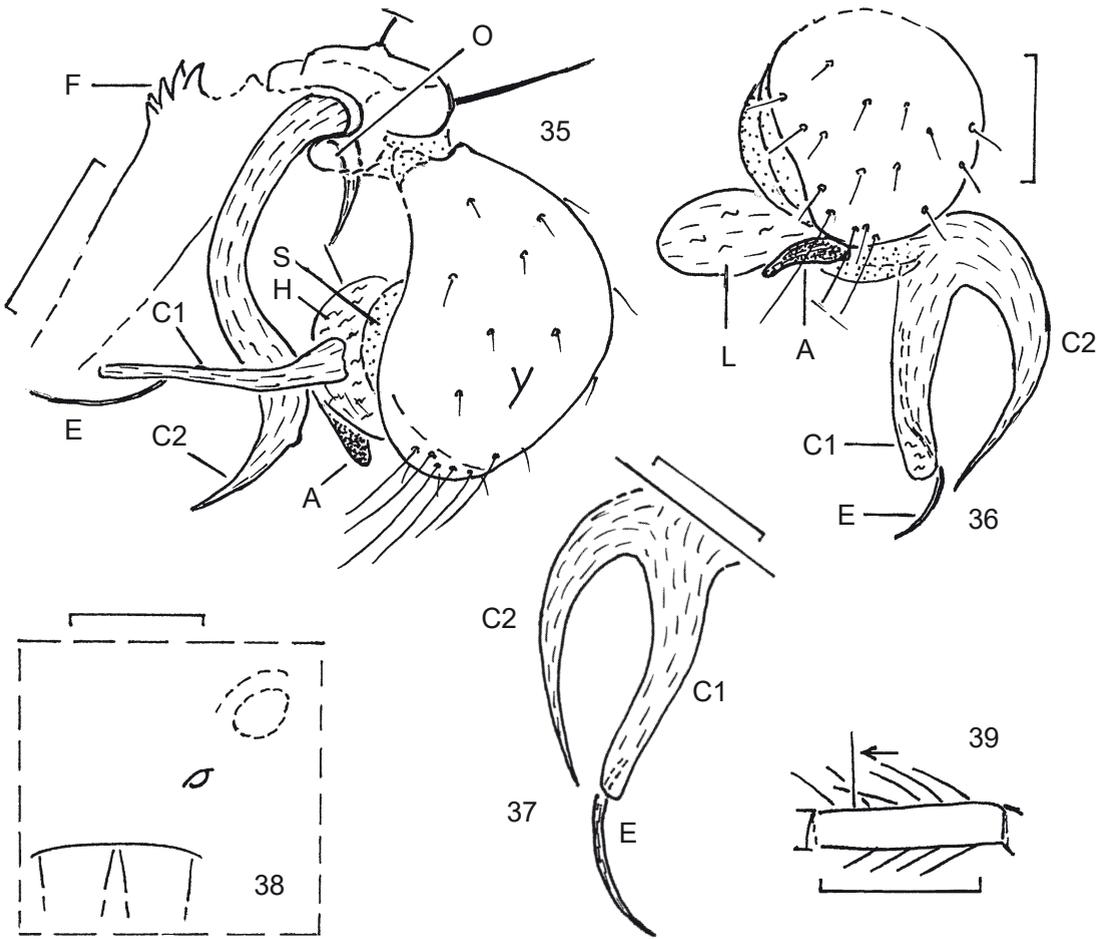
figs. 16-21: *Palaeoleptoneta calcar* n. gen. n. sp. (Leptonetidae: Palaeoleptonetinae), ♂; 16) attempt of a reconstruction of the deformed eyes and their position; 17) retro-lateral aspect of the right leg IV; hairs are not drawn; 18) retroventral aspect of the left metatarsus IV; 19) cribellum and widely spaced deformed anterior spinnerets; 20) retro-lateral aspect of the left pedipalpus (parts are hidden); 21) retro-lateral-apical aspect of the right pedipalpus and dorsal aspect of the left pedipalpus (drawn from the ventral aspect of the fossil), 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, F = femoral outgrowth, N = needle-shaped apophysis, R = roll, S = large cymbial spur T = tibia. Scale bars 0.5 in fig. 17, 0.1 in figs. 16 and 19, 0.2 in the remaining figs.;



figs. 22-26: ?*Pholcochyrocer baculum* n. sp. (Pholcochyroceridae), ♂; 22-23) left and right aspects of the prosoma, outlines, parts (mainly the eyes) are hidden; 24) retro-lateral aspect of the right metatarsus and tarsus I; 25) retro-lateral aspect of the right pedipalpus which is strongly deformed and partly hidden, bulbus expanded; 26) retro-lateral aspect of the deformed left pedipalpus with the bulbus expanded. B = bulbus, C = conductor, D = dorsal apophysis of the femur, E = embolus, F = femur, L = large tegular apophysis, P = patella, Y = deformed questionable cymbium. Scale bars 0.5 in figs. 22-24, 0.2 in figs. 25-26;



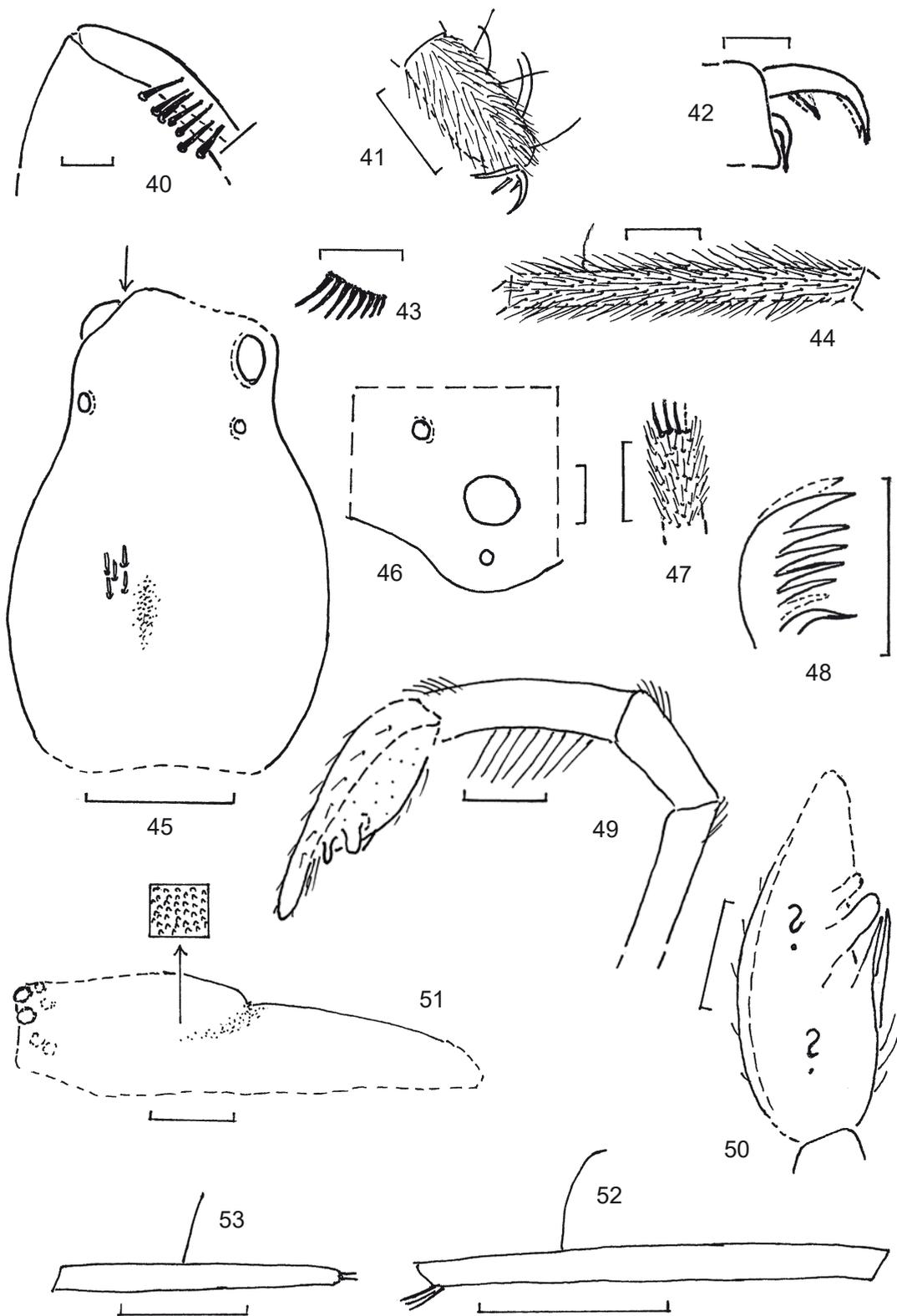
figs. 27-36: *Pholcochyrocer pecten* n. sp. (Pholcochyroceridae), ♂; 27) dorsal aspect of the eyes, attempt of a reconstruction of the deformed eye field; 28) dorsal aspect of the left femur I. Hairs are not drawn; 29) retrolateral aspect of the right tibia I. Hairs are not drawn; 30) retrolateral aspect of the right metatarsus IV. Note the relatively short bent hairs of the calamistrum (C); 31) retrolateral (slightly apical) aspect of the right tarsus IV and the tip of the metatarsus. Hairs are not drawn except the auxiliary hairs (arrow)



below the tarsal claws; 32) retrolateral aspect of the right pedipalpal tibia; 33) right pedipalpus, dorsal aspect of femur and patella, and ventral-basal aspect of the bulbus; 34) prodorsal aspect of the partly deformed right pedipalpus; 35) retrolateral aspect of the right pedipalpus; 36) apical aspect of the left pedipalpus; only few hairs are drawn. A = strongly sclerotized bulbus apophysis, C = calamistrum, C1, C2, C3 = branches of the conductor, E = embolus, F = femoral comb; H = questionable haematodocha, L = large scinny apophysis, O = ventral tibial outgrowth, S = subtegulum. Scale bars 0.5 in fig. 29, 0.2 in the remaining figs.;

fig. 37) *Pholcochyrocer guttulaeque* WUNDERLICH 2008 (Pholcochyroceridae), holotype ♂, dorsal aspect of the left embolus (E) and branches of the conductor (C). Scale bar 0.2;

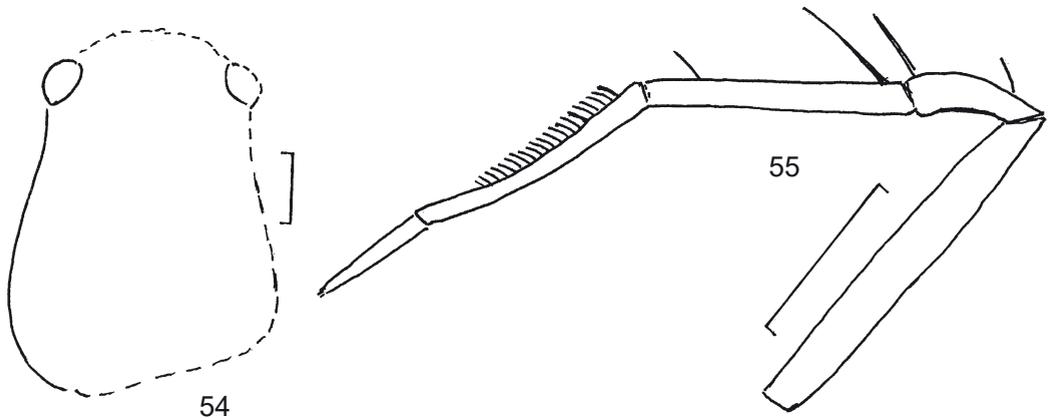
figs. 38-39: *Burlagonomegops ?eskovi* PENNEY 2005 (Lagonomegopidae); 38) juv. F2017/BU/AR/CJW, retroanterior aspect of the left part of the prosoma. Note the large deformed posterior median eye (dotted), and the small anterior lateral eye; 39) juv. F1918/BU/AR/CJW, prolateral aspect of the right metatarsus II. The arrow points to the trichobothrium. Scale bar 0.2;



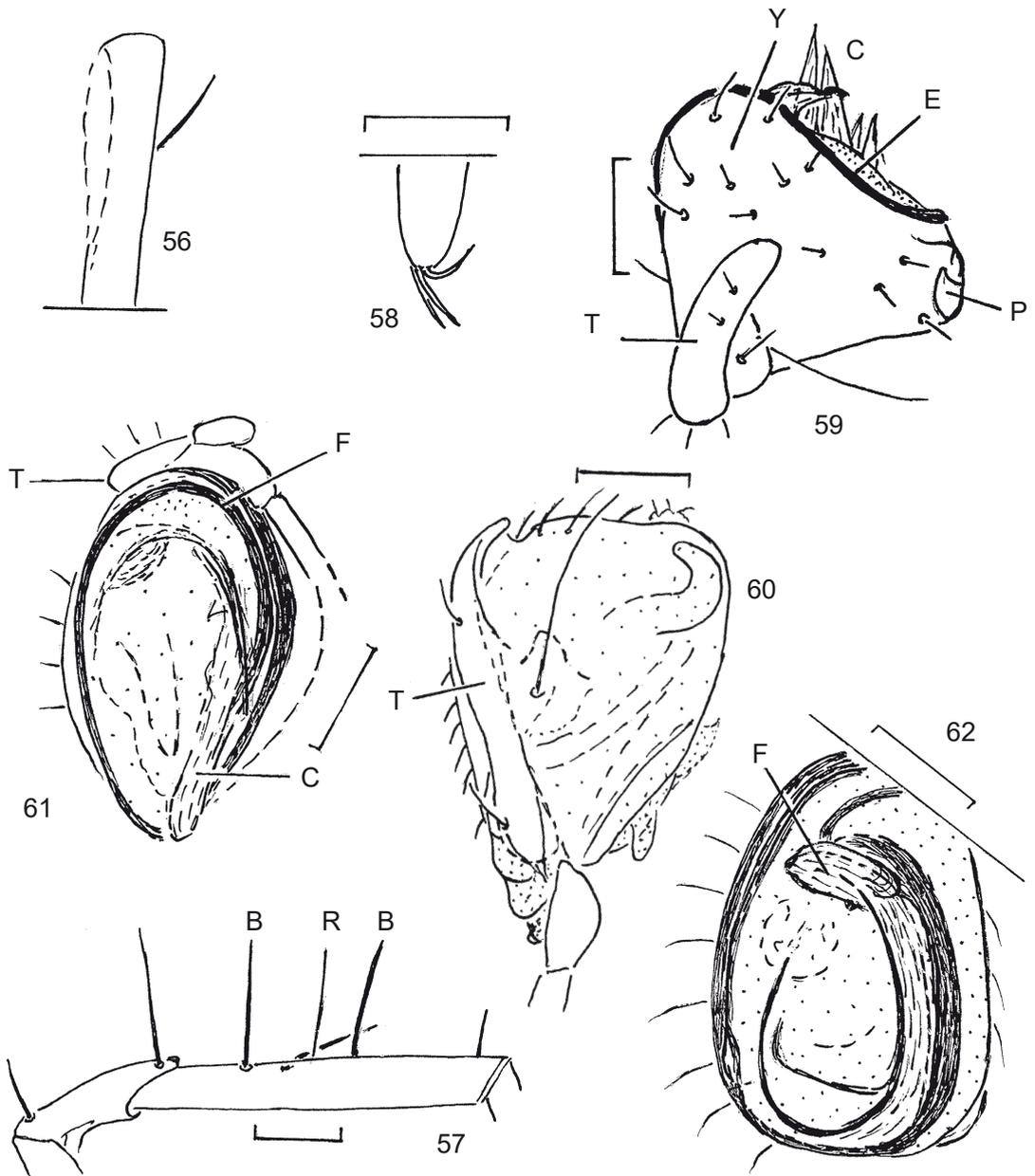
figs. 40-44: *Lagonoburmops plumosus* n. gen. n. sp. (Lagonomegopidae), ♀; 40) anterior aspect of the distal part of the left chelicera. Normal hairs are not drawn; 41) oblique retroapical aspect of the right tarsus IV. Note the long trichobothria; 42) prolateral aspect of the tip of the left tarsus II. Hairs are not drawn; 43) apical aspect of the ventral “preening comb” of bristles on the tip of the right metatarsus IV; 44) prodorsal aspect of the right metatarsus II. Note the long dense hairs (not all are drawn) and the distal position of the erect trichobothrium. Scale bar 0.2 in figs. 40, 41 and 43, 0.1 in fig. 42, 0.5 in fig. 44);

figs. 45-50: *Myanlagonops gracilipes* n. gen. n. sp. (Lagonomegopidae), ♂; 45) dorsal aspect of the deformed prosoma, slightly from the right side. Only few hairs are drawn. The arrow points to the hidden position of the left anterior lateral eye; 46) dorsal-retroanterior aspect of the right eyes above the prosomal margin; 47) retroventral aspect of the tip of the left metatarsus IV with the apical “preening comb” of bristles; 48) prolateral aspect of the tarsal claws III; 49) retrolateral (slightly apical) aspect of the left pedipalpus. Only few hairs are drawn; 50) proventral aspect of the left pedipalpus. The structures of the bulbus are only insufficiently observable, artefacts may exist. Scale bar 0.5 in fig. 45, 0.3 in fig. 48, 0.2 in the remaining figs.;

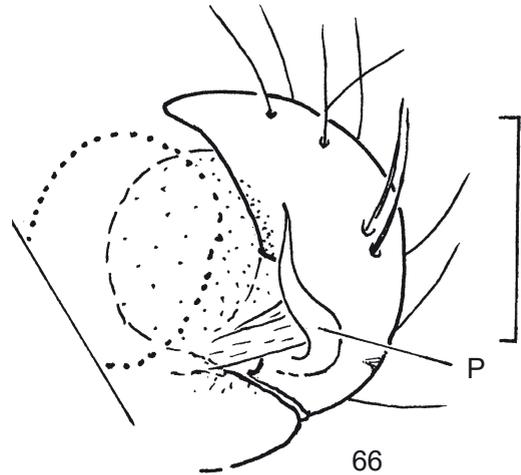
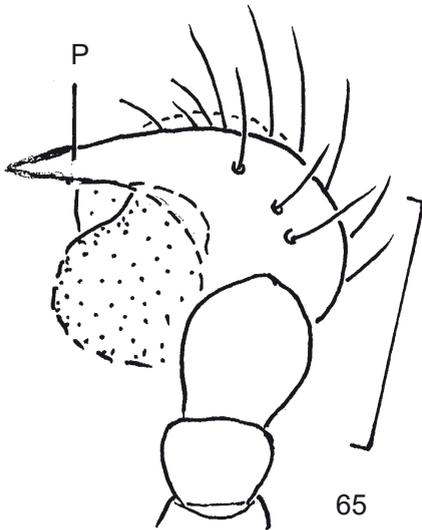
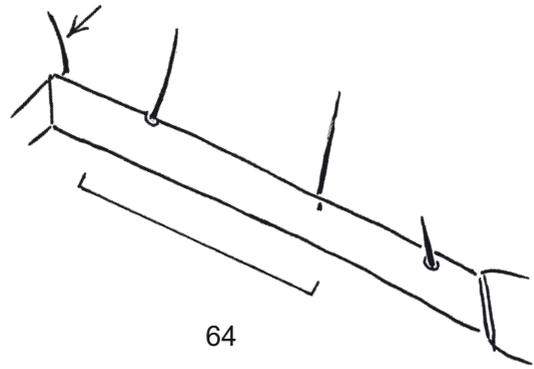
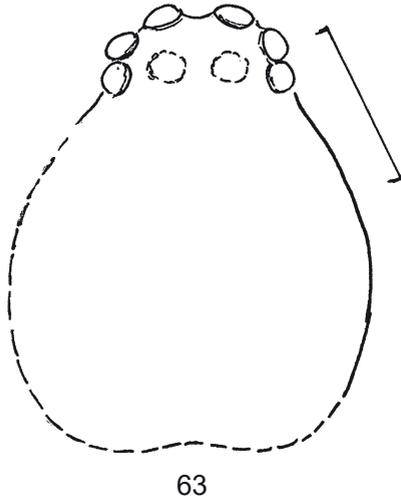
figs. 51-53: *Micropalpimanus* sp. indet. (Micropalpimanidae), ♀; 51) lateral aspect of the prosoma. The arrow points to the enlarged part of the rugose cuticula; 52) oblique aspect of the right metatarsus IV with its long trichobothrium. Note the the apical bristle-shaped hairs of the “preening comb”; 53) dorsal aspect of the right tarsus I. Note the long and straight sensory hair in a prolateral position. Normal hairs are not drawn. Scale bars 0.2;



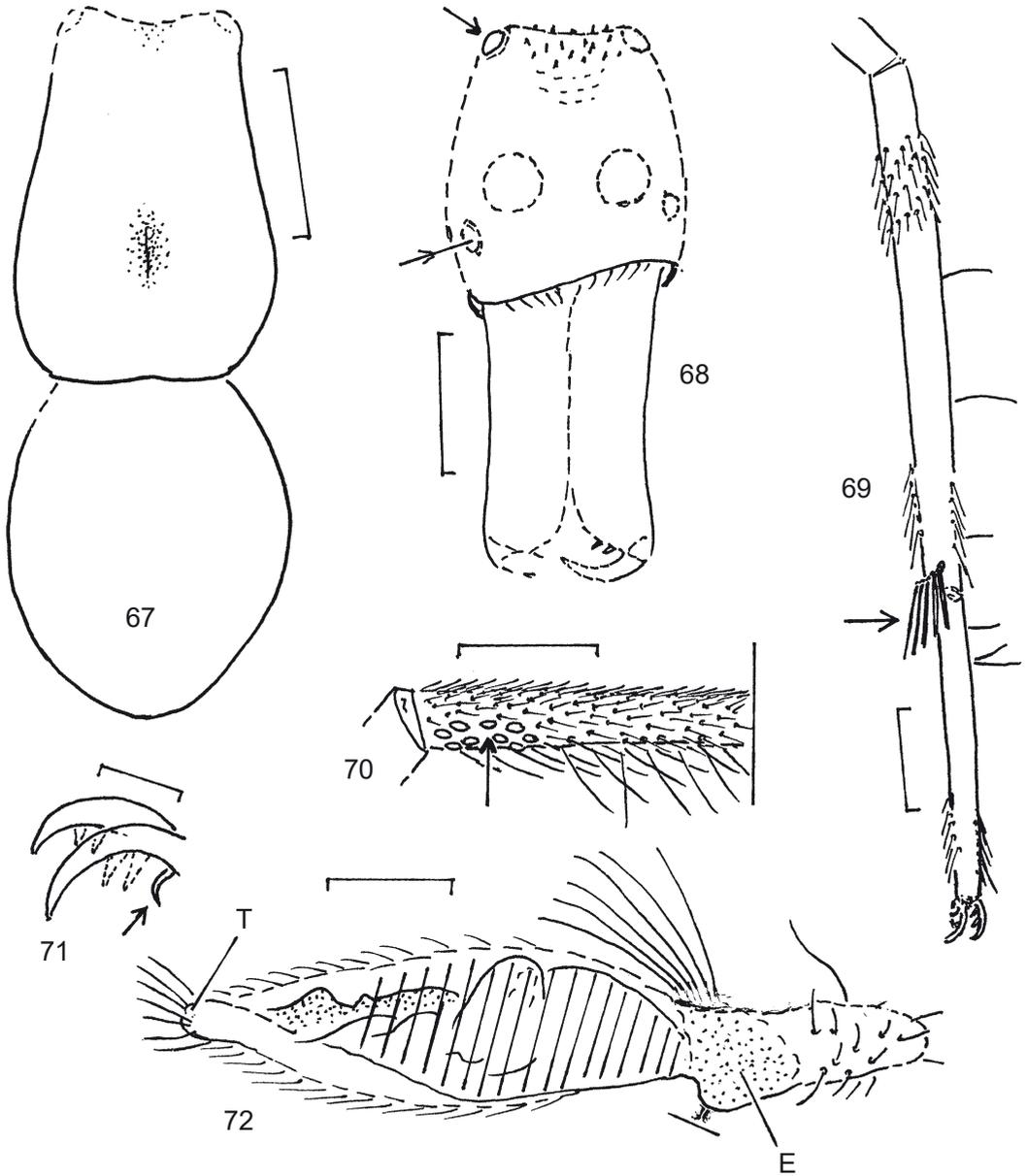
figs. 54-55: *Oculoborus curvatus* n. gen. n. sp. (Uloboridae), ♀; 54) dorsal aspect of the prosoma. Only the large posterior lateral eyes are surely observable and drawn; 55) lateral aspect of a loose leg IV. Hairs are not drawn. Trichobothria and probably some bristles are apparently not preserved. Scale bar 0.2 and 0.5;



figs. 56-62: *Leviunguis bruckschi* n. gen. n. sp. (Theridiosomatidae), ♂; 56) dorsal aspect of the distal part of the deformed left femur I. The bristle is 0.1 mm long. Hairs are not drawn; 57) retrolateral aspect of the right patella and tibia. Note the long tibial trichobothrium (R), the long dorsal tibial bristles (B) and the long prolateral tibial bristle; 58) prodorsal aspect of the tip of the right tarsus I with its claws. Hairs are not drawn; 59-60) apical and dorsal aspect of the deformed right pedipalpus; 61) ventral aspect of the deformed left pedipalpus; 62) retrolateral aspect of the right pedipalpus (the distal part is hidden). B = bristle, C = conductor, E = embolus, F = parembolic apophysis, P = questionable paracymbium, R = trichobothrium, T = outgrowth of the tibia, Y = cymbium. Scale bars 0.05 in fig. 58, 0.1 in the remaining figs.;



figs. 63-66: *Hypotheridiosoma paracymbium* n. gen. n. sp. (Theridiosomatidae), ♂; 63) dorsal aspect of the prosoma; 64) retrolateral and slightly dorsal aspect of the left tibia I. The arrow points to the proapical bristle; 65) dorsal-posterior aspect of the left pedipalpus; 66) retrolateral aspect of the left pedipalpus. Strongly dotted: Bubble around the bulbus. P = paracymbium. Scale bars 0.2 in figs. 63-64, 0.1 in figs. 65-66;



figs. 67-72: *Archaelagonops salticoides* n. gen. n. sp. (Lagonomegopidae, ♂; 67) dorsal aspect of the body; 68) anterior aspect of the prosoma which is slightly deformed. The arrows point to two questionable eyes; 69) prodorsal aspect of the left metatarsus and tarsus III. Note the preening comb (arrow). Only few hairs are drawn; 70) prodorsal aspect of the basal part of the left metatarsus II. Some of the scale-shaped hairs (arrow) are drawn; 71) prolateral aspect of the tarsal claws of the right leg III. The arrow points to the unpaired claw. Only few of the long teeth of the paired claws are partly observable; 72) retrodorsal (?) aspect of the deformed left pedipalpus which is partly cut off. E = tibial depression, T = tip of the long cymbium. Scales: 1.0 in fig. 67, 0.5 in fig. 68, 0.05 in fig. 71, 0.2 in the remaining figs.

**DESCRIPTION OF THE FIRST FOSSIL RICINULEI IN AMBER FROM BURMA (MYANMAR), THE FIRST REPORT OF THIS ARACHNID ORDER FROM THE MESOZOIC AND FROM ASIA, WITH NOTES ON THE RELATED EXTINCT ORDER TRIGONOTARBIDA**

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**Abstract:** The first Mesozoic (Cretaceous) as well as Asian members of the order Ricinulei (Arachnida) are described from Burmese (Myanmar) amber, *?Poliochera cretacea* n. sp., a member of the extinct family Poliocheridae. The suborders Neoricinulei SELDEN 1992 and Palaeoricinulei SELDEN 1992 are downgraded to superfamilial rank (n. stat.), the Poliocheroidea SCUDDER 1884 resp. Ricinoidoidea EWING 1929. Fossil Ricinulei have only been known from the Carboniferous up to now. Carboniferous Ricinulei have been found to be distinctly larger than extants. The existence of trichobothria is regarded as a basal (autapomorphic) pattern of the (land-living) Arachnida, and their absence in the Ricinulei and the Trigonotarbida may be a common loss (of their ancestor) which may support the sister group relationships of these orders.

**Key words:** Amber, Arachnida, Asia, Burma, Carboniferous, Cretaceous, evolution, fossils, Mesozoic, Myanmar, Palaeozoic, pedipalpus, Ricinulei, secondary copulatory organ, trichobothria, Trigonotarbida.

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CJW = collection of J. WUNDERLICH – Photos: I C 34–36.

Ricinulei and the probably related Trigonotarbida are two “small” (not diverse) orders of the class Arachnida which includes 13 or 14 orders. Only three of these – the Palaeozoic orders Haptopoda (a dubious monophyletic taxon), Phalangiotarbida and Trigonotarbida – are extinct.

During the last years the sister group relationships of several arachnid orders became clearer:

- Araneae -- Amblypygi,
- Opiliones -- Acari (?),
- Ricinulei -- Trigonotarbida (more likely than Acari),
- Schizomida -- Telephonida,
- Solifugae -- Pseudoscorpiones.

Ricinulei is a distinctive tropical relict order of the class Arachnida which is poor in taxa today; only a single extant family is known, see tab. 1. The only fossils known up to now are Palaeozoic (Carboniferous) members of two families of Europe and North America. The huge gap of about 300 million years has been filled now with first Mesozoic (Cretaceous) fossils in Burmese (Myanmar) amber (photos) which lived about 100 million years ago and shows that the extinct superfamily Poliocheroidea (= suborder Palaeoricinulei) still existed in the Mid Cretaceous. According to the existence of eyes the fossil taxon in amber is a member of the extinct (Carboniferous) superfamily but not of the (almost) eye-less extant superfamily Ricinoidoidea (= suborder Neoricinulei).

Our knowledge of fossil Ricinulei is still quite poor; fossils are unknown from Australia, South America, Africa, and most parts of Asia. NENILIN (1988) already proposed a more widespread distribution of the Ricinulei during the Mesozoic, see SELDEN (1992: 604), and the discovery of the present Asian fossils verifies this supposition.

Well preserved tarsi and pedipalpi (\*) were unknown in the fossil Ricinulei, and remarkably not a single male copulatory organ has been reported from fossils. Are most of the known fossils nymphs or females? An adult fossil male has apparently never been found up to now. Eight-legged Ricinulei may wrongly suggest that these specimens are adult, but most probably all nymph stages have eight legs like the adults. The well and three-dimensionally preserved present holotype of the new species in amber allows important conclusions. Special features are the excellently preserved tarsi and a pedipalpus as well, in which even sensory organs can be detected (figs. 4, 7, photo 35).

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(\* ) The Cretaceous fossil holotype shows the absence of a POINTED third tarsal claw as in extant Ricinulei (see figs. 2, 7); the first well preserved pedipalpus of a fossil Ricinulei (fig. 4) has the same pattern and small size like extant Ricinulei.

**Main diagnostic (autapomorphic) characters of the Ricinulei (\*)** (see the figs. 1–7 and the photos 34–36):

- Existence of a wide anterior prosomal “hood” (CUCULLUS) which is movable, it can be raised and may cover the mouth parts when lowered,
- metatarsus and tarsus of the male leg III are modified – strongly in adults, less in nymphs in which dorsal outgrowths exist – as a secondary COPULATORY ORGAN (fig.1) (\*\*),

- basically two pairs of widely spaced EYES (fig. 3, photo 34) (only remains of eye lenses may exist in extant species) (a narrow eye field is regarded as plesiomorphic),
- contiguous leg COXAE (fig. 6),
- a modified (blunt, not pointed or bent) UNPAIRED TARSAL CLAW (figs. 2, 7),
- ELONGATED LEG II (fig. 1, photo) which is distinctly the longest and used for prey capturing but not as a walking leg,
- PEDIPALPUS (figs. 1, 4, photo 35): Very small, coxae fused, tibia and tarsus fused to a “tibio-metatarsus”, used for egg transport in females (\*\*\*),
- SIX-LEGGED LARVAE (not the nymphs which are eight-legged).

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(\*) Certain authors mixed in their “diagnoses” autapomorphic characters as well as synapomorphies with related taxa, symplesiomorphies, convergences and simple similarities with other taxa (see below). Problems in finding out true autapomorphies may exist if the sister group of a given taxon is not (surely) known.

(\*\*) It has the same function for sperm transfer as a secondary copulatory organ like the pedipalpus in male spiders (in both orders a penis is absent). In certain taxa of the extremely diverse order of mites the male leg III or IV functions as secondary copulatory organ – a remarkable convergence with the Ricinulei! (In some mite taxa exists a penis). – A male copulatory organ of the Trigonotarbida is unknown.

(\*\*\*) See WESTHEIDE & RIEGER (1996: 489, fig. 677).

### **Common characters of Ricinulei and Trigonotarbida.** See below: Relationships.

**Basic (symplesiomorphic) characters of the Ricinulei** are the characters of the Arachnida like four pairs of legs, two body parts (prosoma and opisthosoma) (\*), similar chelicerae and pedipalpi, as well as certain characters of the Tetrapulmonata like similar mouth parts (lungs are absent).

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(\*) The arachnid prosoma and opisthosoma are still called “carapax” and “abdomen” – body parts of crabs and insects – by certain careless or incompetent authors. Curiously SELDEN (1992: 596) started with the term “prosoma” and changed later to “carapace” in the same paper.

**Further characters:** Distinct eye lenses are absent in the extant taxa – but patches of clear cuticula may exist, and the animals react to optical stimuli – contrarily two pairs of well developed eyes existed in the fossil Cretaceous and Carboniferous taxa (photo) (\*). Legs, number and articles: The three stages of juveniles have only three pairs of legs as well as a reduced (stump-shaped) pair of fourth legs; at least the last two of the three stages of the nymphs possess four pairs of legs like the present fossil in amber (photo). (The adults possess four pairs of legs like other adult arachnids). The articles of the legs are coxa, trochanter (two-jointed in legs III and IV to trochanters I and II), femur, patella, tibia, metatarsus and tarsus. In Ricinulei tarsus I is unarticulate (undivided), but the tarsi II–IV are segmented, in adults their sequence is 5/4/5. Inadults possess less tarsal articles; the nymph holotype of the present fossil in amber has three tarsal

articles on leg III, and only two tarsal articles on leg IV (fig. 5). In extant nymphs from Brasil (coll. JW) I found a sequence of 4/3/2 segments in a second stage of legs II–IV, and 5/4/5 in a third stage. Leg II of the Ricinulei is already very long and used for prey capturing by the nymphs. The body length of extant Ricinulei is usually 5–10 mm, but usually 10–18 mm in the Carboniferous fossils (only 5.3 mm in *Terpsicroton* which may be based on a nymph). I suppose that several Carboniferous Ricinulei may not be adult but nymphs; nymphs have four pairs of legs like adults, see above (\*\*). Therefore adult Carboniferous species may have been even larger than the fossil specimens which have been reported up to now.

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(\* ) Eyes of the fossils have been overlooked by PETRUNKEVITCH in different papers.

(\*\* ) The tarsi of most fossils are not preserved but they are important to determine the stage. The “restored” tarsi of a Ricinulei – see figs. 4a and 4b in MOORE (1955: 158) – are not convincing. The holotype of *Curcilionoides adompha* BRAUCKMANN 1987 has partly well preserved tarsi; it may be a nymph of the third stage or an adult female, but – according to the thorn-like structure on tarsus III which most probably is nothing else than an artefact – it surely is not a mature male.

**Relationships** (see DUNLOP (1996), DUNLOP et al (2009), and VAN DER HAMMEN 1979):

The extinct – late Silurian to early Permian – order Trigonotarbida may be related to the Ricinulei: In both orders a flattened body exists as well as a laterigrade position of the legs (like in most Arachnida besides the Araneae), a prolonged prosoma (modified as the cucullus in the Ricinulei). (The male copulatory organ of the Trigonotarbida is unknown) (\*). In both orders exist furthermore.....

- similar opisthosomal tergites which are divided in median and lateral plates (fig. 1) (rarely modified), and fusion of at least tergites 2 and 3 into a diplotergite,
- a common feature of the pedipalpal claw/pincer, see DUNLOP et al. (2009) and fig.4,
- a complicated coupling mechanism between pro- and opisthosoma, and
- the absence of trichobothria which have probably been lost in their common ancestor (see below).

**Differences between both orders** (see above, the apomorphies of the Ricinulei). In the Trigonotarbida.....

- a cucullus is absent, but an anterior outgrowth exists which is narrowed,
- a secondary copulatory organ is absent (\*),
- at least a single pair of MEDIAN eyes exists, additional lateral eyes exist in certain basal taxa, as well as additional tiny eyes,
- all legs possess a single trochanter,
- most coxae are wider spaced,
- leg II is not elongated,
- a pointed and bent tarsal claws exist (fig. 8) (compare figs. 2 and 7),
- the pedipalpus is leg-shaped large, possesses a free tarsus but not a fused tibio-tarsus as in fig. 4,

- 12 opisthosomal segments exist in contrast to 9 segments in the Ricinulei,
- 2 segments of the pygidium exist in contrast to 3 segments in the Ricinulei.

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(\*) Within all the described FOSSIL Ricinulei a secondary male genital organ on leg III has never been described, and the same applies for the Trigonotarbida.

**Phylogeny and suprafamilial taxa:**

Two pairs of well developed eyes existed in the Carboniferous fossils – see SELDEN (1992) – and in the present Cretaceous fossil in Burmese amber (photo), but distinct eye lenses are absent in all extant taxa; so DISTINCT eye lenses in the Ricinulei have apparently been lost during the last 100 million years. The Carboniferous species were distinctly larger than the extant members, this apparently is a case of dwarfism, see above (“Further characters”).

According to SELDEN (1992: 601) “The Palaeoricinulei and Neoricinulei are separated in time, so it is possible that the Neoricinulei are derived from the Palaeoricinulei rather than the two groups sharing a common ancestor ... If this were the case, then the Poliocheridae is the group most likely to be the ancestor of Neoricinulei. It is rational to envisage sizes of the coxae changing and the eyes atrophying over time to produce the neoricinuleids from the Poliocheridae.”

Both suborders are based on only weak differences, (1) on the only fairly distinct shape and size of certain coxae, and (2) on the reduction of eye lenses. Compared, e. g., with the clearly distinct conditions of the suborders of spiders – Mesothelae and Opisthothelae – I question that the division of the Ricinulei in two suborders is justified. Therefore I downgrade the two suborders, and regard (a) the extant taxa as members of the monotypic superfamily Ricinoidea EWING 1929 (**n. stat.**) (= Neoricinulei SELDEN 1992 (**n. syn.**), including only the family Ricinoididae EWING 1929, and (b) the fossil taxa as members of the superfamily Poliocheroidea SCUDDER 1884 (**n. stat.**) (Palaeoricinulei SELDEN 1992) (**n. syn.**), including the families Poliocheridae SCUDDER 1884 and Curculioididae COCKERELL 1916.

† Poliocheroidea (= Palaeoricinulei)	† Poliocheroidea (= Palaeoricinulei)	Ricinoidea (= Neoricinulei)
Carboniferous	Cretaceous	extant
> 300 m. years ago	ca. 100 m. years ago	
coxa II	smaller than III–IV	larger than III–IV
eye lenses	well developed (fig. 3)	tiny remains only or none
† Curculioididae, † Poliocheridae	† Poliocheridae	Ricinoididae
America, West Palaeartic	Asia: Burma (Myanmar)	Tropical Americas, West and Central Africa

Tab. 1. Comparison of the extant and fossil/extinct (†) suprageneric taxa of the Ricinulei

**Similarities, and convergences:**

Trichobothria (of legs and pedipalpi) are absent in the Ricinulei like in the Trigonotarbida and the Solifugae (\*). The ricinuleid two-partite body is a bit similar (e. g.) to spiders (Araneae) but the connection of pro- and opisthosoma is quite different. The – unpaired – metasoma (pygidium) at the end of the opisthosoma which is absent in spiders may remind of short – paired – spinnerets of spiders at first sight. Secondary male copulatory organs exist in both orders but they are situated on quite different prosomal appendices: On the leg III in Ricinulei, on the pedipalpus in Araneae. The egg-carrying behaviour is similar in some spider families like Pholcidae and Pisauridae but spiders mainly use their chelicerae, and bear the eggs continuously. Ricinulei are furthermore a bit similar in some respect to certain Acari (e. g. ticks) whose larvae also usually have only three pairs of legs – but see above –, and certain authors related the mites' gnathosoma to the ricinuleid cucullus, but this suggestion is not accepted by most recent authors. The long and tactile ricinuleid leg II reminds of long second leg of certain Opiliones. The divided ricinuleid tarsi (fig. 1) are similar to certain beetles, and their shape in the dorsal aspect remembers certain Coleoptera: Curculionidae, see the name of the extinct ricinuleid family Curculioididae.

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(\* ) DUNLOP (1996: 202) regards the absence of trichobothria in Ricinulei and Trigonotarbida as plesiomorphic in contrast to SELDEN et al. (1991) who regard this pattern as derived. In my opinion the loss of trichobothria two times – in the Solifugae and in the taxon Ricinulei (plus?) Trigonotarbida – is more likely than the independent origin for at least five times in the remaining orders of arachnids. So the opinion of SELDEN et al. appears more likely to me. Remark: "Water Scorpions" possessed already trichobothria.

**Ecology and behaviour:**

Ricinulei move slowly and live in litter, detritus and leaf mould, usually in (rain) forests. American members are not rarely cave-dwellers; such life style is not rare in relict taxa. Their ground-living life style is apparently the reason for the rarity/absence in ambers. The tactile long second leg is raised by these arachnids and used for prey capturing; the animals walk on the remaining three pairs of legs. Ricinuleids feed on small arthropods like Collembola. A single egg is produced at a time and carried by the female below the prosomal hood (the cucullus) with the help of the pedipalpi for the transport to a hiding place. Distinct eye lenses are absent in extant ricinuleids, but remains of lenses exist, and the arachnids react to optical stimuli. Extinct Carboniferous Ricinulei possessed well developed eyes like the present fossil in amber (fig. 3), see above.

**Diversity:**

Two superfamilies are known, see tab. 1: (1) The extant Ricinoidea and (2) the extinct Poliocheroidea, see above.

(1) Extant taxa: More than 60 species of the single family Ricinoididae are known, including the West-Central African genus *Ricinoides* and the neotropical (mainly South American) genera *Cryptocellus* and *Pseudocellus*, see SELDEN (1992: 603, fig. 3a).

(2) Fossil taxa are known from (a) the Carboniferous of the North America and Europe, see SELDEN (1992: 603, fig. 3b) and PLATNICK's World Catalog of Spiders (Internet),

15 species of the genera *Amarixys* and *Curculioides* (Curculioididae) as well as *Poliochera* and *Terpsicroton* (Poliocheridae). A further Carboniferous fragment of a fossil from China – the only and questionable member of the order Ricinulei from Asia – has been published by LAURENTIAUX-VIEIRA & LAURENTIAUX (1963) as a member of *Poliochera* or *Curculioides*. According to SELDEN (1992: 632) this fossil is not a member of the Ricinulei but probably of the Crustacea or Scorpions. – (b) A Cretaceous species from Asia (Burma/Myanmar) is described in this paper; it may be the member of the genus *Poliochera* of the family Poliocheridae.

### Description of the new fossil species from Burma (Myanmar)

?*Poliochera cretacea* n. sp. (figs. 3–7), photos: Part I C p. 351, nos. 34–35

The name of the species points to its Cretaceous age.

**Material** (bought from a German dealer who got material directly from a Burmese dealer): Holotype female nymph 2 or 3 in Mid Cretaceous amber from Burma (Myanmar), and a separated piece of amber, F2336/BU/CJW, later probably SMF.

**Preservation and syninclusions** (see the photos): Most parts of the specimen are excellently preserved (see the photos) in a single layer at the surface of a clear yellow piece of amber, its opisthosoma is dorsally distinctly depressed, and most leg articles are depressed, usually laterally. The remains of the right legs I–III are partly oxidated, and apparently had contact to the surface of the fossil resin for a longer time. Cut off are both first legs near their middle or more basally (the right one), the right leg II through the femur, the left leg II near the end of the metatarsus. The mouth parts are hidden by an emulsion and the lowered cucullus, the right pedipalpus is well preserved, the left pedipalpus is hidden or lost, coxae I–II are hidden, most leg articles are deformed by the high pressure of the fossil resin for million of years, tiny particles and bubbles/droplets cover parts of the body and legs including the eyes, the two distal articles of the pygidium are retracted. – In the same piece of amber a tiny leg of an insect (probably a beetle) just in front of the cucullus, a tiny deformed Diptera with long antennae, remains of ½ insect at a spider's thread at its end, and a tiny ballet of excrement of an insect are preserved. A small globular particle below the left leg III is surely not an egg of the Ricinulei, remains of plants, tiny splinters of amber, tiny droplets exist also. – In the separated piece of amber remains of plants like “stellate hairs” are preserved, few remains of tiny insects like Diptera, ballets of insects excrements, spiders threads, and

a small bubble filled with a tiny gas bubble which is movable in a fluid – preserved for 100 million years (!).

**Diagnosis** (nymph 2 or 3): Some leg articles bear dorsal “thorns” (fig. 5), tergites covered with short hairs, the anterior tergite bears two transverse rows of short hairs (fig. 3) (the remaining tergites bear hairs in a more irregular position), opisthosomal lines (fig. 3) in a lateral position; pedipalpus (fig. 4): tibio-tarsus about 4 times longer than high, the fixed finger of the pincer bears a longer distal and a quite short more basal tooth.

**Description** (nymph 2 or 3):

Measurements (in mm): Body length 2.3, prosoma: Length 1.0, width 1.0, cucullus: Length at least 0.3, width ca. 0.8, diameter of an anterior eye ca. 0.08; opisthosoma: Length ca. 1.6 (1.3 in the dorsal aspect), width 1.4; pedipalpal tibio-tarsus: Length 0.38, height less than 0.09; leg I: Femur ca. 0.55, leg II: Femur 1.1, patella 0.4, tibia 0.8, metatarsus at least 0.9 (the distal part is cut off), femur III 0.4, femur IV (see fig. 5) 0.7.

Colour medium to dark grey brown.

Prosoma (fig. 3, photos) as wide as long, laterally only fairly convex, very fine corniculate, bearing a weak longitudinal depression in the anterior half, most of the short hairs are rubbed off, two pairs of widely spaced and well developed eyes (they are partly hidden by tiny bubbles), each pair is not widely spaced, situated in the middle of the length of the prosoma. Colulus lowered and hiding the mouth parts, probably 3.8 times wider than long. – Pedipalpus (fig. 4, photo) with long patella and tibio-tarsus, movable finger of the pincer long and smooth, fixed finger bearing a tiny and a longer distal tooth, the tibio-tarsus bears some longer hairs and several sensory pits; see the well-studied pedipalpus of an extant species: TALARICO et al. (2008). – Legs (figs. 5–7) (most articles are deformed, usually depressed laterally, some are cut off, see above) slender, II distinctly the longest, the femora are the longest articles and bear dorsal “thorns”, tarsus III is 3-segmented, tarsus IV is 2-segmented (tarsi I and II are not preserved), the tarsal segments III are short as in extant taxa (fig. 1), but the segments of tarsus IV are distinctly longer and more slender, the tarsi bear a pair of stiff hairs near the long paired claws and an unpaired median outgrowth (O in fig. 7), the modified median claw is blunt, stout and straight. Coxae IV are long, pointed medially and contiguous (I–II and most parts of III are hidden). – Opisthosoma (fig. 3, photos) (it is dorsally strongly depressed) in dorsal aspect 1.14 times longer than wide, finely corniculate, laterally deeply inclined between tergites and sternites, most hairs are rubbed off, but two transverse rows of the anterior tergite are preserved. The four tergites are divided laterally longitudinally, the second one is the largest. The Pygidium is large, its two basal segments are retracted. The sternites are covered with small/tiny bubbles, the second sclerite is the largest, the anterior one (fig. 6) is relatively slightly prolonged.

**Relationships:** According to the well developed eyes (the coxae II are hidden) *cretacea* should be a member of the extinct superfamily Poliocheroidea which has only been known from the Carboniferous up to now. The opisthosoma is divided in transverse tergites as in the Carboniferous family Poliocheridae SCUDDER 1884 and in extant taxa, and not divided longitudinally by a median line. Like in the genus *Poliochera* SCUDDER 1884 body and legs possess a tuberculate cuticula, but “elongate depressions” – see SELDEN (1992: 622) – are absent in the present specimen – which is only based on a nymph – in contrast to members of the Carboniferous genus *Poliochera*; therefore I regard *cretaceus* only with hesitation as a member of *Poliochera*.

**Distribution:** Lower or Mid Cretaceous (about 100 million years old) amber forest of Burma (Myanmar). **Remark:** No extant or fossil member of the order Ricinulei has previously been reported from Asia or from Burmese or other Cretaceous ambers. Fossil members of the genus *Poliochera* have been described from North America.

**Further material in Burmese amber** (bought from the same dealer as the holotype):

**Ricinulei indet.**, probably the same genus and species:

(1) Two nymphs, coll. ALEX BEIGEL., no. BU-32.

The eight-legged arachnids are fairly decomposed and covered with a thin emulsion, almost completely preserved. Syninclusions are, e. g., a juvenile spider indet., a larger spiders leg which has 3 tarsal claws (Mygalomorpha? Dipluridae?), 1 Opiliones, some Acari, some Diptera and Coleoptera, 2 Myriapoda, some insects indet., a leaf and detritus.

Measurements (in mm): Body length 4.0, prosomal length 1.3, femur I 0.9, femur II 1.3. The body is very strongly flattened; an emulsion hides parts of the body including the area of the eyes, and the pedipalpi as well.

(2) Exuvia of a nymph, F2345/BU/CJW. Photo 36

The eight-legged exuvia is preserved in an almost globular piece of amber which includes numerous particles of detritus and insects excrement. It is well preserved, partly deformed, some leg articles are lost; its body length is almost 3 ½ mm.

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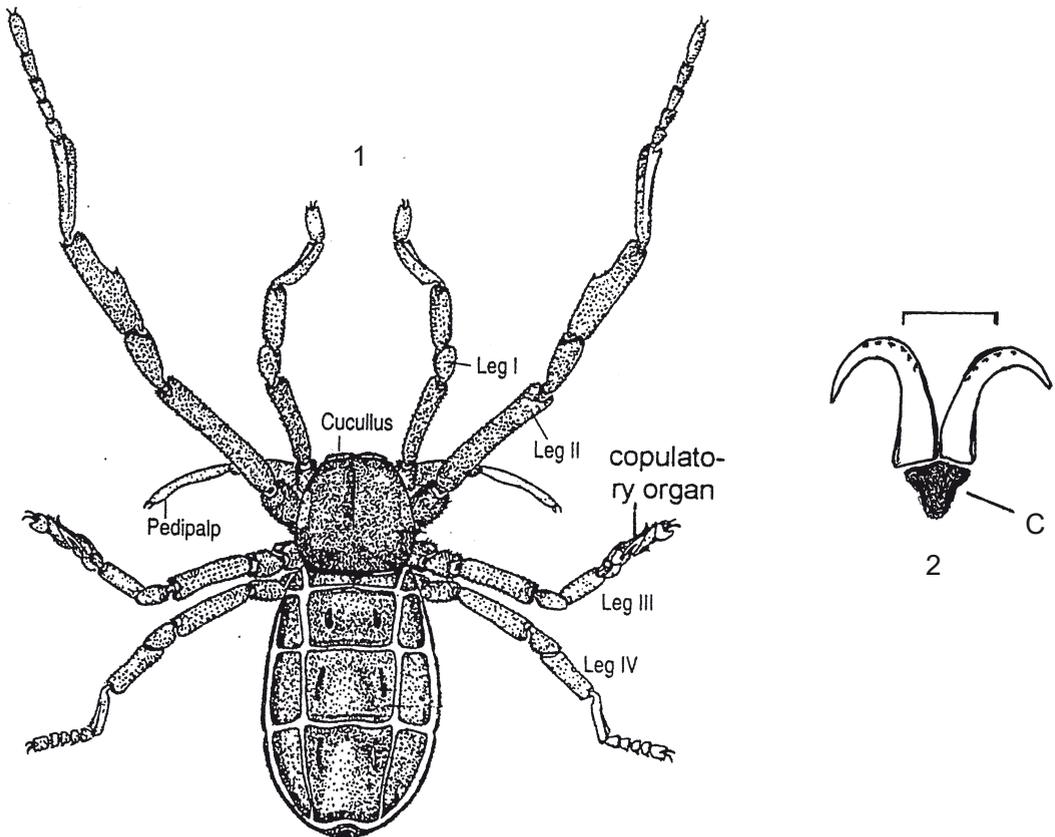
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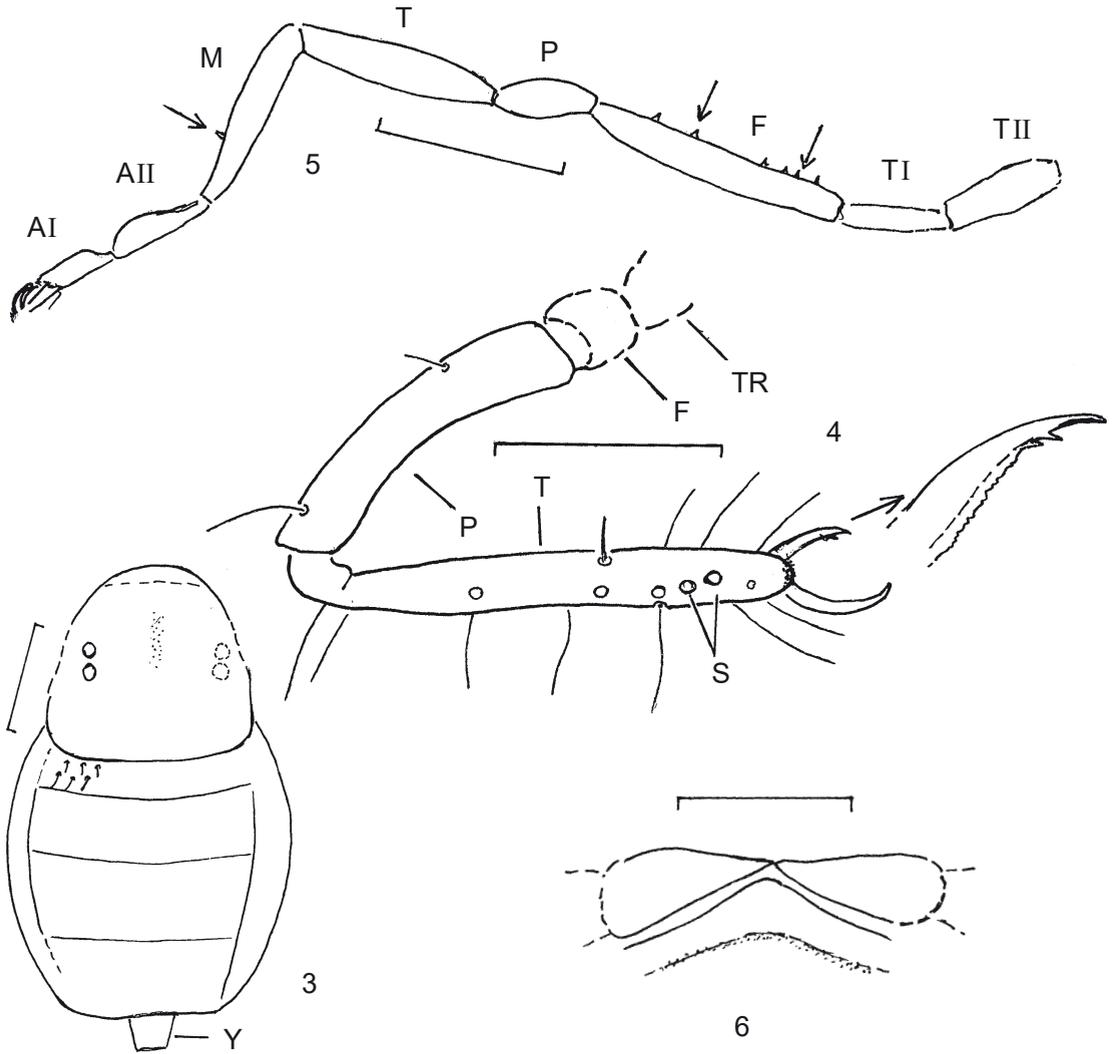
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Figs. 1-2) Extant Ricinulei indet.:

1) dorsal aspect of an adult male, body length about 5 mm. Note the "hood" (cucullus) of the anterior part of the prosoma, the absence of eye lenses, the plates of the opisthosoma, the very small pedipalpi, the large second leg, and the secondary copulatory organ of the modified third leg (metatarsus and tarsus); fig. 2) apical aspect of the claws of the right tarsus IV of the male nymph 3 from NO-Brasil (CJW). C = modified blunt unpaired claw. Scale bar 0.1 mm;

figs. 3-7: ?*Poliochera cretacea* n. sp. (Poliocheridae), female nymph 2 or 3 in Cretaceous amber from Burma (Myanmar); 3) dorsal aspect of the body. Note the 2 pairs of widely spaced eyes. Only few hairs are drawn on the anterior tergite; 4) prolateral and slightly dorsal aspect of the right pedipalpus which is folded in this natural position. The fixed finger of the pincer (arrow) is enlarged to show its teeth. The articles are somewhat deformed. Only few hairs are drawn. I am not sure about the correct terms of the articles; 5) oblique retrolateral and slightly ventral aspect of the left leg IV. Some

articles are deformed. The coxa is not drawn, few of the dorsal "thorns" (arrows) are drawn; 6) coxae IV and anterior part of the opisthosoma; 7) apical aspect of the right tarsus IV with its claws. Only few long hairs are drawn. AI, AII = two tarsal articles, C = strongly sclerotized cone-shaped modified median claw, F = femur, H = stiff setae, M = metatarsus, O = dorsal-apical outgrowth, P = patella, R = retroclaw, S = sensory pits T = tibio-tarsus, TI, TII = trochantera I and II, TR = trochanter, Y = pygidium. Scale bars 0.1 mm in fig. 7, 0.2 in fig. 4, 0.5 mm in the remaining figs.;

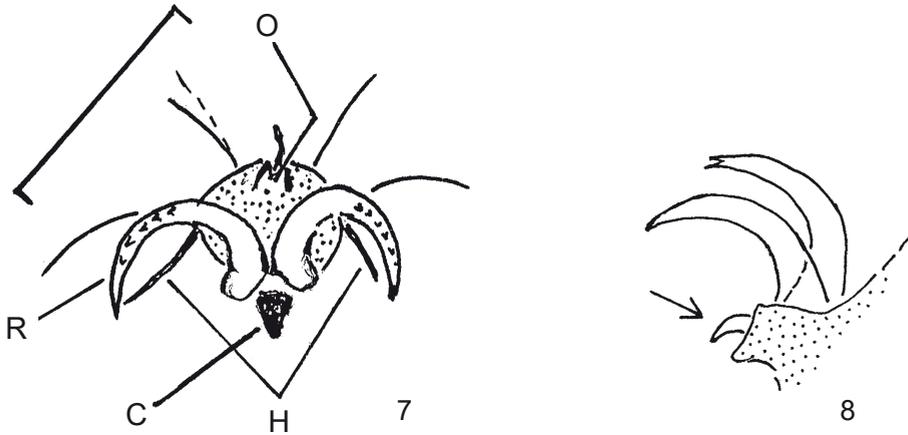


fig. 8) A member of the extinct order Trigonotarbida, lateral aspect of the tarsal claws. The arrow points to the bent and pointed unpaired claw. No scale. Drawn after a photo of *Gilboarachne griersoni*, taken from SHEAR et al. (1987).

**CORRECTIONS AND ADDENDA TO VOL. 6 OF THE BEITR. ARANEOL.  
(2011)**

JOERG WUNDERLICH, 69493 Hirschberg, Germany.

Pages 115 ff, SEGESTRIIDAE:

The genus *Ariadna* AUDOUIN 1826: See the paper on *Ariadna* in the present volume.

Pages 110, 115, MITURGIDAE:

The genus *Prochara* O. PICKARD-CAMBRIDGE 1872 is actually a member of the family Miturgidae and not of the Liocranidae/Zoridae. Its single species – *lycosiformis* – has probably been introduced to Sicily from Australia via Israel.

Pages 230, 231 and 253: THERIDIIDAE, the genera *Ruborridion* and *Theridion* : I found that a trichobothrium on metatarsus III – which is absent in *Ruborridion* but usually existing in *Theridion* – is also absent in *Theridion hannoniae* DENIS in which the labium is long and the coxae IV are only fairly spaced in contrast to *Ruborridion* WUNDERLICH 2011. (The species strongly related to *hannoniae* have not yet been studied). I regard the loss of the metatarsal III trichobothrium as convergently evolved in both taxa. A note in this respect has to give on the pages 230, 231 and 253. – Furthermore I found the coxae IV widely spaced in some *Theridion varians* (CJW) quite similar to *Ruborridion musivum*.

Page 182, SEGESTRIIDAE:

Key no. 5(4) – –: Read “*gallica* WUNDERLICH 2012” instead of “sp. indet.”, and add “figs. 22–26” (under *A. europaensis* in that paper); See also below (*A. gallica*); see the paper on the genus *Ariadna* in this volume.

Page 372–773, LINYPHIIDAE: ERIGONINAE:

The genus *Styloctetor* (with *S. romanus*) has to add to the key.

Page 486, CTENIZIDAE:

“?*Ummidia* sp. indet.”.

Material: 1♂ in Eocene Baltic amber (not Bitterfeld deposit), coll. FRIEDHELM EICHMANN Ar 38 (not coll. HEINRICH GRABENHORST Ar-38).

Page 493, OONOPIDAE:

*Orchestina* (*Baltorchestina*) *rectangulata* WUNDERLICH 2011 (p. 493) (in amber from the Bitterfeld deposit) is a homonym of *Orchestina* (*Baltorchestina*) *rectangulata* WUNDERLICH 2008 (p. 65) (in Baltic amber), and is replaced herewith by the name *Orchestina* (*Baltorchestina*) *angulata* **nov. nom.**

Page 545, OONOPIDAE: GAMASOMORPHINAE:

Spiders described under Oonopidae: Gamasomorphinae (the genus *Escaphiella*) are really members of the family Tetrablemmidae.

Page 552, PRAETERLEPTONETIDAE.

Lung covers exist in *Praeterleptoneta tibialis* WUNDERLICH 2011 but feathery hairs are absent.

Pages 569, 570, 575, MESOTHELAE, ARANEAE:

Poison glands exist actually in the Mesothelae. These glands have to add in the list p. 569 (autapomorphic characters of spiders) as well as basally on p. 575. P. 570 “poison glands” has to eliminate below “OPISTHOTHELAE” and has to add with a question mark below “ARANEIDA” as well as below “ARANEAE”.

The basically not flattened body (but raised from the ground), and the prograde leg position may be further apomorphic characters of the Araneae. Most Arachnida – even the most archaic Scorpions as well as the basal Opiliones and Acari – possess a flattened body and a laterigrade or mediograde leg position in contrast to most Araneae, including the most archaic Mesothelae, which body is not flattened. Probably the reason for the evolution of these apomorphic characters is the subterranean life style and the digging behaviour of the archaic spiders.

**OECOBIUS AMBOSELI SHEAR & BENOIT 1974 (ARANEAE: OECOBIIDAE), A RECENTLY TO DENMARK AND EUROPE INTRODUCED SPIDER SPECIES**

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**Abstract:** An abundant population of *Oecobius amboseli* SHEAR & BENOIT 1974 (Araneae: Oecobiidae) has been discovered in a basement room of the Aarhus University, Denmark. The tropical species was previously known only from Africa (Kenya, Uganda, Egypt: in buildings). *O. amboseli* is probably in an initial phase of worldwide spreading by human transport. Therefore, the origin of the Danish population is uncertain. This is the first record of the family Oecobiidae in Denmark and of *O. amboseli* in Europe.

**Key words:** Araneae, spreading, territory behaviour.

Specimens of an *Oecobius* species were discovered in October 2009 in a basement room of the Department of Bioscience (building 1135, room 022) of Aarhus University, Denmark. The genital organs of the collected specimens did not comply with those of the known European species, see WUNDERLICH (1995), but both epigyne and male pedipalpus are identical with those illustrated by EL-HENNAWY (2004) for *Oecobius amboseli* SHEAR & BENOIT 1974. The species was described from a single female collected in the Massai Amboseli Reserve, Kenya, with no further details given.

Subsequently it has been collected from house walls in Uganda and from inside houses in Egypt, EI HENNAWY (2004). The synantropic occurrence in all cases except probably the type locality casts doubt in the true origin of the species, so it must so far be assumed to be East African. However the finds in Egypt and now in Denmark indicate that the species is in an initial phase of possibly worldwide spreading by human transport, as has been the case for several other *Oecobius* species, e. g. for *O. navus* BLACKWALL 1859 in buildings in Central Europe. For the same reason it is impossible to state with any certainty the place of origin of the Danish population.

When discovered there was already an abundant population of at least several hundred individuals. The room was used for growing wheat seedling for aphid cultures. It was not temperature-controlled but usually maintained a rather stable temperature of 20–22 °C. The cultures also attract fungus gnats, drosophilids and other Diptera. Additionally there were Psocoptera from the drain pipes, and where humid organic matter accumulated. Thus, there should have been abundant potential prey for spiders in this room, which also housed *Ostearius melanopygius* (Linyphiidae) and a strong population of *Pholcus phalangioides* (Pholcidae). *Oecobius* webs were found on the floor and walls; often they were so dense that neighbouring webs were in contact. Spider individuals of all sizes could be seen roaming around whenever boxes or trays were moved. At the time of writing (January 2012) the population was as abundant as ever, probably counting thousands including juveniles. It had spread to the neighbouring rooms and was found at least 10–15 m down the hallway.

The abundance of the species in the cellar in Aarhus allowed some preliminary biological observations to be made. For example, the interesting “sequential displacement” behaviour described by BURGESS (1976) for the gregarious *Oecobius civitas* was often observed: when one spider was induced to leave its web it would quickly enter another nearby web whose owner would be displaced, only to repeat the same sequence of events at a third web, etc. MESTERTON-GIBBONS & ADAMS (1998) interpreted this behaviour as a unique case of of the antibourgeois strategy, i. e. a territory owner withdraws without fighting when challenged by an intruder. This unusual behaviour may be explained by presumably high costs of fighting combined with an abundance of territories/webs. In fact, there were many unoccupied webs in the cellar and the “chain reaction” stopped when a spider entered such a web.

### **Short description of *Oecobius amboseli*:**

Material: Numerous specimens University of Aarhus, Denmark; 4♂5♀ coll. J. WUNDERLICH.

Measurements (in mm): Body length ♂ 1.8–2.2, ♀ 2.2–2.8, prosoma: Length ca. 0.7, width ca. 0.8, tibia I 0.6–0.7 (both sexes).

Colour quite variable, prosoma yellowish brown, medially and marginally more or less darkened, clypeus darkened, sternum light grey, legs uniformly yellow to fairly grey and annulated, opisthosoma grey, dorsally with numerous white spots, medially frequently darkened, posterior spinnerets darkened dorsally.

Calamistrum absent in the male, well developed in the female, almost along the basal two thirds. Tarsus IV bears a row of four long retrolateral bristles and two dorsal-distal bristles, two short additional ventral-distal bristles may exist. – ♂-pedipalpus (figs. 1–2): Cymbium with three apical bristles, radix apophysis slender, embolus strongly sclerotized, slender and bent. Epigyne (fig. 3) with a large groove, strongly sclerotized margins and an anterior projection which is directed posteriorly.

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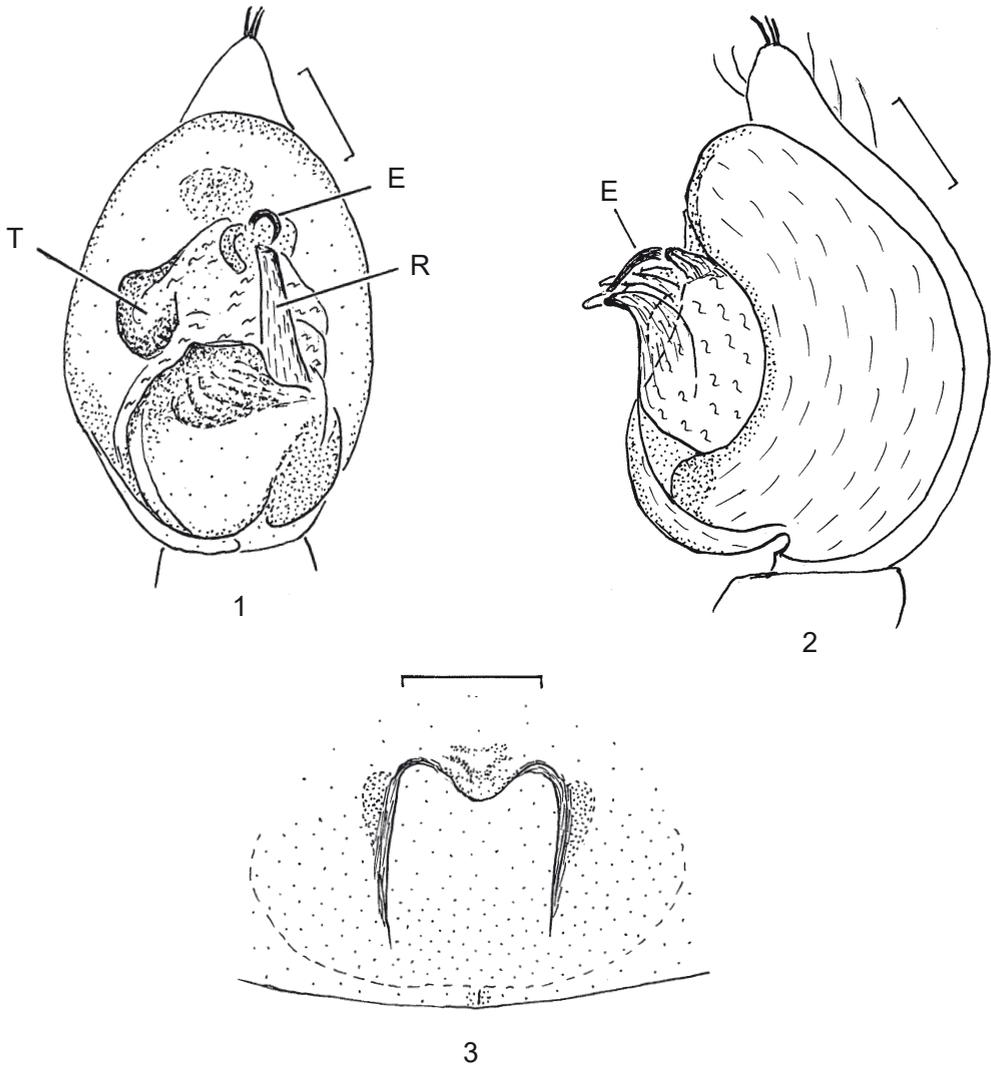
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Figs. 1-3: *Oecobius amboseli* SHEAR & BENOIT 1974 from Denmark; 1-2) ♂, ventral and prolateral aspect of the right pedipalpus; 3) ♀, epigyne. E = embolus, R = radix apophysis, T = terminal apophysis. Scale bar 0.1 mm.

## SEVEN NEW SPECIES OF THE SPIDER GENUS *OTACILIA* THORELL 1897 (ARANEAE: CORINNIDAE) FROM CHINA, LAOS AND THAILAND

PETER JÄGER, Senckenberg Research Institute (SMF), 60325 Frankfurt a. M., Germany & JOERG WUNDERLICH, 69493 Hirschberg, Germany.

**Abstract:** The following **new species** of the genus *Otacilia* THORELL 1897 (Araneae: Corinnidae) are described from Southeast Asia: *O. bicolor* from Laos (♂♀), *O. christae* from Laos (♂), *O. kao* from Thailand (♂♀), *O. loriot* from Laos (♂), *O. namkhan* from Laos (♂♀), *O. paracymbium* from China, Yunnan (♂), and *O. vangvieng* from Laos (♂). The relationships of *Otacilia* and *Phrurolithus* C. L. KOCH 1839, and the limit of *Otacilia* are discussed.

**Key words:** Southeast Asia, spiders, taxonomy.

Corinnidae is a family of spiders which is diverse in the tropics. Numerous species are ant-shaped. *Otacilia* THORELL 1897 is one of the most diverse genera of the subfamily Phrurolithinae and even of the Corinnidae in South East Asia, see DEELEMANN-REINHOLD (2001), ZHANG et al. (2009), FU et al. (2010), HU & ZHANG (2011), and ONO (2009), hundreds of undescribed species may exist. In this paper we add 7 species to the 21 species which were already known.

According to DEELEMANN-REINHOLD (2001: 411) „all species (< of *Otacilia* >) are known from small distribution ranges.“. The spiders of this genus are restricted to South East Asia; all are dwellers of leaf litters like most other Corinnidae including the genus *Phrurolithus* C. L. KOCH 1839 which also occurs in South East Asia.

## PHYLOGENETICS, RELATIONSHIPS, AND PRELIMINARY LIST OF DIAGNOSTIC CHARACTERS OF *OTACILIA* AND *PHRUROLITHUS*

According to its chaetotaxy, the profile of the prosoma, the development of the scutum of the ♂-opisthosoma, body size and colour as well as its copulatory structures *Otacilia* in the current sense is a very diverse genus compared to *Phrurolithus*; see, e. g., *O. christae* n. sp., *O. yangi*, ZHANG et al., *O. namkhan* n. sp. – *Otacilia ornata* DEELEMEN-REINHOLD 2001 has recently transferred to the genus *Abdosetae* FU et al. 2010, and the relationships of *O. christae* n. sp. are unsure. In our opinion *Otacilia* most probably is a paraphyletic taxon. Unfortunately the generotype – *Otacilia armatissima* THORELL 1897 from Burma (Myanmar) – is only known in the female sex, and for a revision of the „*Otacilia*-complex“ the male of *armatissima* has to be known absolutely.

*Otacilia* in the current wide sense is strongly related to *Phrurolithus*: In both genera the narrow cephalic part widens abruptly to the thorax, all patellae and legs III–IV are bristleless or bearing a single dorsal femoral bristle only, leg scopulae are absent, the tarsal claws are smooth, the claw tufts consist of several well developed spatulate hairs; GRIMM (1986: 47) reports erroneously the absence of claw tufts in *Phrurolithus*. Teeth of the margins of the fang furrow: According to GRIMM (1986: 47) the promargin in *Phrurolithus* bears denticles only but actually both margins bear two teeth in both genera.

Spiders of both genera are ant-mimicking like other Phrurolithinae. In several genera of this subfamily the gnathocoxae bear a ventral depression but this depression is absent in *Otacilia* like in *Phrurolithus*. In some taxa of both genera the posterior median eyes are oval, in others they are circular or almost so (apparently variable within the same species).

Differences of *Otacilia* and *Phrurolithus*: Probably no clear cut between these genera can be found currently; the paraphyly of *Otacilia* may be the reason. In most members of the subfamily Phrurolithinae the chelicerae bear anteriorly in the basal half either a single bristle (fig. 5) or two bristles (fig. 34). In all members of *Phrurolithus* exists only a single bristle, in *Otacilia* exist one or two bristles, see tab. 1. In all species of *Phrurolithus* the male opisthosoma bears a large dorsal scutum; in most species of *Otacilia* a large opisthosomal scutum exists, too, in certain others it is slightly or strongly reduced, see, e. g., *O. kao* n. sp.. In both genera and most species all femora bear a single dorsal bristle, but two exist on the anterior femora in certain species from China. In *Phrurolithus* the femora III–IV are bristle-less in contrast most species of *Otacilia* with usually a single dorsal bristle on all femora, but in *O. namkhan* all femora are bristleless like in *Phrurolithus*. Femur I bears a single prolateral bristle in *Phrurolithus* but several (most often 4) in *Otacilia*, tibia I bears paired ventral bristles in *Phrurolithus* but one more retroventral than proventral bristle exists in the species of *Otacilia* which are treated in this paper. The size of the tarsal claws is reduced in *Phrurolithus* in contrast to *Otacilia*. Genital organs: In *Phrurolithus* bulb and epigyne are strongly sclerotized in contrast to *Otacilia*, in *Phrurolithus* only a single very large RTA exists (one or two of different size in *Otacilia*), and a strongly sclerotized and usually large retrolateral tegular apophysis which is directed anteriorly (rarely similar in *Otacilia*).

Unusual characters in some new described species: Most species treated in this paper are small or even tiny, but in *O. paracymbium* and in *Otacilia* sp. indet. B the body

length is 4.5 mm, about twice as long as in the remaining species. The order of the legs is usually I/IV/II/III, but it is IV/I/II/III in *O. vangvieng*. In *O. paracymbium* and in *Otacilia* sp. indet. B the legs are longer than in the remaining species. All femora bear a dorsal bristle except in *O. namkhan* in which all femora are bristle-less. The ♂-opisthosoma is covered almost completely with dorsal a scutum in most species, but a scutum is absent in *O. kao* n. sp. and *O. paracymbium* n. sp. In *O. christae* sp. n. bears the opisthosoma a field of long ventral setae similar to the genus *Abdosetae* FU et al. 2010.

Species	number of cheliceral bristles	anterior eyes	distribution
<i>bicolor</i>	1	ME < LE	Laos
<i>christae</i>	2	ME < LE	Laos
<i>kao</i>	2	ME > LE	Thailand
<i>loriot</i>	1	ME > LE	Laos
<i>namkhan</i>	2	ME < LE	Laos
<i>paracymbium</i>	2	ME = LE	China
<i>vangvieng</i>	2	ME < LE	Laos
sp. indet. A	2	ME < LE	Laos (Ban Keng Koung)
sp. indet. B	2	ME > LE	Laos (Tad Vang Fong)

Tab. 1. Two characters and the distribution of the species treated in this paper. ME = anterior median eyes, LE = anterior lateral eyes.

## DESCRIPTION OF THE NEW SPECIES

***Otacilia bicolor* n. sp.** (figs. 1–10, photos 1–6)

**Etymology:** The spider is named after its bicoloured opisthosoma; adjective.

**Material:** Laos, Champasak Prov., Muang Bachiang, Ban Lak 38, That Fane, N15°11'03,0", E 106°07'36,9", 952 m, Bolaven plateau, primary forest, in dry leaf litter and soil, sieving at day, 5♂3♀, P. JÄGER & J. MARTENS leg. 16. III. 2010; holotype ♂ and 4♂3♀ paratypes, SMF; 1♂ paratype, with the same data, SMF.

**Diagnosis:** A single cheliceral bristle (fig. 1), anterior median eyes smaller than anterior lateral eyes, opisthosoma distinctly bicoloured: Dark dorsally, light grey ventrally. ♂-pedipalpus (figs. 1–4) with a long dorsal and a long retrolateral apophysis as well as 2 ventral humps, cymbium distally-ventrally hairy but without a brush of hairs, conductor large and translucent. Epigyne (figs. 6–8) a weakly sclerotized wide plate, receptacula seminis clearly visible in ventral view. Vulva (figs. 9–10): Receptacula seminis transversal, their lateral part dilated; distance copulatory openings > distance CO – epigastric furrow, copulatory duct hidden behind membranous sac, the latter elongated, 2.5 times longer than wide, anteriorly pointed.

**Further characters:** Posterior eye row fairly recurved (photo 5), posterior median eyes distinctly smaller than the lateral eyes (fig. 5), femora darkened (photos 1, 4), chelicerae with a single anterior bristle (fig. 5).

### **Description:**

Measurements (in mm): Body length 1.7 (♂)–2.0, prosoma: Length 0.9, width 0.8; leg I (♂): Femur 0.9, patella 0.33, tibia 0.9, metatarsus 0.8, tarsus 0.5, tibia II 0.65, tibia III 0.53, tibia IV 0.85, metatarsus IV 1.0 in both sexes; ♀: Tibia I 0.9, tibia IV 0.9.

Colour (photos 1–5): Prosoma medium grey brown, legs brown, femora (especially I) partly darkened, opisthosoma dorsally dark grey (♂-opisthosoma dark brown), a spot of white hairs above the spinnerets, ventrally light grey.

Prosoma 1.13 times longer than wide, thoracic part slightly higher than the cephalic part, thoracic fissure well developed, eyes (fig. 5, photos) large, posterior row fairly recurved, posterior median eyes distinctly smaller than posterior lateral eyes, spaced by about their diameter. Posterior margin of the fang furrow with 2 denticles close together, anterior margin with 3 teeth, labium slightly wider than long, sternum as wide as long, fairly spacing the coxae IV. – Legs long, order IV/I/II/III. Bristles: All femora dorsally 1 in the basal half; leg I: Femur prodistally 3–4, tibia pro-/retroventrally 6/7 ventral pairs, metatarsus 4 ventral pairs, leg II: Tibia 6 ventral pairs, metatarsus 3–4 pairs; III–IV: None except the dorsals on the femora. Preening comb of metatarsus III fairly well developed, spatulate hairs exist below the toothed tarsal claws. Autotomy exists between coxa and trochanter. – Opisthosoma oval, hairs short, in the male covered with a large dorsal scutum except in front of the spinnerets, epigaster not scutate. Spinnerets short, anteriors stout, conical and close together, median spinnerets laterally depressed in both sexes, posterior spinnerets slender. Colulus absent, tracheal fold straight. – ♂-pedipalpus (figs. 1–4): Femur with a paired hump in the distal half, tibia with a long dorsal and a long retrolateral apophysis as well as 2 ventral humps, cymbium distally-ventrally hairy but without a brush of hairs, conductor large and translucent, tegular apophysis large, embolus pointed. Epigyne (figs. 6–8, photo 6) a weakly sclerotized wide plate, receptacula seminis clearly visible in ventral view. Vulva: Fig. 9–10. Glandular appendage anteriorad, almost as long as fertilisation duct.

**Relationships:** According to the quite similar structures of the bulbus *O. onoi* DEELEMAN-REINHOLD 2001 from Thailand is most related; the femora in *onoi* are darkened, too, but the opisthosoma is olive grey and the copulatory organs are different, the retrolateral tibial apophysis is v-shaped excavated, the femoral outgrowth as well as epigyne and vulva are different, see DEELEMAN-REINHOLD (2001: Figs. 652–656).

**Distribution:** Laos, Champasak.

***Otacilia loriot* n. sp.** (figs. 11–14, photos 12–16)

**Derivatio nominis:** This species is dedicated to the late VICCO VON BÜLOW (pseudonym: Lorient) acknowledging his tremendous contributions to the German humour; nomen in apposition.

**Material:** Holotype ♂, Laos, Luang Prabang Prov., SE Luang Prabang, Nam Khan, Ban Pak Bak, Houay Kho, 328 m, N. 19°44'09,1", E. 102°16'37,5", leaf litter, along stream, sieving, P. JÄGER leg. 28. II. 2008.

**Diagnosis** (♂; ♀ unknown): A single thin cheliceral bristle, anterior median eyes larger than anterior lateral eyes, prosoma dark brown, legs: Femora, patellae and tibiae dark brown, the remaining articles yellow brown (photos 12–14), opisthosoma dorsally dark brown (photo 12), ventrally light grey brown (photo 13), with a large light spot above spinnerets (photo 16). Pedipalpus (figs. 11–14): Tibia with a long retrolateral apophysis, a more slender long dorsal apophysis which is bent in the prolateral direction, as well as a well developed ventral-basal hump, conductor long, embolus hidden behind conductor in the ventral aspect.

**Description** (♂):

Measurements (in mm): Body length 1.9, prosoma: Length 0.95, width 0.75; leg I: Femur 0.9, patella 0.3, tibia 1.0, metatarsus 0.85, tarsus 0.5, tibia II 0.7, tibia III 0.5, tibia IV 0.8.

Colour (photos 12–16): See the diagnosis.

Prosoma 1.27 times longer than wide, anteriorly abruptly narrowed like in other congeners, profile convex, almost smooth, thoracic fissure distinct but short. Eyes: Posterior row recurved, median eyes distinctly smaller than laterals, anterior eyes close together, the median larger. Basal cheliceral articles fairly large, frontally with a single thin bristle in the basal half, anteriorly distally with long thin and bent plumose hairs like in congeners, posterior margin of the fang furrow bearing 3 small teeth, anterior margin toothed, too, fangs long and slender, labium free, about as long as wide, gnathocoxae large, not depressed, sternum as long as wide. – Legs fairly long and robust, hairs very short. Most bristles long: All femora a single short dorsal one in the basal half; leg I: Femur 4 prolateral bristles, patellae none, tibia pro-/retroventrally 6/7, metatarsus 4 ventral pairs, III–IV bristle-less except the femora. The tarsi bear several spatulate tuft hairs, the claws are smooth and strongly bent, autotomy exists between coxa and trochanter. – Opisthosoma oval, hairs very short, dorsally covered with a large scutum except above the spinnerets (photo 12), epigastric scutum existing (photo 13), colulus well developed, anterior spinnerets stout and converging. – Pedipalpus: See the diagnosis. Femur with distal retrolateral lyriform organ.

**Relationships:** In *O. bicolor* n. sp. exists also a single cheliceral bristle, but the retrolateral tibial apophysis of the ♂-pedipalpus is blunt and wider, the position of the ventral tibial hump is more distally. In *O. namkhan* n. sp. the chelicerae bear 2 bristles each,

the tibial apophyses are quite similar but slightly shorter, the embolus is longer and bent in a semicircle.

**Distribution:** Laos, Luang Prabang.

***Otacilia namkhan* n. sp.** (figs. 15–21, photos 7–11)

**Etymology:** The species is named according to the type locality, the river Khan (= Nam Khan); nomen in apposition.

**Material:** Laos, Luang Prabang Prov., SE Luang Prabang, Nam Khan, Xieng Ngeun District; (a) Ban Keng Koung, 372 m, N.19°40'963", E.102°18'442", along stream, leaf litter, sieving at daytime, P. JÄGER leg. 22. III. 2007, holotype ♂, SMF; (b) Ban Pak Bak, Houay Kho, 328 m, N.19°44'09,1", E.102°16'37,5", leaf litter, at slope of stream, at dusk, sieving, P. JÄGER leg. 23. III. 2007, 1♂ paratype, SMF; (c) Ban Nong Di, 281 m, N19°41'03,5", E.102°21'31,2", along stream, leaf litter, sieving at daytime, P. JÄGER leg. 21. III. 2007, 1♀ paratype, SMF; (d) between Ban Khon Why and Xieng Ngeun, Houay Tham, 363 m, N.19°44'51,2", E192°13'15,4", along stream, leaf litter at rocks, sieving at daytime, P. JÄGER leg. 24. III. 2007, 1♀ paratype SMF; (e) Ban Keng Koung, ca. 700 m, N19°40'963", E102°18'442", valley, secondary forest, dry stream bed, dead wood, sieving, P. JÄGER leg. 24. II. 2008, 1♂ paratype, SMF; (f) Ban Keng Koung, ca. 372 m, N19°40'963", E.102°18'442", N-side of Nam Khan, along stream bed, bamboo, few bananas and mango, sieving, P. JÄGER leg. 25. II. 2008, 13♂ paratypes, SMF; (g) same locality, leaf litter, close to village, sieving, P. JÄGER leg. 27. II. 2008, 2♂ paratypes, SMF.

**Diagnosis:** All femora bristle-less, two bristles on each chelicera, anterior median eyes smaller than anterior lateral eyes, prosoma medium to dark brown, pedipalpus (figs. 15–18): Embolus semicircular, femoral hump in proximal half; epigyne/vulva (figs. 19–21): Receptacula seminis transversal, median part dilated; distance between copulatory openings equal to distance copulatory openings and epigastric furrow; copulatory ducts clearly visible, running anteriorly in membranous sac, the latter only slightly longer than wide.

### **Description:**

Measurements (in mm): Body length 1.8–2.5, prosoma: Length 0.95–1.2, width 0.85–1.0; leg I of a large ♂: Femur 1.1, patella 0.45, tibia 1.15, metatarsus 0.95, tarsus 0.55, tibia II 0.8, tibia III 0.65, tibia IV 1.1.

Colour (photos 7–11): Prosoma medium to dark brown, medium part and sternum lighter, legs yellow brown, femora and tibiae distally strongly darkened, opisthosoma dorsally dark brown, ventrally mainly yellow brown but dark posteriorly in the middle; without light patch above spinnerets.

Prosoma 1.12–1.2 times longer than wide, flat, hairs indistinct, fovea well developed; chelicerae bearing two anterior bristles which are well developed, fangs long, posterior

margin of the fang furrow bearing two fused teeth, anterior margin with 3 teeth, labium as wide as long, sternum longer than wide, fairly elongated between coxae IV. – Legs fairly long, order I/IV/II/III, hairs indistinct. Bristles: All femora bristle-less; leg I: Femur 3–5 prolaterals in the distal half, tibia pro/retrolaterally 7/8, metatarsus 4 ventral pairs, legs III–IV completely bristle-less. (Remark: In one male within the sample of 13 paratypes the right tibia I apparently is a regeneration, and bears only 4 pairs of ventral bristles). – Opisthosoma oval, dorsally completely covered with a scutum (photos 7, 10), epigaster not scutate (photos 8, 11). – ♂-pedipalpus (figs. 15–18): Tibia with two longer apophyses, the retrolateral with slender tip with ventral hump running from prolateral side medially, conductor well developed, embolus describing a semicircle. – Epigyne/vulva (figs. 19–21) as in diagnosis. Glandular appendage antero-laterad, as long as fertilisation duct.

**Relationships:** See *O. loriot* n. sp.

**Distribution:** Laos, Luang Prabang.

***Otacilia vangvieng* n. sp.** (figs. 22–25, photos 17–20)

**Etymology:** The species is named according to the type locality, Vang Vieng; nomen in apposition.

**Material:** Laos, Vientiane Prov., w Vang Vieng, Tham Pou Kham, 260 m, N18°55.549', E102°23.734', in front of limestone cave, leaf litter, sieving, P. JÄGER & F. STEINMETZ leg. 13. III. 2007, holotype ♂, SMF.

**Diagnosis** (♂; ♀ unknown): Two cheliceral bristles, anterior median eyes smaller than the anterior lateral eyes, prosoma medium grey, legs distinctly annulated, opisthosoma dorsally dark grey, ventrally light grey, no light patch above spinnerets (photos 17–20). Leg IV > I. Pedipalpus (figs. 22–25): RTA triangular with distal bristle and basal ventral hump, dorsal tibial apophysis short and narrow, conductor long, more than half the length of the tegulum.

**Description** (♂):

Measurements (in mm): Body length 2.0, prosoma: Length 1.0, width 0.85; leg I: Femur 1.1, patella 0.4, tibia 1.1, metatarsus 1.0, tarsus 0.5, tibia II 0.8, tibia III 0.57, tibia IV 1.0.

Colour (see the diagnosis, photos 17–20); spinnerets light grey like in the related species.

Prosoma 1.18 times longer than wide, profile not convex, hairs short, thoracic fissure short, eye field fairly wide, posterior row slightly recurved, posterior median eyes circular, anterior median eyes smaller than anterior lateral eyes. The basal cheliceral articles bear 2 thin bristles, fang long and slender, posterior margin of the fang furrow with 3 denticles which are close together. Labium slightly wider than long, gnathocoxae stout,

coxae IV not widely spaced by the sternum. – Legs long and slender, order IV/II/III/III, hairs indistinct. (The right leg I may be regenerated: It is colour-less, slightly shorter than the left leg I, and its bristles are shorter). All femora bear a dorsal bristle in the basal half. Leg I: Femur 4 long prolaterals, tibia pro/retroventrally 6/7, metatarsus 4 ventral pairs. Legs III–IV are bristle-less besides a single femoral bristle. – Opisthosoma oval, hairs short, completely covered with a dorsal scutum (photo 17), epigaster not scutate (photo 18). – Pedipalpus (figs. 22–25): Ventral femoral hump weakly developed, dorsal tibial apophysis slender, retrolateral tibial apophysis quite short, wide, and bearing a bristle, conductor very long, widened apically, embolus hidden in ventral view.

**Relationships:** In *O. bicolor* and *O. loriot* the tibial apophyses of the ♂-pedipalpus are longer and the conductor is shorter.

**Distribution:** Laos, Vang Vieng.

***Otacilia kao* n. sp.** (figs. 26–36, photos 21–29)

**Etymology:** „Kao“ is part of the name of the type locality; nomen in apposition.

**Material:** Thailand, Trat Prov., Gulf of Thailand, Koh Chang, (1) Hat Sai Kao, 48 m, N12°06'46.7", E102°16'15.2", forest at a stream, in foliage, fern and bushes, collected by hand by P. JÄGER & S. BAYER, leg. 30. X. 2009, holotype ♂, SMF; (2) 3 km S Hat Sai Kao, 37 m, N12°04'46.2", E 102°16'48.2", partly empty river bed, secondary forest, collected by hand at night, P. JÄGER & S. BAYER leg. 2. XI. 2009, paratype ♀, SMF.

**Remark:** Both sexes were collected in the same region but not in the same locality; therefore their conspecificity may be not quite sure.

**Diagnosis:** Opisthosoma not scutate in both sexes, two cheliceral bristles, anterior median eyes larger than anterior lateral eyes, medium grey, ventrally-laterally light grey. ♂-pedipalpus (figs. 26–27): Tibia with a single large retrolateral apophysis, tegular apophysis (= remnant of the conductor) straight, embolus strongly bent. Epigyne (figs. 28–29, 35, photo 29) with long oval receptacula seminis, vulva (fig. 30) distinguished from females of species described in this paper by obliquely longitudinal spermathecae (as in *Otacilia*. sp. indet. B, figs. 48–51); distance between copulatory openings equal to distance between copulatory openings and epigastric furrow; membranous sac more than two times longer than wide, anteriorly dilated. Glandular appendage much shorter than fertilisation duct anteriorad; wall of the receptacula seminis reticulate.

**Further characters:** Legs not annulated (photos 21, 26), posterior eye row straight to slightly procurved, anterior median eyes largest, chelicerae with a pair of anterior bristles (fig. 34), shape of the area of the tracheal spiracle triangular in females (fig. 36, photo 28).

## Description:

Measurements (in mm): ♂: Body length 3.3, prosoma: Length 1.4, width 1.2; leg I: Femur 1.5, patella 0.5, tibia 1.9, metatarsus 1.5, tarsus 1.2. ♀: Body length 4.1, prosoma: Length 1.8, width 1.4; leg I: Femur 2.35, patella 0.65, tibia 3.0, metatarsus 2.1, tarsus 1.65, tibia II 2.3, tibia III 1.4, tibia IV 2.4.

Colour (photos 21–28): Prosoma and legs light yellow to orange brown, opisthosoma medium to light grey, with a spot of white hairs above the spinnerets.

Prosoma 1.17 to 1.29 (♀) times longer than wide, almost smooth, cuticula finely scale shaped as in other congeners, anteriorly abruptly narrow as in other congeneric species, thoracic part slightly higher than the cephalic part (fig. 34), thoracic fissure well developed and long, eyes large, anterior median eyes distinctly largest, posterior median eyes smallest and spaced by their diameter, posterior row straight to slightly procurved (♀), chelicerae with strong paired anterior bristles (fig. 34, photos 23, 25), the anterior margin of the fang furrows bears 3 teeth, the posterior margin with 2 denticles close together (fig. 32). The labium is wider than long – Legs: Male (fig. 33) (only the right leg II is still existing): Femur with a dorsal bristle in the basal half and 3 prodistal bristles, tibia with 8 ventral pairs, metatarsus with 4 pairs. Most tarsal and metatarsal trichobothria are apparently rubbed off. Female: Order IV/II/III. Bristles: All femora a single dorsal one in the basal half, femur I prodistally 5 bristles, tibia I 11, metatarsus I 4 ventral pairs (fig. 33). Patellae bristle-less; III–IV: Only the dorsal femoral one. Metatarsal preening comb well developed. Tarsal claws toothed, claw tuft consisting of spatulate hairs. Tarsi I–II bear 2 long trichobothria and few short ones in the distal half, metatarsus I bears a long trichobothrium near its end and some short trichobothria. – Opisthosoma oval, hairs short, not scutate in both sexes but dorsally anterior-medially and epigaster leathery in the male (photos 21–22). Area of the tracheal spiracle (fig. 36, photo 28) triangular in female, fairly sclerotized, similar to the fossil species *Eohahnia ?succini* PETRUNKEVITCH 1958 (Hahniidae), see WUNDERLICH in Beitr. Araneol., 3 (2004: 1469: Fig. 66), colulus absent, few hairs in its position, anterior spinnerets stout, conical and close together, median spinnerets very large in the female and laterally depressed, posterior spinnerets long and slender. ♂-pedipalpus (figs. 26–27): Femoral outgrowth strongly bent, retrolateral tibial apophysis long, its tip bent to the cymbium, embolus also strongly bent, tegular apophysis blunt and straight. – Epigyne (figs. 28–29, photo 29) with long oval receptacula seminis, vulva: Fig. 30, with sclerotized „bubbles“ interpreted as remnants of fused furrows; see JÄGER & PRAXAYSOMBATH (2009: 34).

**Relationships:** In *O. paracymbium* n. sp. from China a dorsal opisthosomal scutum is absent, too, but the structures of the ♂-pedipalpus are quite different. Several other Chinese species – e. g. *O. linpan* HU & ZHANG 2011, *O. hengshan* HU & ZHANG 2011 – are related according to the paired cheliceral bristle and the structures of the bulbus but in these species the opisthosoma bears transverse bands at least in their posterior part, the shape of the pedipalpal tibial apophysis, of the embolus and of epigyne/vulva are different.

**Distribution:** Thailand: Koh Chang.

***Otacilia paracymbium* n. sp.** (figs. 37–40, photos 30–33)

**Etymology:** The species name refers to the existence of a paracymbium; nom. in apposition.

**Material:** China, Sichuan, Emei Shan, 750 m, in the field of a village near a stream, holotype ♂, P. JÄGER leg. 29. III. 1999, SMF.

**Diagnosis** (♂; ♀ unknown): Opisthosoma not scutate (photos 30–31), two cheliceral bristles (photo 32), anterior median eyes and anterior lateral eyes equal in size, medium grey, ventral-laterally light grey. ♂-pedipalpus (figs. 37–40, photo 33): Tibia with a large retrodorsal and 2 small retrolateral apophyses, cymbium with a strong retrobasal paracymbium which is bent retrolaterally (fig. 38, photo 33).

**Further characters:** Legs annulated (photo 31), posterior eye row fairly recurved.

**Description** (♂):

Measurements (in mm): Body length 4.5, prosoma: Length 2.1, width 1.8; leg I: Femur 2.15, patella 0.8, tibia 2.2, metatarsus 2.0, tarsus 1.0, tibia II 1.6, tibia III 1.15, tibia IV 1.9, metatarsus IV 2.0, tarsus IV 1.2.

Colour (photos 30–31): Prosoma medium brown, legs light to medium brown, annulated, femora I–II almost completely darkened, III–IV basally and distally, tibia I in the basal  $\frac{3}{4}$ , tibia III–IV basally and beyond the middle but yellowish near the end, similar metatarsus III–IV, opisthosoma medium grey, ventrally-laterally light grey; a spot of white hairs above the spinnerets.

Prosoma 1.17 times longer than wide, thoracic part slightly higher than the cephalic part, hairs rubbed off, thoracic fissure well developed. All eyes of about the same size, posterior row fairly recurved, posterior median eyes spaced by their diameter, slightly more than from the posterior lateral eyes. Chelicerae with a pair of anterior bristles each as in fig. 34. Labium slightly longer than wide, gnathocoxae without a ventral depression, coxae IV spaced slightly by the sternum. – Legs long, order IV/I/II/III, all femora bear a dorsal bristle in the basal half, I bears additionally 2 or 4 prodistal bristles, tibia I bears pro-/retroventrally 7/8 bristles, metatarsus I 4 pairs of ventral bristles. Legs III–IV bear a single dorsal femoral bristle. Preening comb of metatarsus III well developed. The tarsi bear spatulate hairs under the toothed claws like in the related species. Tarsal trichobothria long and in an irregular position, tarsus I bears a dorsal depression in the distal half which may bear a sensory organ and which has not studied more closely. Coxal organ of leg I large and elevated like in the remaining species which are treated in this paper. – Opisthosoma oval, scuta absent, hairs very short and indistinct, spinnerets short, colulus absent, area of the tracheal spiracle not triangular but curved. – Pedipalpus (figs. 37–40, photo 33): See the diagnosis. The cymbium bears a brush of hairs distally of the embolus which latter is slender and fairly short.

**Relationships:** See *O. kao* n. sp.. In the related species from China as well as in *O. luzonica* (SIMON 1898) from Luzon the opisthosoma bears white spots or bands, the ♂-opisthosoma bears a dorsal scutum and the structures of the ♂-pedipalpus are dif-

ferent, a paracymbium is absent. In *O. paracymbium* n. sp. (female unknown) the legs are also very long.

**Distribution:** China, Sichuan.

***Otacilia christae* n. sp.** (figs. 41–44, photos 41–44)

Derivatio nominis: The species honours CHRISTA DEELEMANN-REINHOLD and her contribution to the knowledge of the South East Asian spider fauna; nomen in genitive case.

**Material:** Laos, Luang Prabang Prov., SE Luang Prabang, Nam Khan, Xieng Ngeun Distr., Ban Keng Koung, 372 m, N.19°40'963", E.102°18'442". In village, at a house, by hand, P. JÄGER leg. 23. II. 2008, holotype ♂, SMF.

**Diagnosis** (♂; ♀ unknown): Opisthosoma ventrally-posteriorly (photo 42) with a large field of bristle-shaped setae. Two cheliceral bristles, anterior median eyes smaller than anterior lateral eyes, colour mainly orange, prosoma darkened marginally and laterally mainly in the anterior half, legs indistinctly annulated, opisthosoma dorsally brown orange, ventrally lighter. Pedipalpus (figs. 41–44): Tibia with a single retrolateral apophysis which is slender and bent hook-shaped, tegulum bearing a long apophysis which originates at the base of the embolus and is directed to the tibial apophysis, conductor reduced, embolus freely visible, long and bent.

**Description** (♂):

Measurements (in mm): Body length 2.2, prosoma: Length 1.2, width 0.95; leg I: Femur 1.3, patella 0.45, tibia 1.5, metatarsus 1.2, tarsus 0.6, tibia II 1.0, tibia III is lost, tibia IV 1.1.

Colour (photos 41–44): See the diagnosis.

Prosoma 1.26 times longer than wide, profile slightly convex, hairs indistinct, thoracal fissure short, eyes large, all about of the same size, anterior median eyes only slightly smaller than anterior lateral eyes, posterior row distinctly recurved, the relatively large posterior median eyes are spaced by only  $\frac{3}{4}$  of their diameter. The chelicerae bear 2 anterior bristles, fangs long and slender, posterior margin of the fang furrow with 2 denticles, labium wider than long, sternum slightly longer than wide. – Legs long, order I/IV/II/III, hairs short. All femora bear a single dorsal bristle in the basal half; bristles of leg I: Femur 4 prolaterally, tibia pro/retroventrally  $\frac{7}{8}$ , metatarsus 4 ventral pairs, legs III–IV bristle-less besides a dorsal femoral bristle. – Opisthosoma (it is slightly defect, deformed) oval, dorsally completely covered with a scutum, epigaster scutate. The posterior part of the opisthosoma (photo) bears ventrally a large field of long bristle-shaped setae. – Pedipalpus (figs. 41–44): See the diagnosis.

**Relationships:** We do not know any strongly related species. According to (a) the existence of long and strong ventral opisthosoma setae – a sexual-dimorphic character

like in *Abdosetae*? –, (b) the existence of a long tegular apophysis, (c) the absence of a second pedipalpal tibial apophysis, and (d) the absence of a conductor. *O. christae* is an outsider of *Otacilia* and may even be the member of an unnamed genus. The discovery of the unknown female may help to solve this question. – In *Abdosetae ornata* (DEELEMAN-REINHOLD 2001) from Borneo – described originally under *Otacilia* – the eyes are also large and long ventral opisthosomal setae exist but the position of these setae is more anterior, the thoracic part is distinctly raised in contrast to *christae*, a second pedipalpal tibial apophysis exists, and a large tegular apophysis is absent. Because of these differences the ventral opisthosomal setae appear more likely to us to be convergently developed in both taxa.

**Distribution:** Laos, Luang Prabang.

***Otacilia* sp. indet. A** (figs. 45–47, photos 45–49)

**Material:** Laos, Luang Prabang Prov., SE Luang Prabang, Nam Khan, Xieng Ngeun District; (a) Ban Keng Koung, 372 m, N.19°40'963", E.102°18'442", disturbed forest, valley, waterfall, dry stream bed, sieving and Winkler apparatus, P. JÄGER leg. 21.–23. II. 2008, 1♀, SMF.

**Diagnosis and short description** (♀): Receptacula seminis round; distance between the copulatory openings three times the distance between copulatory openings and epigastric furrow. Membranous sac widest medially, glandular appendage medium-sized, shorter than fertilisation duct (figs. 45–47). Colour: Figs. 45–49.

**Distribution:** Laos, Luang Prabang.

***Otacilia* sp. indet. B** (figs. 48–51, photos 34–40)

**Material:** Laos, Bolikhamsay Prov., Nam Kading National Protected Area, Tad Vang Fong Training Centre, secondary forest, leaf litter, bark of tree, foliage, by hand at night. P. JÄGER & L. NOPHASEUD leg. 23. III. 2011, 1♀ SMF.

**Diagnosis** (♀): Two cheliceral bristles, anterior median eyes larger than anterior lateral eyes, legs quite long and slender, prosoma and legs light to medium brown, legs not annulated, opisthosoma dorsally dark grey, ventrally medium grey, light spot above spinnerets absent, epigyne/vulva (figs. 48–51): Receptacula obliquely longitudinal (as in *O. kao* n. sp.) but with membranous sac three times longer than wide, and similarly wide along its entire length. Distance between copulatory openings slightly more than distance between copulatory openings and epigastric furrow; glandular appendage very short, much shorter than fertilisation duct.

**Description** (♀):

Measurements (in mm): Body length 4.5, prosoma: Length 1.8, width 1.5; leg I: Femur 2.3, patella 0.6, tibia 2.9, metatarsus 3.0, tarsus 1.7, tibia II 2.25, tibia III 1.4, tibia IV 2.35.

Colour (photos 34–40): See the diagnosis.

Prosoma 1.2 times longer than wide. Eyes: Posterior row straight, anterior median eyes distinctly largest, posterior lateral eyes distinctly larger than posterior median eyes. The chelicerae bear two bristles. Legs quite long and slender. Bristles of leg I: Femur a single dorsally and a row of 7 long prolateral ones, tibia ventrally 9/10, metatarsus 4 ventral pairs. Legs III–IV bear only a single short femoral bristle. Epigyne with sclerotized spheres/bubbles under cuticle (interpreted as remnants of fused furrows, see JÄGER & PRAXAYSOMBATH 2009: 34).

**Relationships:** In *O. paracymbium* n. sp. (female unknown) the legs are also quite long and slender but the anterior median eyes are smaller. *O. kao* n. sp. has a similar general bauplan of the internal duct system (longitudinal spermathecae, short glandular appendages, etc.).

**Distribution:** Laos, Bolikhamsay.

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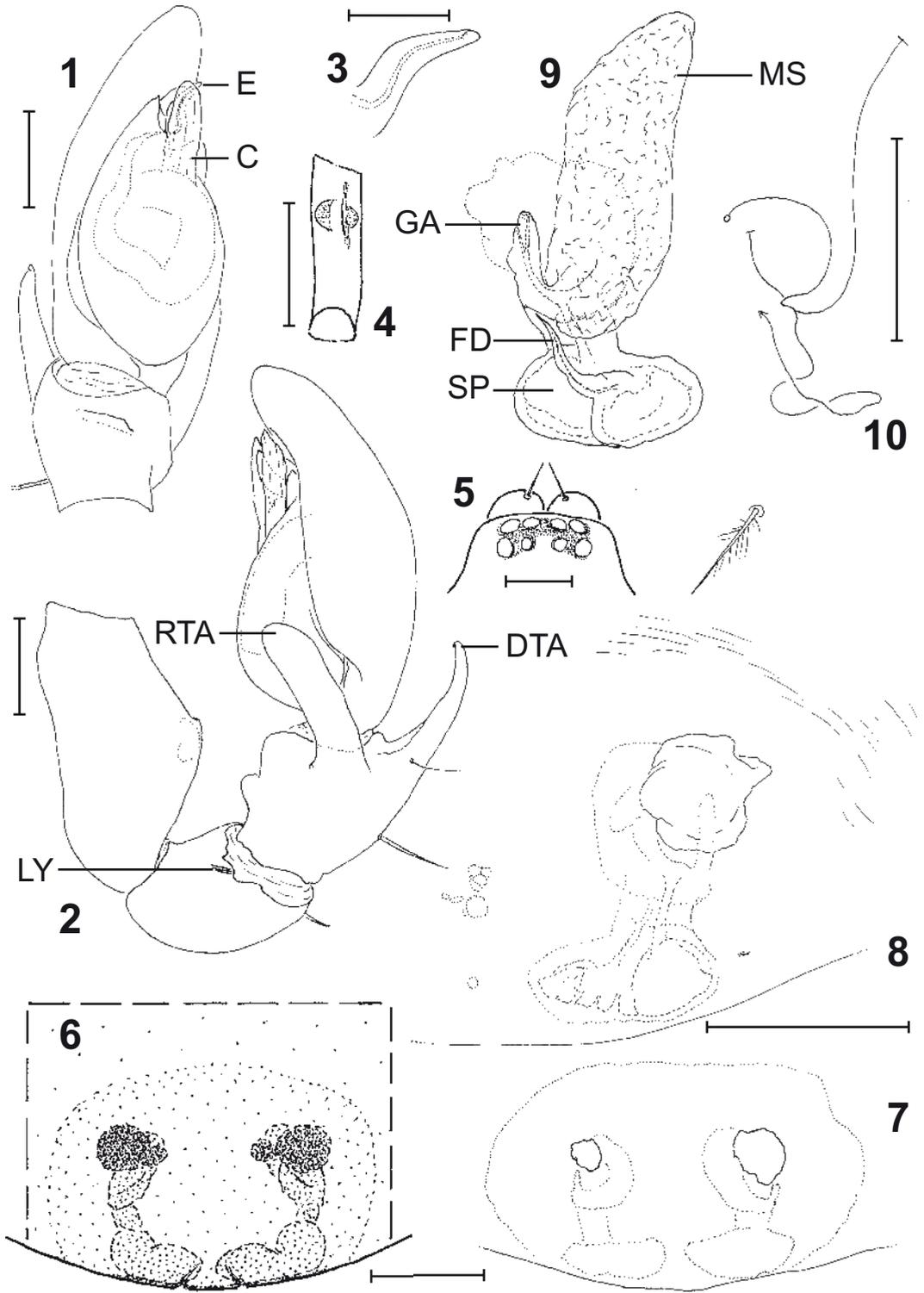
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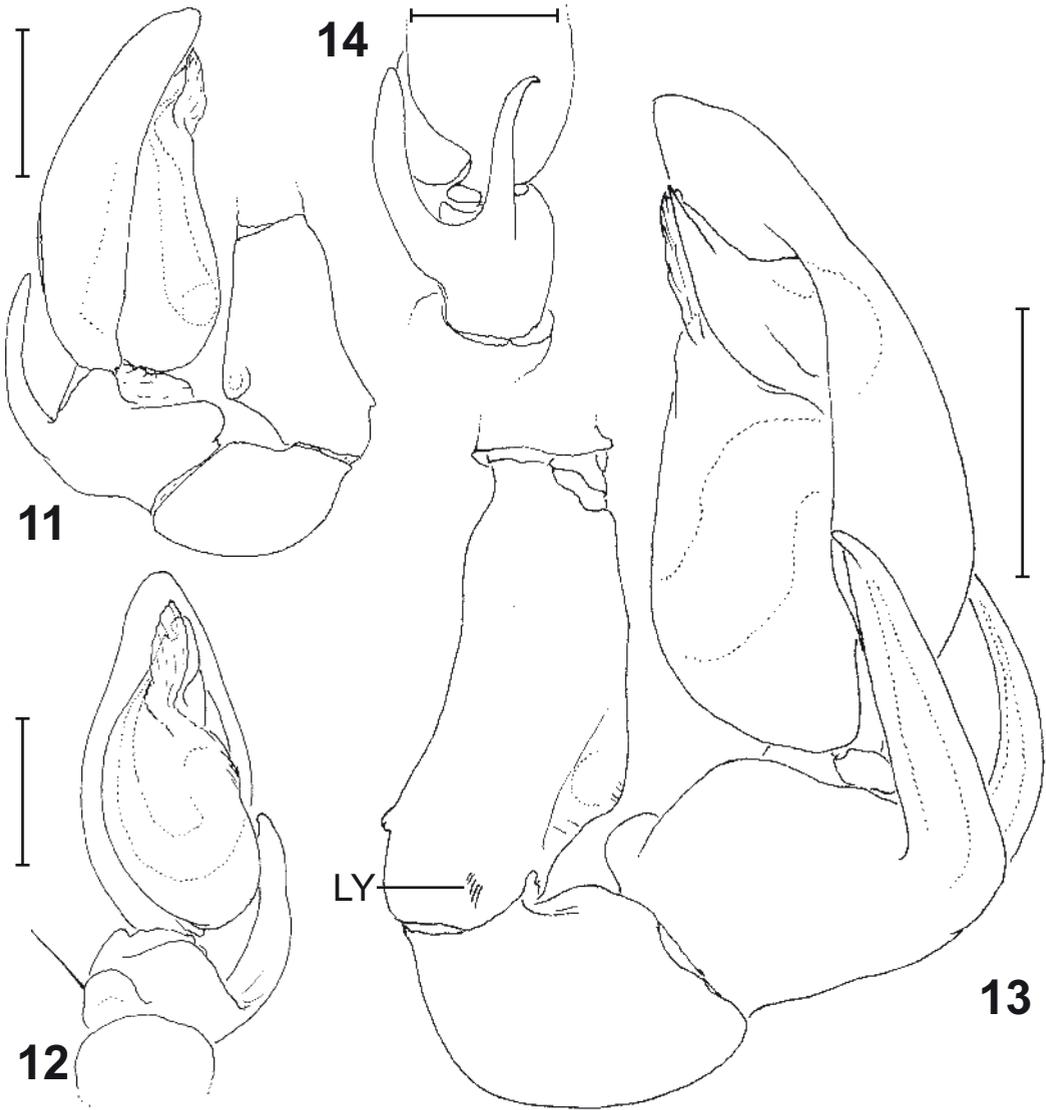
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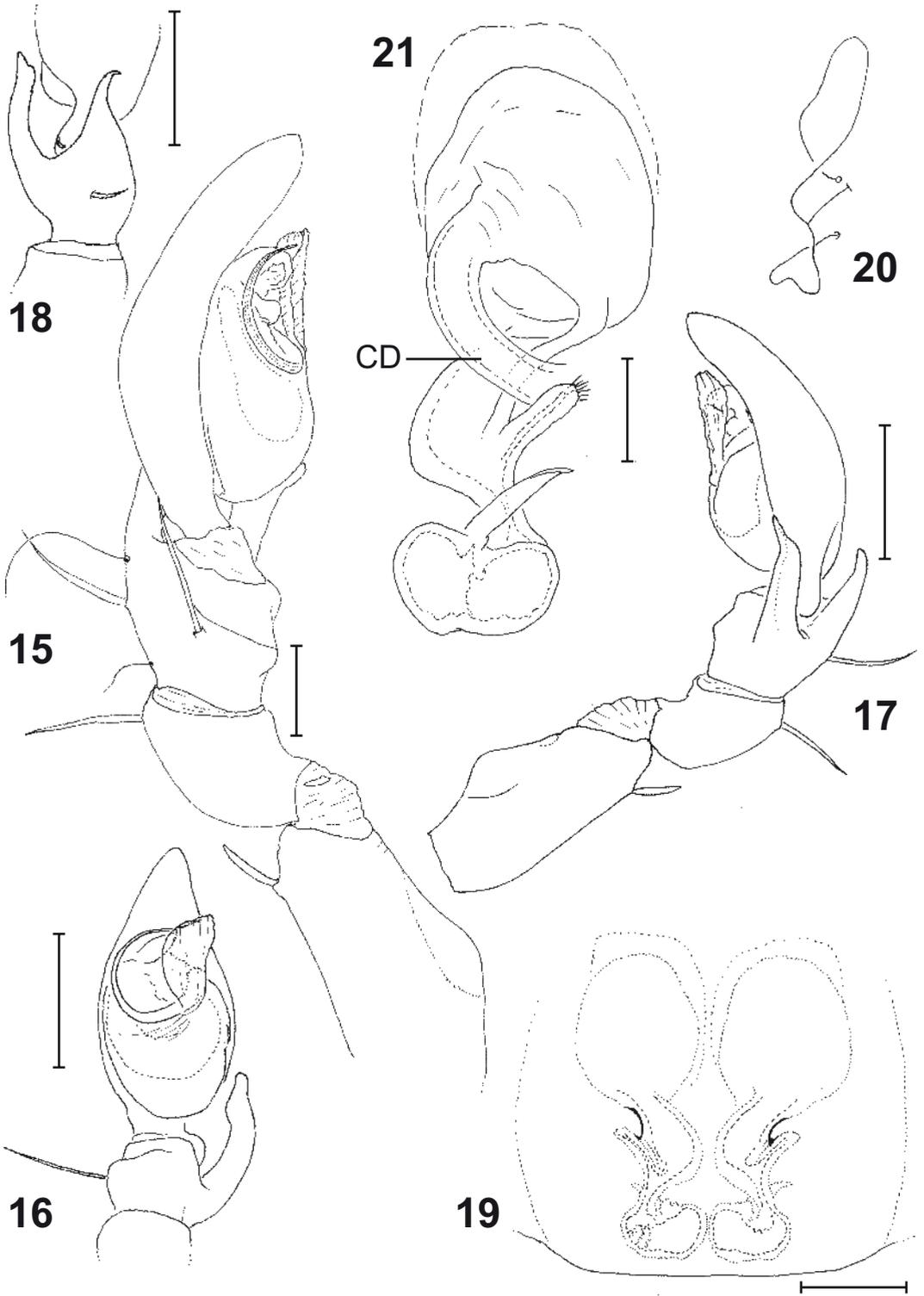


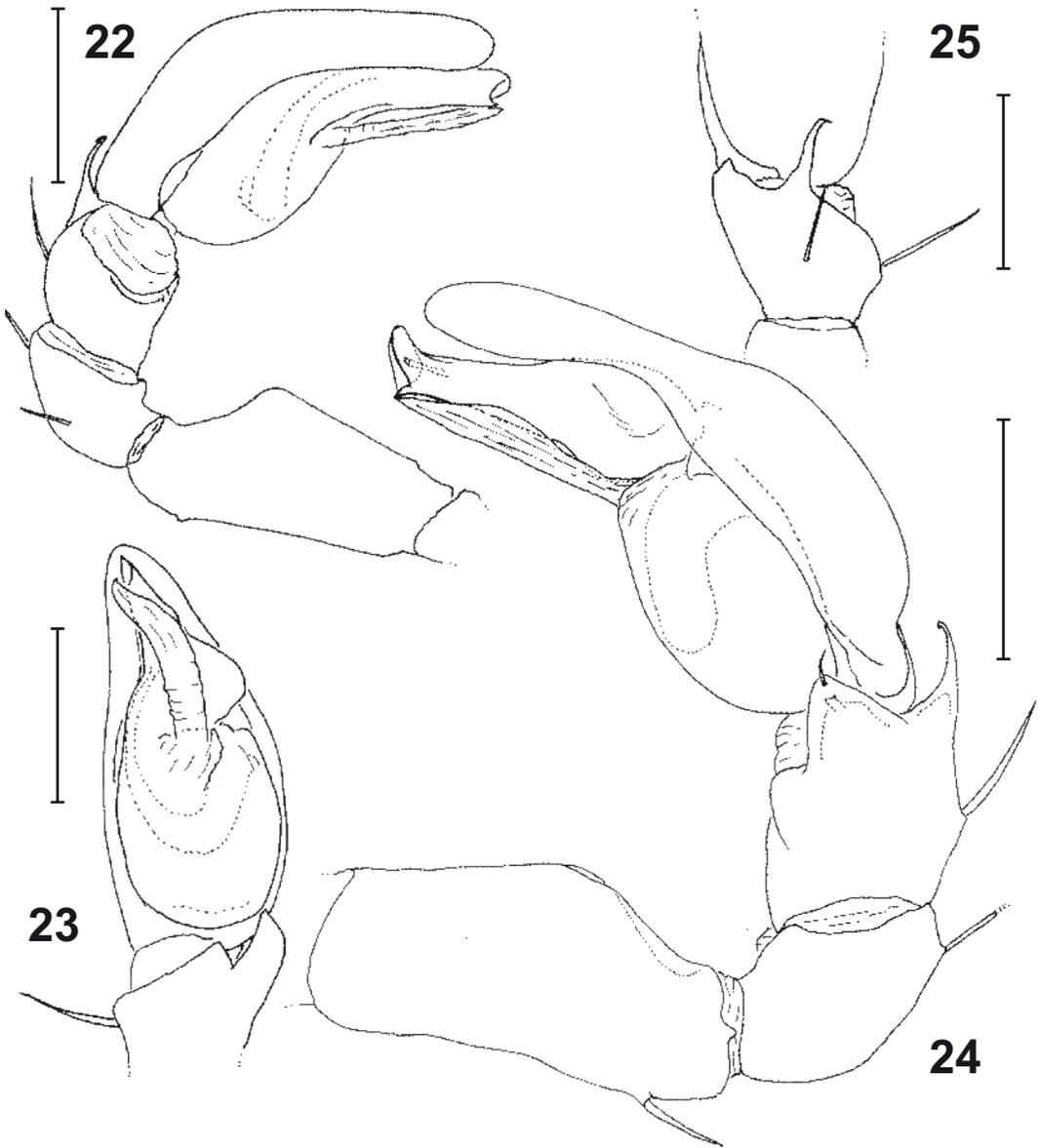


Legends to the drawings:

Figs. 1-10: *Otacilia bicolor* n. sp.; 1-2) ♂, ventral and retrolateral aspect of the left pedipalpus; 3) distal part of the embolus, 4) ♂, ventral aspect of the left pedipalpal femur; 5) ♂♀, dorsal aspect of the anterior part of the prosoma; 6-8) ♀, epigyne ventral (the few hairs are not drawn; one feathery hair is shown; 9) left half of the vulva, dorsal view; 10) schematic course of the internal duct system. – C = conductor, E = embolus, DTA = dorsal tibial apophysis, FD = fertilisation duct, GA = glandular appendage, LY = lyriform organ, MS = membranous sac, RTA = retrolateral tibial apophysis, SP = spermatheca. Scale bars (in mm): Figs. 1-2, 8-10: 0.1, 3: 0.05, 4-6: 0.2.

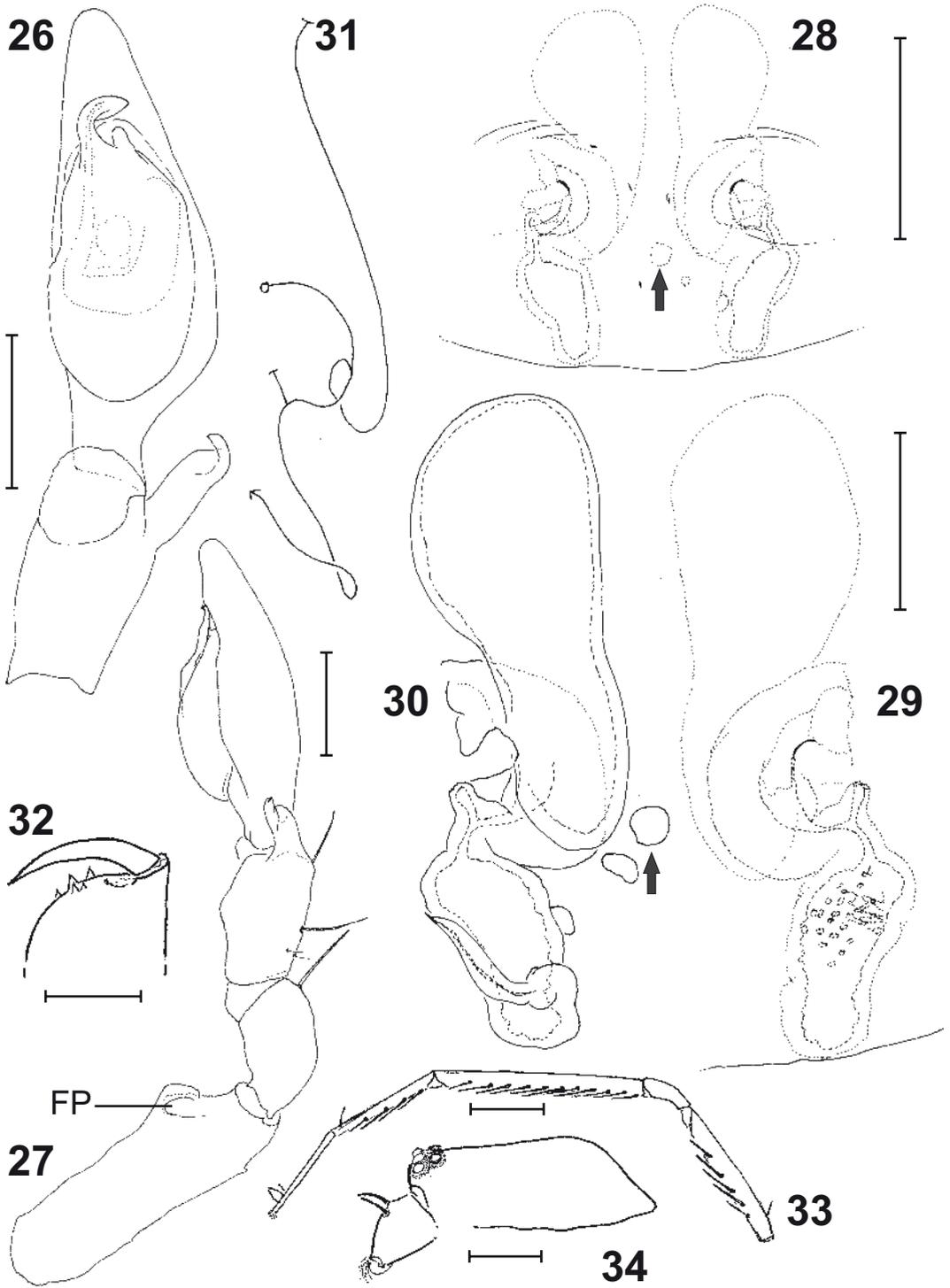
Figs. 11-14: *Otacilia loriot* n. sp., ♂; 11-13) prolateral, ventral and retrolateral aspect of the left pedipalpus; 14) dorsal aspect of the left pedipalpal tibia; scale bars 0.2.

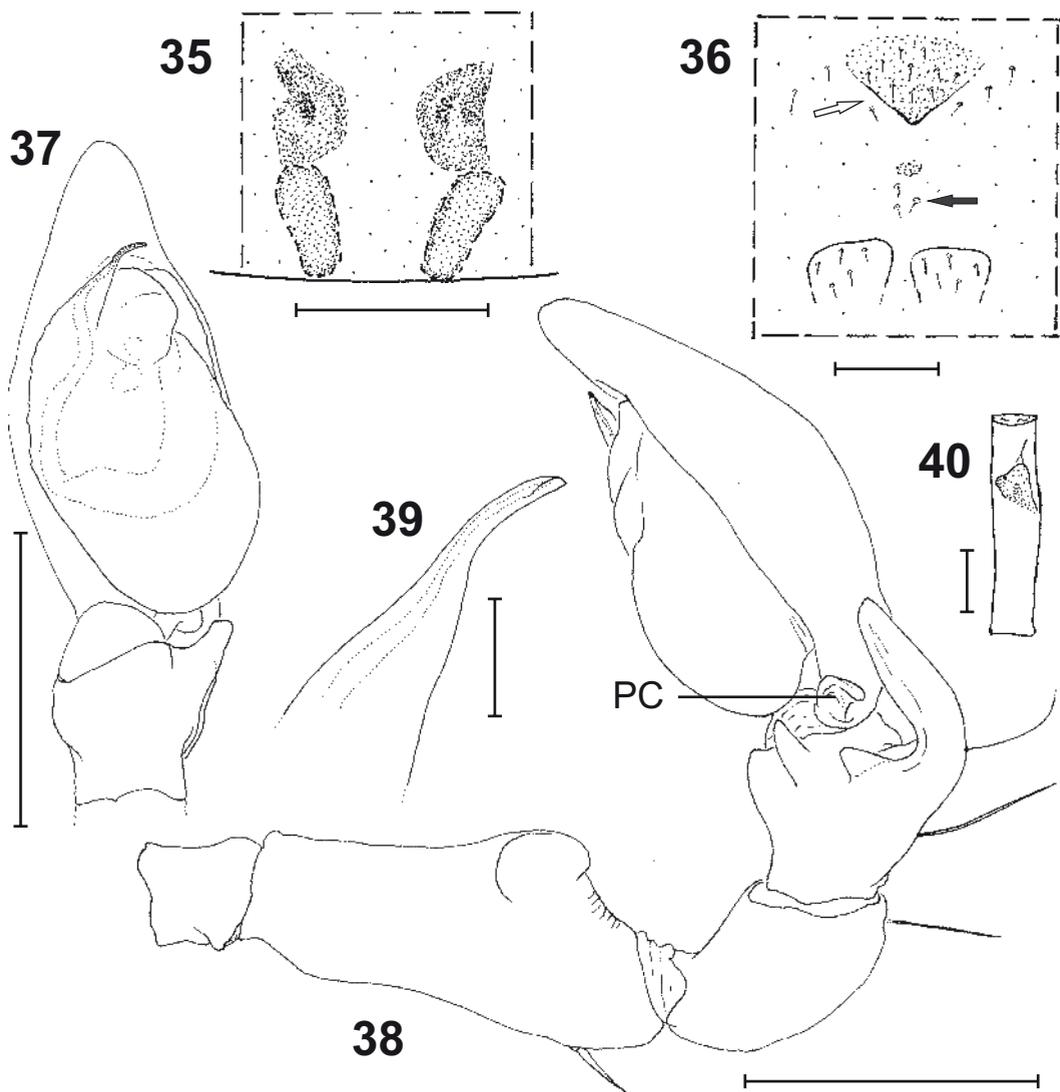




Figs. 15-21: *Otacilia namkhan* n. sp.; 15-17) prolateral, ventral and retrolateral aspect of the left ♂-pedipalpus; 18) ♂, dorsal aspect of the left pedipalpal tibia; 19) ♀, epigyne/vulva, ventral view; 20) schematic course of the internal duct system ventral; 21) dorsal aspect of the left half of the vulva. – CD = copulatory duct. Scale bars: Figs. 15, 19-20: 0.1, 16-18: 0.2, 21: 0.05.

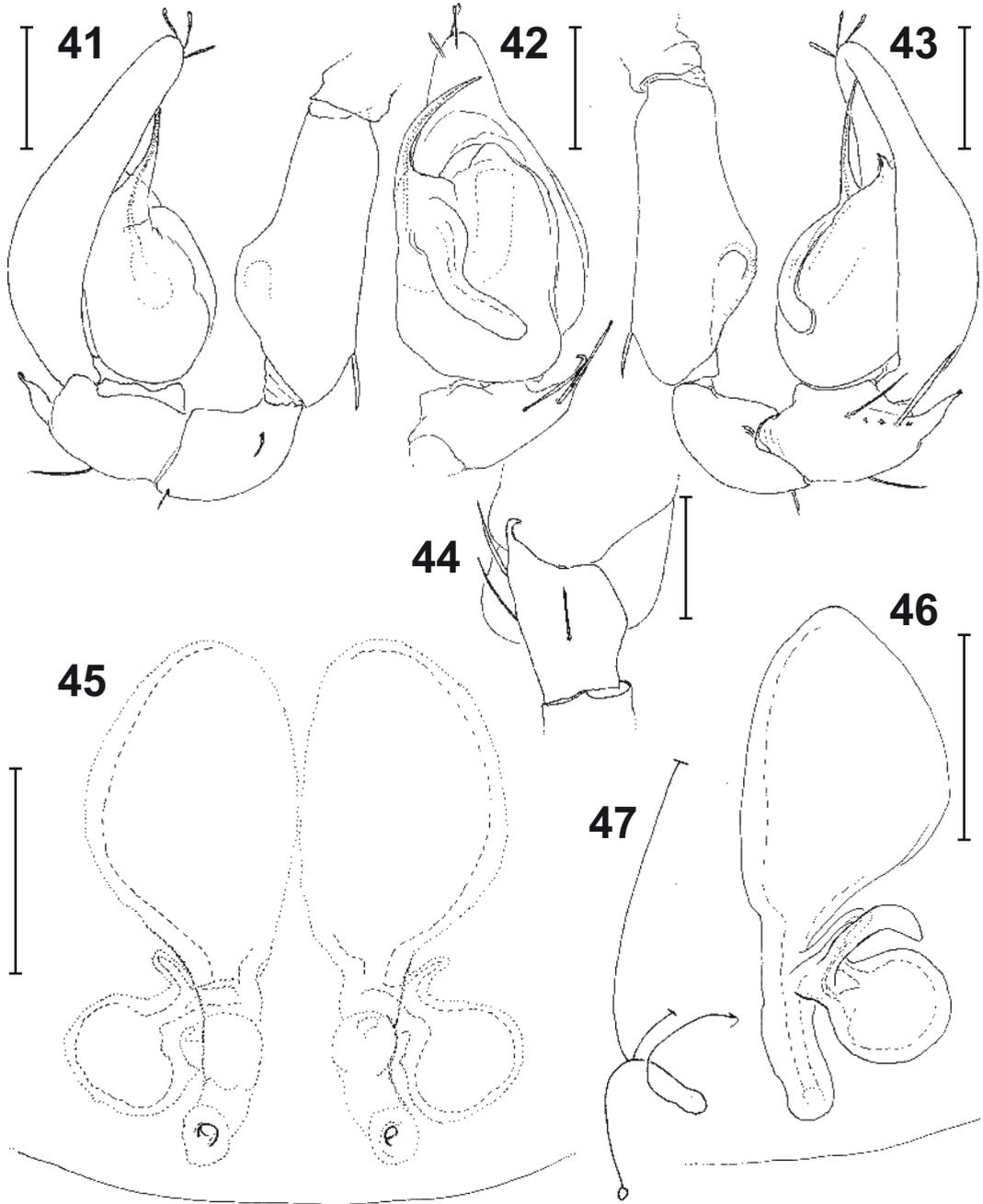
Figs. 22-25: *Otacilia vangvieng* n. sp., ♂; 22-24) prolateral, ventral and retrolateral aspect of the left ♂-pedipalpus; 25) dorsal aspect of the left pedipalpal tibia. Scale bars 0.2.

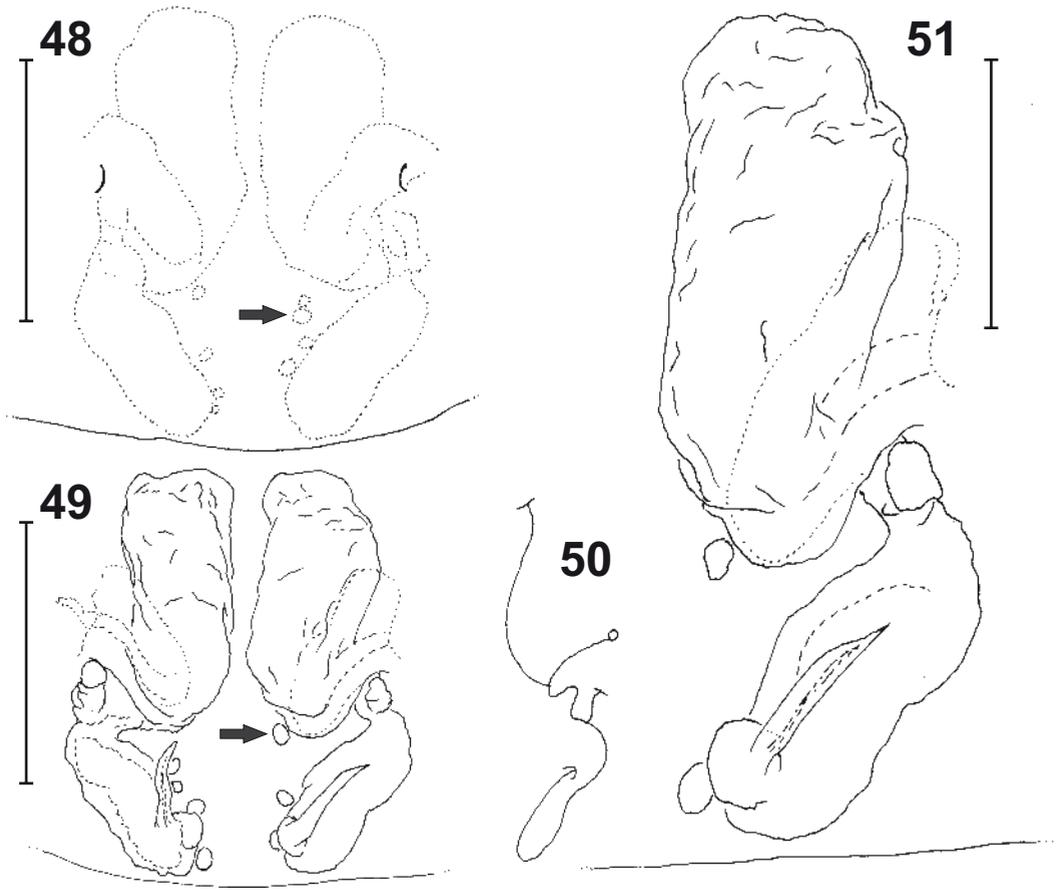




Figs. 26-36: *Otacilia kao* n. sp.; 26-27) ventral and retrolateral aspect of the left ♂-pedipalpus; 28-29) Epigyne, ventral. 30) ♀, vulva; the black arrows point to the sclerotised bubbles; 31) schematic course of the internal duct system, dorsal; 32) ♀, ventral aspect of the distal part of the left chelicera; 33) ♀, prolateral aspect of the right leg I; 34) ♀, lateral aspect of the prosoma; 35) epigyne ventral; 36) ♀, triangular area of the tracheal spiracle (light arrow) in front of the field of the spinnerets which is expanded. The black arrow indicates the area of the colulus (a colulus is absent). Only few hairs are drawn. – F = femoral process. Scale bars: Figs. 26-28, 32, 35-36: 0.2, 29-31: 0.1, 33: 1.0, 34: 0.5.

Figs. 37-40: *Otacilia paracymbium* n. sp., ♂; 37-38) ventral and retrolateral aspect of the left pedipalpus; 39) tip of the embolus, ventral; 40) ventral aspect of the left pedipalpal femur. PC = paracymbium. Scale bars: Figs. 35-36, 40: 0.2, 37-38: 0.5, 39: 0.05.





Figs. 41-44: *Otacilia christae* n. sp., ♂; 41-43) prolateral, ventral and retrolateral aspect of the left pedipalpus; 44) dorsal aspect of the left pedipalpal tibia. Scale bars 0.2.

Figs. 45-47: *Otacilia* sp. indet. A, ♀ from Laos, Ban Keng Koung; 45) epigyne, ventral; 46) vulva, right half, dorsal; 47) schematic course of the internal duct system, dorsal. Scale bars: 0.1.

Figs. 48-51: *Otacilia* sp. indet. B, ♀ from Laos, Tad Vang Fong; 48) epigyne ventral; 49, 51) vulva, dorsal; 50) schematic course of the internal duct system, dorsal. The arrows point to the sclerotized bubbles (see the text). Scale bars: Figs. 48-50: 0.2, 51: 0.1.

**A REVIEW ON THE SPIDER GENUS *ARGIOPE* AUDOUIN 1826 WITH SPECIAL EMPHASIS ON BROKEN EMBOLI IN FEMALE EPIGYNES (ARANEAE: ARANEIDAE: ARGIOPINAE).**

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„While a published monograph may appear to provide definite solutions, and readers infer that the author is certain of his findings, more likely the work only identifies and illuminates tantalizing problems. Especially to those with no experience with taxonomic problems, a published monograph has an unfortunate aura of authority.“ Herbert Levi (1983: 256)

**Abstract:** *Argiope* species are revised with special emphasis on broken male emboli in female epigynes. Broken emboli proved suitable for matching conspecifics and recognising cryptic species in species swarms with similar females. Material of 47 species from 63 countries was included in this study: 92 males, 834 females and 316 broken emboli were examined. Broken emboli are documented for 32 species, those of 27 species are illustrated for the first time, those of 8 species have been known and illustrated before. 19 species are illustrated by means of in situ emboli, 9 of them are not recorded as broken emboli. In total, emboli of 41 species are illustrated. The male of *A. luzona* could be confirmed by means of broken emboli stuck in the epigyne.

One new species is described: *Argiope hinderlichi* spec. nov. (female; Laos, Lak Sao, Nong Khiao). The male of *Argiope jinghongensis* Yin, Peng & Wang 1994 is redescribed and the female is described for the first time. *Argiope doleschalli* Thorell 1873 and *Argiope bivittigera* Strand 1911 are removed from the synonymy of *A. reinwardti* Doleschall 1859. *A. crenulata pictula* Strand 1911 is removed from the synonymy of *A. modesta* Thorell 1881 and raised to species rank. *A. boetonica* Strand 1915 is removed from the synonymy of *A. appensa* (Walckenaer 1841) and considered a junior synonym of

*A. pictula*. *A. squallica* Strand 1915 is removed from the synonymy of *A. brunnescentia* Strand 1911. *Argiope submaronica* Strand 1916 is removed from the synonymy of *A. argentata* (Fabricius 1775), and *A. savignyi* Levi 1968 is recognised as junior synonym of *A. submaronica*. Further, the following synonymies are proposed: *Argiope bruennichi nigrofasciata* Franganillo 1910 and *Argiope acuminata* Franganillo 1920 as junior synonyms of *A. bruennichi* (Scopoli 1772), *Argiope lobata retracta* Franganillo 1918 as junior synonym of *A. lobata* Pallas 1772, *Argiope papuana* Workman 1900 as junior synonym of *A. picta* L. Koch 1871. *Argiope avara angulicosta* Strand 1911, *A. a. ocelligera* Strand 1911, *A. a. tristipes* Strand 1911, *A. aetherea tangana* Strand 1911 and *A. lihirica* Strand 1913 are removed from the synonymy of *A. aetherea* and placed in the synonymy of *A. brunnescentia* Strand 1911. *Argiope aetherea keyensis* Strand 1911 is removed from the synonymy of *A. aetherea* and placed into synonymy of *A. modesta* Thorell 1881. *Argiope maja* Bösenberg & Strand 1906 is misplaced, transferred to the genus *Nephila* Leach 1815 and proposed as junior synonym of *Nephila clavata* L. Koch 1878. *Argiope thai* Levi 1983 was misplaced and is transferred to the genus *Cyrtophora* Simon 1864 and proposed as junior synonym of *C. moluccensis* (Doleschall 1857).

In most cases distribution ranges of species were confirmed by the material included in this study. *Argiope chloreis* Thorell 1877 is recorded as first record for Laos and northernmost record for the species, *A. jinghongensis* from Thailand and Laos for the first time. *A. comorica* Bjørn 1997 is recorded the second time in general and the first time from the Island Mayotte, a female close to *A. tapinobata* Bjørn 1997 is recorded from Namibia. The record of *A. pulchella* from Sumbawa extends its range farther east.

A map is provided with records of the new species, new Asian country records and Asian species previously not included in large revisions. Habitus photos of 41 species are provided in the Senckenberg online database, 9 of which are included in this paper.

**Key words:** Taxonomy, new species, first description, first record, Southeast Asia, Indochina, Greater Mekong Region, Africa, Americas, Europe

## INTRODUCTION

*Argiope* species are famous for their colourful opisthosomal patterns of the showy females and the strong sexual size and colour dimorphism (Levy 1983). *Argiope* species are also known for their sexual cannibalism: in *Argiope bruennichi* (Scopoli 1772) no male survived a second insertion (Schneider *et al.* 2006), and in *A. aurantia* Lucas 1833 the heart beat of the male stopped when the second palp was inserted resulting in a whole-body-plug of the male (Foellmer & Faibairn 2003). Ghione & Costa (2011) found in experiments with *Argiope argentata* (Fabricius 1775) that male emboli break without a female attack. During the copulation process emboli break usually on a predetermined breaking point (crack) and emboli or parts of them plug copulatory openings. Bjørn (1997) suggested that the breaking off may be an active process as haemato-

dochal zones were involved. Whether broken emboli are a real barrier for a potential second male in all species was not clear, as in some openings several emboli were found (Bjørn 1997, present study). Nessler *et al.* (2006) and Uhl *et al.* (2007) showed in macerated female copulatory organs, that the very distal embolic tip is plugging the copulatory duct in *Argiope bruennichi*. Similarly plugging was found by Grasshoff (1970a: fig. 8c; 1970b: fig. 8c; 1984: figs 18, 21, 25, 27) for *Kilima conspersa* Grasshoff 1970, *Larinia chloris* (Audouin 1826) and species of the genus *Caerostris* Thorell 1868 respectively. Paternity success in *Argiope bruennichi* was increased by plugging the female's insemination duct (Nessler *et al.* 2006, 2007). Moreover, Nessler *et al.* (2007) showed that the spur of the median apophysis promotes the breakage of the embolus tip. For a review on mating plugs (also including broken emboli) in spiders in general see Uhl *et al.* (2010).

No matter whether or in which way emboli represent an effective barrier for a subsequent successful insertion of a male or not, broken emboli provide a good taxonomic help to identify a female spider when its colouration has faded (Levi 2004) or when it belongs to a group with similar females and only weak diagnostic characters. An excellent example is the American species pair *Argiope blanda* O. Pickard-Cambridge 1898 and *A. argentata* (Fabricius 1775), whose males are clearly identified by the absence or presence of an embolic pendant (Figs 115, 119, 123, 126, 131, 152–153, 157). Broken emboli can also help matching conspecifics when male and female are not found together in one web or in copula (Levi 1983, Bjørn 1997, present study). They provide in most cases good evidence whereas colour and size dimorphism makes it difficult to match male and female of the same species (Strand 1915: 217). Additionally, broken emboli can be illustrated in the case the male sex is not known which again can help in future identification of the male. In one case of the literature investigated male and female were matched together (Yin *et al.* 1997: figs 19a–i, sub *Argiope versicolor*), but the broken embolus illustrated betrayed that the broken embolus and the embolus in situ were different and thus the assumed matching was wrong. Broken emboli were already used by Grasshoff (1984: 729) to match male and females in the genus *Caerostris*.

The genus *Argiope* is distributed worldwide with currently 85 valid species with a centre of its diversity in Southeast Asia including New Guinea and adjacent islands (44 spp.). From other regions distinctly fewer species are known: Australia: 15 spp., Africa: 11 spp., Americas: 8 spp., Europe: 3 spp. (synonyms of *A. bruennichi* and *A. lobata*), Central Asia 1 sp. Three further species have exceptionally large distribution ranges: *A. trifasciata* (Cosmopolitan), *A. bruennichi* (Palaeartic), and *A. lobata* (Old World) (Platnick 2011).

The most fundamental revision on *Argiope* was published by Levi (1983) on Western Pacific representatives reporting on and providing an identification key for 49 species and listing 55 new synonymies. Bjørn (1997) revised African *Argiope* species, and, again, Levi (2004) American representatives. Compilations on Chinese and Japanese species were published by Yin *et al.* (1997), Song *et al.* (1999) as well as Chikuni (1989) and Tanikawa (2009) respectively, those on Indian species by Tikader (1982) and Sebastian & Peter (2009), from Philippines by Barrion & Litsinger (1995). Recently new species were described by Levi (2004) from Brazil and Argentina, by Motta & Levi (2009) from Brazil, and by Ono (2010) from Vietnam. Jäger & Praxaysombath (2009, 2011) described and re-collected *A. dang* from Laos and reported *A. pulchella* Thorell 1881 (illustrating the variation of copulatory organs), *A. aemula* (Walckenaer 1842), and *A. catenulata*

(Doleschall 1859) from Laos. Recently, Cheng *et al.* (2010) published a first molecular approach on few *Argiope* species focusing on evolution of web decoration.

In the present paper, initially *Argiope* specimens collected by the author from Laos and Thailand were reviewed. Additionally, the collection deposited in the Senckenberg Research Institute, including unidentified and identified material, was examined. One new species is recognised and described. Species are commented and illustrated especially by means of broken emboli. New country records for species are listed.

A marginal aspect of this paper is to stress the importance of Natural History collections for systematic studies. Therefore an evaluation of the material examined is provided in the results chapter. Scientific collections received in the near past less and less attention in political terms, i.e. financial support. This paper demonstrates the necessity of not only maintaining these but actively working on this material and reviewing it after main revisions of taxa have been done.

According to Levi's (1983: 256) warning and advice (see leitmotif above) some taxonomic problems may be solved in this paper, but some problems can be just indicated. Future work must continue finding answers to open questions.

## Material and Methods

Adult spiders were considered with only few exceptions, i.e., when immature spiders could be unambiguously identified. Spiders are preserved in 70% denatured ethanol. Female copulatory organs were dissected and observed in 96% lactic acid, if necessary, i.e. if an illustration of a new species was made or to investigate whether broken tips of emboli were present. Broken emboli were removed from epigynes using ultra-thin pins fixed to wooden sticks. They were drawn in a Boveri dish with white artificial sand to choose the best orientation. Usually the embolus was drawn in a mesal view as in an intact palp. Sometimes it was necessary to shift the embolus slightly to show important details. To allow a better comparison especially with illustrations in Levi (1983, 2004) and Bjørn (1997) as well as within the present paper all right emboli were mirrored and all emboli are shown to the same scale. In some cases the tip of the broken embolus is shown in detail and with a higher magnification to allow unambiguous identification with particular details. In few cases emboli could only be removed by damaging the epigyne. This was the case in species with a long scapus (e.g., *A. aurantia*, *A. protensa*) or when only a very small part of the embolus was left behind (e.g., *A. aemula*). These procedures were made exclusively with non-type material. Only entire broken emboli were recognised as such. It was not searched for broken tips in every epigyne (cf. Uhl *et al.* 2007), which would have exceeded the scope of the study and which have not been possible in every case.

Style of description follows Jäger & Praxaysombath (2009: *Argiope dang*), terminology Levi (1983) and Bjørn (1997). Eye measurements are according to Bjørn (1997: fig. 3). Localities in the material lists are ordered according to continents, countries and in some cases to provinces or similar entities. Numbers behind the SMF collection number (Lxx) referring to Laotian localities and to the numbering in Jäger (2007: L1–L36) and Jäger & Praxaysombath (2009: L37–L78; 2011: L79–L103). Collection

numbers are SMF numbers, belonging to the regular Senckenberg collection. In some taxa, among these in Argiopinae, the Roewer collection was not included in the regular Senckenberg collections, but placed separately. These series are indicated as RIIxxxxx and will appear in the online database of Senckenberg (<http://sesam.senckenberg.de>) as 99xxxxx. Totals of material examined for each species is given in parentheses in the beginning of the material list. Material was generally identified by the author. Exceptions are either listed (e.g., Roewer det., Strand rev.) or self-explanatory, for instance in cases of original type material. Photos could not be provided in the manuscript for all species and are therefore uploaded to the online database of Senckenberg (<http://sesam.senckenberg.de>). Particular specimens are marked behind the collection numbers with “www”. Photos are displayed in the database under “General Data” (“Allgemeine Daten”). In general, Senckenberg material was examined. In some cases material from other collections was included. In the case of *A. comorica* and *A. ranomafanensis* the material from Tervuren Museum was on loan by Manfred Grasshoff and therefore included in this review. Type material of the difficult *aetherea*-group from Chinese collections was borrowed to check details in a direct comparison of specimens.

Abbreviations:

ALE — anterior lateral eyes  
AME — anterior median eyes  
AW — anterior width of dorsal shield of prosoma  
OL — opisthosoma length  
OW — opisthosoma width  
PL — prosoma length  
PLE — posterior lateral eyes  
PME — posterior median eyes  
PW — prosoma width  
I–IV/XII — legs I–IV / months I–XII

Museum collections:

HNU — Hunan Normal University, Changsha, China (X.J. Peng)  
MHBV — Museum of Hebei University, Baoding, China (F. Zhang)  
NMID — National Museum of Ireland, Dublin, Ireland (N. Monaghan, M. Nolan)  
NMNH — National Museum of Natural History, Leiden, Netherlands  
(J. Miller, K. van Dorp)  
RMCA — Royal Museum for Central Africa, Tervuren, Belgium (R. Jocqué)  
SKU — Songkhla University, Hat Yai, Thailand (B. Ponksee)  
SMF — Senckenberg Research Institute, Frankfurt, Germany (P. Jäger)

## Results

In the arachnological collections of the Senckenberg Research Institute 41 *Argiope* species in more than 400 series were available, additional 6 species were examined from other collections. Ninety-two males, 834 females, and 316 broken emboli have been examined which originate from 63 countries. Thus, approximately 50% of the described *Argiope* species worldwide (Platnick 2011) are found in the SMF collection. Ninety-two series (< 25%) of the catalogued part of the SMF collection had to be newly determined, i.e. either specimens were misidentified or the nomenclature had to be updated. Additionally, three species represented only by immatures (*A. florida*, *A. doboensis*, *A. ericae*) and several species from original literature and descriptions were included in this study. The oldest record of the Senckenberg collections concerning the genus *Argiope* has been collected in 1872 (Karl von Fritsch & Rein leg. in Casablanca, Morocco, *A. bruennichi*). The arachnological collections in Senckenberg have been established in 1834 (Wider's collection from Germany, Odenwald including type material).

Table 1: Species treated in this paper with number of adult males and females, broken emboli and list of countries (Note: doubtful records are not included in the country list, immatures are listed in parentheses only when these were the only specimens examined; Islands such as Canary Islands are listed as zoogeographically independent entities from their political countries). \*epiynes of only few specimens were investigated for broken emboli.

Species	males	females	emboli	countries
<i>Argiope manila</i>	-	5	4	Philippines.
<i>Argiope aemula</i>	3	24	9	India. Sri Lanka. Japan. China. Laos. Indonesia: Sumatra, Java, West Nusa Tenggara, Sulawesi, Aru Islands. Philippines. Papua New Guinea.
<i>Argiope catenulata</i>	1	13	-	Laos. Indonesia: Sumatra, Sulawesi, West Nusa Tenggara, Papua Province.
<i>Argiope bivittigera</i>	-	6	8	Indonesia: Maluku Islands.
<i>Argiope reinwardti</i>	-	5	6	Indonesia: Java.
<i>Argiope doleschalli</i>	-	1	1	Indonesia: Maluku Islands.
<i>Argiope</i> sp.	-	1	2	Indonesia: Maluku Islands.
<i>Argiope boesenbergi</i>	-	5	2	Japan.
<i>Argiope amoena</i>	1	18	23	Japan.
<i>Argiope magnifica</i>	-	6	5	Papua New Guinea.

Species	males	females	emboli	countries
<i>Argiope bruennichi</i> *	5	102	3	Germany. Switzerland. France. Spain. Italy. Hungary. Croatia. Macedonia. Greece. Azores. Morocco. Lebanon. Iran. Japan.
<i>Argiope aurantia</i> *	1	37	4	USA. Mexico. El Salvador.
<i>Argiope lobata</i>	2	56	7	France. Portugal. Spain. Canary Islands. Italy. Hungary. Greece. Israel. Syria. Iran. India. Senegal. Tanzania.
<i>Argiope australis</i>	1	18	11	Cape Verde Islands. Gaboon. Tanzania. Namibia. South Africa.
<i>Argiope sector</i>	12	20	20	Saudi Arabia. Tunisia. Egypt. Senegal. Cape Verde Islands.
<i>Argiope</i> sp. cf. <i>tapinobata</i>	-	1	1	Namibia.
<i>Argiope coquereli</i>	-	7	6	Madagascar.
<i>Argiope flavipalpis</i>	1	34	3	Ivory Coast. Cameroon. Congo. Kenia. Ruanda. Tanzania
<i>Argiope ranomafanensis</i>	-	6	-	Madagascar.
<i>Argiope protensa</i>	1	8	6	Australia.
<i>Argiope trifasciata</i>	14	21	2	USA. El Salvador. Venezuela. Peru. Brazil. Argentina. Haiti. Balkan. Azores. Canary Islands. Senegal. Egypt. Ruanda. Tanzania.
<i>Argiope florida</i>	-	- (1)	-	USA.
<i>Argiope doboensis</i>	-	- (1)	-	Indonesia: Maluku Islands.
<i>Argiope chloreis</i>	-	1	-	Laos.
<i>Argiope argentata</i>	14	73	109	USA. Mexico. Panama. Cuba. Lesser Antilles. Ecuador. Venezuela. Peru. Colombia. Honduras. Trinidad. Martinique. French Guyana. Brazil. Argentina.
<i>Argiope blanda</i>	-	9	12	Mexico. El Salvador.
<i>Argiope submaronica</i>	-	2	2	Brazil.
<i>Argiope ericae</i>	-	- (2)	-	Brazil.
<i>Argiope anasuja</i>	8	54	-	India. Maldives.
<i>Argiope minuta</i>	1	10	-	Japan.
<i>Argiope hinderlichi</i> spec. nov.	-	2	3	Laos.
<i>Argiope jinghongensis</i>	3	4	2	China. Laos. Thailand.
<i>Argiope aetheroides</i>	1	-	-	China.

Species	males	females	emboli	countries
<i>Argiope luzona</i>	1	7	8	Philippines.
<i>Argiope pulchella</i>	5	67	49	Bangladesh. Birma. Thailand. Laos. Indonesia: Sumatra, Java, West Nusa Tenggara.
<i>Argiope pulchelloides</i>	1	1	-	China.
<i>Argiope dang</i>	2	6	1	Laos.
<i>Argiope cameloides</i>	1	-	-	China.
<i>Argiope modesta</i>	-	13	2	Indonesia: Java, West Nusa Tenggara, Maluku Islands.
<i>Argiope pictula</i>	1	11	2	Indonesia: Sulawesi.
<i>Argiope appensa</i>	1	11	1	Philippines. Indonesia: Sulawesi. Palau. Micronesia. Papua New Guinea.
<i>Argiope brunnescentia</i>	-	37	1	Papua New Guinea.
<i>Argiope squallica</i>	1	-	-	Papua New Guinea.
<i>Argiope bougainvilla</i>	-	25	-	Papua New Guinea.
<i>Argiope aetherea</i>	3	20	-	Indonesia: Maluku Islands, Papua Province. Papua New Guinea. Australia.
<i>Argiope picta</i>	7	85	1	Indonesia: Maluku Islands, Papua Province. Papua New Guinea. Australia.
<i>Argiope comorica</i>	-	1	-	Comores.
Total	92	834	316	63

Females of *A. bruennichi* and *A. aurantia* were investigated for emboli only in few cases due to their hidden epigynal openings. Therefore these cannot be compared with others statistically. However, species with females exhibiting openly accessible epigynal depressions are generally comparable in terms of presence or absence of broken emboli. There are striking differences between species. Apart from the fact that broken embolus tips were difficult to detect, the presence of longer emboli is comparable. Females of species close to *A. aetherea* (with embolic pendant situated distant from embolus tip: *A. modesta*, *A. pictula*, *A. appensa*, *A. brunnescentia*, *bogainvilla*, *Aetherea*, *A. picta*), for instance, had only rarely broken emboli in their epigynes (7 in 203 females). The same is true for *A. anasuja* and *A. minuta* with no embolus found in 64 females. In some species, e.g. *A. argentata* or *A. pulchella* in almost all females at least one embolus were found.

41 species have been examined with adult females, 26 species with adult males. Seven species have been found without broken emboli in epigynes. In 13 species, where no males were available, broken emboli were found. Considering single identification

events, the percentage with females found without males in the same series but with broken emboli present was similarly high: in 103 series with exclusively females available broken emboli could be found (ca. 25 %). All this stresses the usefulness of emboli for identification purposes.

## TAXONOMY

### ARANEIDAE Simon 1895

#### *Argiope* Audouin 1826

Species are listed in an order following Levi (1983, 2004) and Bjørn (1997). It seems that males offer better features to group species systematically, whereas female epigynes are in many cases similar between groups and the opisthosomal pattern and shape seem to vary within groups.

Levi (1983: 259) grouped the following species with *A. ocula* Fox 1938 and *A. macrochoera* Thorell 1891. But he presumed that similar structures (scape) in the female epigyne are convergently developed. Males are necessary to make statements of the systematic position of *A. manila* and *A. macrochoera*. For the first description of a broken embolus in *A. manila* see below.

#### *Argiope manila* Levi 1983 (Figs 1–2)

**Material examined (5 females, 4 emboli).** PHILIPPINES. **Holotype female [without emboli]** (SMF 31458, www), Luzon, Levi det. 1981. **1 female paratype** (SMF 31439), Levi det. 1981. **3 female paratypes [2 females with 2 emboli each, 1 freshly moulted female without emboli]** (SMF 31459), Luzon, Levi det. 1981.

A broken embolus is illustrated for the first time (Figs 1–2). Broken emboli were recognisable by their long sperm ducts (SD in Fig. 2) extending beyond the broken embolus tip (not to be confused with tiny bristles!) or by a black sclerotised portion of the embolus tip visible best in the posterior view. Special and probably diagnostic feature is the prominent bulge (B in Fig. 2; present in all three emboli investigated) situated distally to

the opening of the sperm duct, which latter is situated on a small apophysis (A in Fig. 2). Another smaller outgrowth (O in Fig. 2) is situated on the proximal side of the opening. Placement of this species is doubtful. A comparison of male emboli of this and other species may give hints for its relationship. Most similar conformation of the embolus tip is that of *A. jinghongensis*.

### ***Argiope aemula* (Walckenaer 1841) (Figs 3–7)**

*Argiope aemula nigripes* Thorell 1877: 364 (description of female; female holotype from Sulawesi, Kendari, MSCN, not examined). Levi 1983: 273 (synonymisation with *A. aemula*).

**Note.** This synonymy was not included in Platnick (2011).

**Material examined (3 males, 24 females, 9 emboli).** INDIA. **2 females** (SMF 31457, www), Mumbai (Bombay), Levi det. 1981. SRI LANKA. **1 female [without emboli]** (SMF 34492), Diyaluma, waterfall, G. Schmidt leg. XII.1981, G. Schmidt det. JAPAN. **1 female** (SMF 56479), Okinawa, Iriomotejima Island, Nishi-geda river, A. Tanikawa leg. 17.VIII.1993, A. Tanikawa det. CHINA. **1 female** (SMF 31436), Guangzhou Province, Kanton (Guangdong city), Levi det. 1981. **1 female** (SMF 31435, www), Hongkong, Levi det. 1981. **1 female** (SMF 31605), Lilang, Levi det. 1982. LAOS: BOLIKHAMSAY. **1 male** (SMF), E end of Sayphou Loyang, Lak Sao, L90, between N 18°11'49.87", E 104°57'36.36", and N 18°11'47.85", E 104°58'18.51", 530 m altitude, town with arable fields, bushes, trees, plantation, by hand, by night, P. Jäger & S. Bayer leg. 8.XI.2009. **1 female** (SMF), Ban Na Deua (= Ban Nadua), L88, northern slopes of Phou Samkeng, 7.9 air km WSW of Lak Sao, N 18°11'9.00" E 104°53'55.00", 520 m altitude, limestone forest, vegetation at forest margin, rice fields, by hand, P. Jäger & S. Bayer leg. 8.XI.2009. INDONESIA: SUMATRA. **1 female** (SMF 61152, ex RII 827), Roewer det. 1931 sub *A. reinwardti* (1 female = *A. pulchella*). **2 females, 6 juvenile females** (SMF 31434), Fort de Kock (=Bukkittinggi), Jacobson leg. 1924, Levi det. 1981. **3 females [1 female without emboli, 1 female: 3 emboli, 1 female: 2 emboli]** (SMF 31433), W Sumatra, Schütz leg. 14.IV.1914, Levi det. 1981. **1 male** (SMF 61152), without data. JAVA. **3 females [2 emboli]** (SMF, RII 4477), Roewer det. 1934. **1 female** (SMF 31601), Levi det. 1981. **1 female [2 right emboli]** (SMF 3477), Java?, Strubell leg. 1908, Strand det. WEST NUSA TENGGARA. **2 females** (SMF 3476), Soembawa [Sumbawa], Wawó [Wawu], B. Rensch leg. 1927. SULAWESI. **1 female** (SMF 3459), SE-Celebes, Elbert leg. 1909. ARU ISLANDS. **1 female** (SMF 3478, www), Terangan, Popjetur, H. Merton leg. 1908. PHILIPPINES. **1 male** (SMF 61155, www), Laguna, Luzon, Mt. Maquiling, Baker leg. PAPUA NEW GUINEA. **1 female** (SMF 3457), New Ireland, Marrahat [not found; there is Mahagat on Tatau Island N of New Ireland], E. Wolf leg. 3.V.1909, sub *A. aemula nigripes*.

Only a tiny and very distal tip of the male embolus has been shown to break in this species (Figs 4–7, cf. intact embolus in Fig. 3). One female from Mumbai (SMF 31457, www) showed a pattern in the posterior part of the dorsal opisthosoma which resembles *A. bougainvilla*, whereas the other female showed the typical pattern, but with trans-

versal bands rather than the characteristic lines. However, both females are faded and pattern is not clearly recognisable. Levi (1983: fig. 31) illustrated for these specimens an epigyne with striking differences in comparison with material from other part of the distribution range. Jäger & Praxaysombath (2011) recorded the species for the first time from Laos. The male from Vientiane had an extensive black patch in the posterior two third of the dorsal opisthosoma as well as a distinct irregular lateral pattern.

### ***Argiope catenulata* (Doleschall 1859)** (Figs 8–9)

**Material examined (1 male, 13 females).** LAOS. **1 male** (SMF 61298, www), Vientiane, L24, wall, by hand, by day, P. Jäger leg. 30.XI.2009. INDONESIA: SUMATRA. **3 females** (SMF 31430), W Sumatra, Schütz leg. 14.IV.1914, Levi det. 1981. **5 females** (SMF 31431, www), Fort de Kock (=Bukittinggi), 920 m altitude, Jacobson leg. 1924, Levi det. 1981. **1 female** (SMF 31432), Padang, Levi det. 1981. SULAWESI. **1 female** (SMF, RII 4192), Tondano, Levi det. 1981. WEST NUSA TENGGARA. **1 female [+ 1 in-det. juvenile]** (SMF 3518), Lombok, Sadjang, Elbert leg. 29.IV.1909, Strand det. 1910. PAPUA PROVINCE. **1 female** (SMF 18113), Merauke, Fr. Monulphus leg. 1956–1957, Chrysanthus det. + ded. VIII.1966, Coll. O. Kraus. **1 female** (SMF 22250), Merauke, Fr. Monulphus leg. 1956–1957, Chrysanthus det., Coll. Wiehle.

No broken emboli have been found in this study. Yin *et al.* (1997: fig. 4h) illustrated one embolus, which is, however, not indicated as broken embolus (Li, in litt.). For an embolus in situ see Fig. 8. The spermathecae of this species are uniquely bent laterad (Fig. 9). Jäger & Praxaysombath (2011) recorded the species for the first time from Laos.

The following four species (*A. bivittigera*, *A. reinwardti*, *A. doleschalli*, *Argiope* sp.) exhibit a similar opisthosomal pattern (three transversal dorsal bright patches; Photos 1–20) and epigynes having a broad median septum in posterior view (MS in Fig. 22). Levi (1983: 259) suggested that all members of this group may belong to the same species, “since they are allopatric”. In another paragraph he suggests for *A. reinwardti* that different forms may be species on its own or subspecies (Levi 1983: 278). He illustrated two male palps of *A. reinwardti*. These show a distinctly different shape of embolus as well as of the median apophysis. An investigation of broken emboli revealed strong differences between embolus forms corresponding with characters in females (colouration, shape of epigyne, sternal protuberances). Considering the diversity of other SE Asian *Argiope* (e.g., *aetherea* group, see below) and on the other hand the low variability of copulatory organs of widespread species such as *A. aurantia* and *A. bruennichi* over their entire range, all these forms are considered having species status, according to the distinct and consistent differences in copulatory organs, size and colouration. However, due to limited material available, especially males and fresh material in larger amounts, not in all cases final conclusions can be drawn. Two additional species within this group which were not examined are *A. buehleri* Schenkel 1944 and *A. niasensis* Strand 1907. The latter is transferred to this group tentatively according to its broad epigynal septum, the pentagonal shape of the opisthosoma and the characteristic opisthosomal pattern

illustrated by Strand (1907: fig. 3). Levi (1983) designated a neotype with indistinct opisthosomal pattern (“washed out”) and placed it incertae sedis. A similar case of an island speciation and allopatric distribution pattern is known from *Herennia* in SE Asia (Kuntner 2005) and *Nephilengys* in the Indian Ocean (Kuntner & Agnarsson 2011).

### ***Argiope bivittigera* Strand 1911** (Figs 10–14, Photos 1–5)

**Material examined (6 females, 8 emboli).** INDONESIA: MALUKU ISLANDS. **1 female syntype** (SMF 3539, www), Kai Islands, between Elat and Ohilim, H. Merton leg. 8.VI.1908, Strand det. sub *A. doleschalli* b. **2 female syntypes [1 female: 2 emboli]** (SMF 3538, www), Kai Islands, Dula, H. Merton leg. V.1908, Strand det. sub *A. doleschalli* b. **1 subadult female syntype** (SMF 3537), Kai Islands, Elat, H. Merton leg. 2.VI.1908, Strand det. sub *A. doleschalli* b. **2 females [each 2 emboli]** (SMF 3535), Kai Islands, between Elat and Ohilim, H. Merton leg. 8.VI.1908, Strand det. sub *A. doleschalli*. **1 female [2 emboli]** (SMF 3536), Kai Islands, Elat, H. Merton leg. 2.VI.1908, Strand det. sub *A. doleschalli*.

Levi (1983: figs 50–51) illustrated an adult female of this species rather than a penultimate instar of *A. reinwardti*, as he suggested. Epigynes of both species can be clearly distinguished by their shape in posterior view with narrower atrial holes in *A. bivittigera*, from which it was extremely difficult to remove the broken emboli. Moreover the posterior epigynal margin is slightly bilobate in ventral view (Fig. 12). Note that the additional material of the present species identified by Strand as *A. doleschalli* was collected by Merton at the same day and at the same place as the syntypes of *A. bivittigera* (cf. Jäger 2010 on a similar case from the family Pisauridae indicating Strand’s attitude to determine different species if not genera from the same locality and from material belonging in fact to the same species!) Size ranges for the species are: PL 6.4–7.9, PW 5.4–7.0, AW 2.8–3.5, OL 10.1–10.8, OW 8.5–10.1. Colouration as in Photos 1–5. Spermathecae rather spherical in lateral view (arrow in Fig. 14; elongate in *A. reinwardti*, cf. Fig. 23).

### ***Argiope reinwardti* (Doleschall 1859)** (Figs 15–28, Photos 6–14)

**Material examined (5 females, 6 emboli).** INDONESIA: JAVA. **Female holotype [2 emboli, 1 on each side]**, NMNH. **1 female [2 emboli, 1 on each side]** (SMF 61731, www), G. Heberer leg. 1927–1928, H. Wiehle det. sub *A. reinwardti*, ex. Coll. Wiehle. **1 female [1 embolus]** (SMF 61730, www), same data as for SMF 61731. **1 female** (SMF 61732, www), same data as for SMF 61731. **1 female [1 left embolus]** (SMF 31600, www), Bogor, Cibodas, Levi det. 1982.

Male emboli exhibit a distinctly longer straight part than in *A. bivittigera*. In 3 broken emboli the distal tip was broken (Figs 15–16, 18). The females from the Senckenberg collection exhibit slightly longer broken emboli than the type material (15–18; cf. 19–20). Further diagnostic characters could be the seven only slightly humped protuberances on the sternum and the almost entirely yellow sternum (Photos 7, 10, 13). Moreover, the second (middle) transversal bar on the dorsal opisthosoma has a convex anterior margin (Photos 9, 12), whereas in *A. bivittigera*, *A. doleschalli* and *Argiope* sp. it is straight (Photos 1, 15) or indistinct (Photo 19). However, one female (Photo 6) of *A. reinwardti* shows an intermediate state.

***Argiope doleschalli* Thorell 1873** (Figs 29–31, Photos 15–18)

**Material examined (1 female, 1 embolus).** INDONESIA: MALUKU ISLANDS. **Female holotype [1 left embolus]**, Ambon, Doleschall described as *Epeira (Argyropes) trifasciata*, NMNH). Name preoccupied: *A. trifasciata* Forsskål 1775. *Argiope doleschalli* Thorell 1873: 520 (new name).

The species was synonymised by Levi (1983: 276) with *A. reinwardti*. The broken embolus found in the epigyne of the female holotype is distinctly different from all other emboli known in this group: It is shorter and stout with a small and straight distal tip (Fig. 29). The female is best recognised by 4 distinct sternal protuberances (Photo 17–18). The sternal median stripe is restricted to a narrow zone (Photo 16). Moreover the opisthosoma and parts of the dorsal shield of the prosoma (especially posterior margins) are littered with small dark-brown wart-like structures (Photo 15).

***Argiope* sp.** (Fig. 32, Photos 19–21)

**Material examined (1 female, 2 emboli).** INDONESIA: MALUKU ISLANDS. **1 female [2 emboli]** (SMF 3520, www), Aru Islands, Kobroor, Seltoetti, H. Merton leg., Strand det. sub *A. concinna*.

PL 4.5, PW 3.7, AW 2.1, OL 6.3, OW 5.0. According to the smaller size, the distinctly smaller and differently shaped embolus (Fig. 32) it is considered a species on its own. Since there are potential names available (*A. concinna* Thorell 1881, *A. barbipoda* Strand 191), whose type material could not be checked, no identification can be provided. Examination of types (and searching for broken emboli in adult females) of above listed species as well as others listed as synonyms within this species group, e.g., *A. celebesiana* Merian 1911 or *A. reinwardti sumatrana* (Hasselt 1882), could discover more species.

***Argiope boesenbergi* Levi 1983** (Fig. 33)

**Material examined (5 females, 2 emboli).** JAPAN. **2 females [1 female: 2 emboli]** (SMF 3464, www), Saga, Kompira [Daimon, Kinryu-machi, Saga-shi], W. Dönitz leg. 1887, Levi det. 1981. **1 female [only opisthosoma]** (SMF 61156, ex RII 3481), Saga, Kompira [Daimon, Kinryu-machi, Saga-shi], W. Dönitz leg. 1882. **1 female** (SMF 61156), Saga, Kompira [Daimon, Kinryu-machi, Saga-shi], W. Dönitz leg. 1882. **1 female** (SMF 31422), Myianoshita, B. Schmacker leg. 1889, Levi det. 1981.

Both emboli exhibit the same sharp bend of their tip (Fig. 33). Protruding sperm ducts were well visible in epigynal cavities, emboli were difficult to get out.

***Argiope amoena* L. Koch 1878** (Figs 34–35)

**Material examined (1 male, 18 females, 23 emboli).** JAPAN. **1 male [without palps], 12 females [17 emboli], 2 subadult males, 12 immature females** (SMF 3481, www), Saga, Kompira [Daimon, Kinryu-machi, Saga-shi], W. Dönitz leg. 1882. **3 females [1 female: 1 left embolus, 2 females: 1 embolus on each side], 1 subadult female** (SMF 31417), Yokohama, B. Schmacker leg. 1889, Levi det. 1981. **3 females [with emboli]** (SMF 61142), Gifu, Kitagata, Yokohama, G. & B. Lehacker leg. 1889.

Broken emboli are distinctly larger than those of *A. boesenbergi* and *A. magnifica* (Figs 34–35) and are similar to those of *A. sector* in having no appendage or modification. Colour pattern of male and female immatures as well as adults is similar (SMF 3481, www).

***Argiope magnifica* L. Koch 1871** (Fig. 36)

**Material examined (6 females, 5 emboli).** PAPUA NEW GUINEA. **3 females [1 female: 3 emboli, 2 females: each 1 left embolus]** (SMF 3460), New Britain, Toma, E. Wolf leg. 12.–15.V.1909, E. Strand det. sub *A. aemula*. **2 females [without emboli]** (SMF 3479), New Britain, Toma, E. Wolf leg. 14.V.1909, E. Strand det. 1910 sub *A. aemula*. **1 female, 1 subadult female** (SMF 60767, www), Western Highlands, Nondugl Waghi-Valley, leg. VI.1959.

Broken emboli had very long and well recognisable sperm ducts extending into the epigynal depression. Emboli are small (Fig. 36) and were hard to remove.

***Argiope bruennichi* (Scopoli 1772)** (Figs 37–41)

*Argiope bruennichi nigrofasciata* Franganillo 1910: 7, figs 1–2 [fig. 2 depict the characteristic egg-sac of *A. bruennichi*] (description of female, type material not examined).

**Syn. nov.**

*Argiope acuminata* Franganillo 1920: 138 (description of male and female; type material not examined). **Syn. nov.**

**Note.** The type material of Franganillo is either dried or lost, in any case not available (Cardoso & Morano 2010, in litt.). In the Iberian Peninsula three species are recorded: *A. bruennichi*, *A. lobata* and in the South *A. trifasciata* (Cardoso & Morano 2010). From the description as well as from the illustration of *A. b. nigrofasciata* it is clear that this name is a synonym of *A. bruennichi*, whose dorsal opisthosomal pattern of transversal black, white and yellow lines is variable according to strength of single elements but characteristic among the three species in question. The Latin description of *A. acuminata* points also to conspecificity with *A. bruennichi*, especially the two parallel longitudinal lines on the ventral opisthosoma and the median longitudinal sternal line mentioned. I guess that Franganillo examined a juvenile female, whose opisthosoma is in fact much more distinctly acuminate and extending beyond the spinnerets.

**Material examined (5 males, 102 females, 3 emboli).** GERMANY. **1 female [without embolus]** (SMF 61402), Rösrath, Nature Reserve Wahner Heide, Geisterbusch, by sweep-net, P. Jäger leg. 7.VIII.1994. **1 subadult male, 1 subadult female** (SMF 61403), with same data as for SMF 61402, but 10.VII.1994. **1 male, 2 subadult males** (SMF 61404), Troisdorf, Nature Reserve Wahner Heide, Tongrube, by sweep-net, P. Jäger leg. 10.VII.1994. **2 subadult males** (SMF 61401), Mainz, Draisberghof, P. Jäger leg. 11.VII.1997. **1 female** (SMF, RII 4387), near Berlin, Roewer det. 1934. **2 females** (SMF 3506), Frankfurt am Main, K. Koch leg. 1883, Strand rev. **4 females** (SMF 3508), Frankfurt am Main, F. Römer leg. 1902, Strand rev. **1 female** (SMF 3514), Frankfurt am Main, Fechenheim, Mainkur, F. Römer leg. 1901, Strand det. **1 subadult female** (SMF 3516), Frankfurt am Main, C. v. Heyden leg., Strand det. **4 females, few juveniles** (SMF 3515), Schwanheim, A. Knoblauch leg. VIII.1901, Strand det. **3 females** (SMF 3522), Offenbach, Luhrwald, A. Zilch leg. VIII.1935. **1 female** (SMF 3513), between Darmstadt and Messeler Park, Ernst-Ludwigs pond, F. Haas leg. 9.IX.1934. SWITZERLAND. **3 females** (SMF 3512), Lugano, L. Edinger leg. 1904, Strand det. FRANCE. **1 subadult female** (SMF, RII 1900), Riviera, near Nice, Roewer det. 1940. **4 females** (SMF, RII 8992), Marseille, Roewer det. 1943. **1 female** (SMF 3517), S France, A. Knoblauch leg., Strand det. SPAIN. **4 females** (SMF, RII 1796), E-Pyrenees, Roewer det. 1942. **13 females** (SMF 3507), Girona, La Fosca de Palamós, F. Haas leg. 1914. **2 females** (SMF 3510), Prov. Tarragona, Flix, F. Haas leg. 1915. **2 females** (SMF 3511), Cataluna, Province Lerida, Pobla de Segur, F. Haas leg. VII–IX.1918. **1 male [right palp missing, left embolus broken, but hanging on sperm duct at bulb], 1 female [without emboli]** (SMF 34474), Ibiza, Wunderlich det. + ded. 1983. ITALY. **2 females** (SMF, RII 5658), Florence, Roewer det. 1940. **30 females** (SMF, RII 1794), Sardinia, Roewer det. 1938. HUNGARY. **1 female** (SMF, RII 1366), Simontornya, Roewer det. 1928. CROATIA. **1 male** (SMF 10481, www), Istria, Rovinj, Braun leg. VIII.1956, Braun det. XII.1957. MACEDONIA. **2 females** (SMF, RII 9009), Ostrowo lake, meadow, Grell leg.,

Roewer det. 1943. GREECE. **3 females [1 female: 2 emboli + amorphous plugs]** (SMF, RII 815), Crete, Meskia, Roewer leg. VII.1926, det. 1927. AZORES. **1 subadult female [with epigyne fully developed under cuticle]** (SMF 36772), Faial, Horta, hotel garden, G. Schmidt leg. 3.VIII.1987, G. Schmidt det. 1986. MOROCCO. **4 females** (SMF 3521), Casablanca, Karl von Fritsch & Rein leg. 1872, E. Strand det. sub *A. b. africana*. LEBANON. **1 male** (SMF 61135, RII 12636), no further data. IRAN. **1 female** (SMF, RII 10724), Maharlu Lake, Schiras, Löffler leg., Roewer det. 1953. **1 female** (SMF, RII 10729), Maharlu Lake, Schiras, Löffler leg., Roewer det. 1953. JAPAN. **2 males, 1 additional right palp, 8 females, 19 immatures** (SMF 3509), Nagasaki and Kompira [Daimon, Kinryu-machi, Saga-shi], W. Dönitz leg. 1882. **1 female, 1 subadult female** (SMF 31418), Yokohama, Kanagawa, B. Schmacker leg. 1889, Levi det. 1981. DOUBTFUL LOCALITIES. **Holotype female of *Argiope bruennichi orientalis* Strand 1907 [with 1 left embolus]** (SMF 31604, www), Indonesia, Java, Strand det., Levi rev. 1982. **1 female** (SMF 61118), Mexico, Guerrero, Acapulco, E. Seele leg. 10.XI.1966 [label wrong, see below]. In the Senckenberg collection 102 further series of this species are registered, which have not been examined for this study.

Only few females were investigated for broken emboli, since the epigyne would be damaged in old material, when bending it in a ventro-anterior direction. Exclusively historical records, samples from the border of the distribution range or specimens newly identified in the course of this study are listed above. The holotype female of *A. b. orientalis* had one left broken embolus in its epigyne. This exhibited a typical embolus in comparison with those from other males. The locality data (Java) were already questioned by Levi (1983). Preliminary investigations on DNA-sequences showed evidences that it is actually from Western Europe (Krehenwinkel, personal communication). The same is true for the female from Mexico. Most likely the locality data has been confused, since both show the western European haplotype in Krehenwinkel's COI-gene analysis. Similar wrong labeling could be true for *A. lobata* records from Indonesia, Australia and New Caledonia (Levi 1983: map 3) considering the distribution range of the majority of the records. One female of *A. bruennichi* had a shorter scapus (Figs 40–41) which is considered intraspecific variation. Uhl *et al.* (2007, 2010) showed photos of broken emboli in a female epigyne and indicated two areas in male palps where the embolus can break during copulation. Moreover, a tip of embolus is shown in a macerated epigyne plugging effectively the insemination duct (Nessler *et al.* 2006, 2007, Uhl *et al.* 2007).

### ***Argiope aurantia* Lucas 1833 (Figs 42–43)**

**Material examined (1 male, 37 females, 4 emboli).** USA. **4 females** (SMF 10581, www), West Virginia, Wheeling Ohio County, K.W. Haller leg. VIII.-X.1947, Gertsch ded., Coll. O. Kraus, VIII. 1958. **1 male** (SMF 10559, www), Maryland, Kensington, J.M. Davis leg. 30.VIII.1945, Gertsch ded., Coll. O. Kraus, VIII. 1958. **1 female [4 emboli, 2 on each side], 1 subadult female** (SMF 61099, www), Texas. **1 female** (SMF 61136), Tennessee, Sparta, E. Franz leg. 25.IX.1956. MEXICO. **1 female** (SMF 61105), Guerrero, Acapulco, H. Wagner leg. 12.IX.1933. EL SALVADOR. **3 females** (SMF 7811),

Dept. La Union, road Zacatecoluca-Marcos Lampa, km 17 E Zacatecoluca, 100 m altitude, A. Zilch leg. 11.VIII.1951. **3 females** (SMF 7812), Dept. La Union, km 198 of road La Union-Pasoquina, A. Zilch leg. 29.VIII.1951. **13 females** (SMF 7809), Dept. Sonsonate, E of Acajutla, small forest above rock at the beach, A. Zilch leg. 21.X.1951. **3 females** (SMF, RII 10946), Roewer det. 1953. DOUBTFUL LOCALITIES. **3 females** (SMF 31603), Levi det. 1981. **4 females** (SMF 31602), Levi det. 1982. **1 female** (SMF 61113), Santa Catharina [Brazil?]. Further four series are deposited in the Wiehle collection.

Epigynal scapus was strongly truncated in females from El Salvador (SMF 7811) in comparison with illustrations in Levi (2004: fig. 9). In this species it was not searched routinely for broken emboli, as openings are hidden and scapus had to be deformed in every single specimen. Therefore no statements on the frequency of broken emboli in this species can be made. Uhl *et al.* (2010: fig. 1B) showed a photograph of several emboli in a macerated epigyne. Emboli found in this study exhibited a deep V-shaped indentation at the base of the broken embolus (Fig. 42), in one case secretion(?) stuck to the broken embolus (Fig. 43). In *A. bruennichi* the basal indentation is distinctly smaller (Figs 37–38).

Levi (1983: 260) stated that “*A. lobata*, with males known, is not close to any [Asian] group”. Bjørn (1997: 205), in his revision of African species, grouped *A. australis*, *A. coquereli*, *A. lobata*, *A. sector* and *A. tapinobata* together due to the “possession of bluntly rounded lateral abdominal lobes and of a thorn at the concave side of the proximal part of the embolus” and proposed a further subdivision. Due to congruence in characters listed above this group should also include *A. ahngerii* from Central Asia.

### ***Argiope lobata* Pallas 1772** (Figs 44–48)

*Argiope lobata retracta* Franganillo 1918: 122 (description of female; type material not examined). **Syn. nov.**

**Note.** The type material of Franganillo is either dried or lost, in any case not available (Cardoso & Morano 2010, in litt.). In the Iberian Peninsula three species are recorded: *A. bruennichi*, *A. lobata* and in the South *A. trifasciata* (Cardoso & Morano 2010). From the description of *A. l. retracta* it is clear that this name is a synonym of *A. lobata*. No other species at the Iberian Peninsula has such distinct lateral lobes. The shape of lobes and opisthosoma in general can vary strongly (Levi 1983, Bjørn 1997, present study).

**Material examined (2 males, 56 females, 7 emboli).** FRANCE. **1 female** (SMF, RII 8993), Marseilles, Roewer det. 1943. ITALY. **1 female [1 right embolus]** (SMF 61146), Isola dei Conigli, 1.X.1969. PORTUGAL. **1 male [with both emboli intact after copu-**

lation] (SMF 61400), reared from egg-sac by P. Jäger, 23.VI.1993. **2 subadult males [1 with palpal structures recognizable under cuticle], 1 subadult female, 9 juveniles** (SMF 61407), reared from egg-sac by P. Jäger, 2.II.1993. SPAIN. **11 females, 1 subadult female** (SMF 3548), Girona, La Fosca de Palamós, F. Haas leg. 1914. **1 female [1 right embolus]** (SMF 61055), Cataluna, Barcelona, A. Holm leg. 1929. **8 females** (SMF 3547), Tarragona Province, Flix, F. Haas leg. 1915. CANARY ISLANDS. **1 female** (SMF 61405), Tenerife, Teno Alto [N 28°20'41.52", W 16°52'49.36"], grassland, P. Jäger leg. 16.VIII.1993. ITALY. **1 subadult female** (SMF, RII 13850), Latium, Roewer det. 1960. **1 subadult female, 4 juvenile females** (SMF, RII 1795), Sardinia, Roewer det. 1938. **12 females** (SMF, RII 1793), Sardinia, Roewer det. 1938. HUNGARY. **1 female [1 right embolus]** (SMF 35910), Hortobagy, Kiskunsag, Trojan leg. 18.VIII.1983, Starega det. 1984, Coll. Starega. GREECE. **2 females, 1 subadult female** (SMF, RII 816), Roewer det. 1927. **2 females, 3 juvenile females** (SMF, RII 1774), Crete, Roewer det. 1929. **1 female, 2 subadult females** (SMF, RII 817), Crete, Roewer det. 1928. **2 males, 2 females** (SMF 56963, www), Argios Georgios, SW Sitia, Pref. Lasithi, by hand, H. Eikamp & U. Kluge leg. 14.07.2006. ISRAEL. **1 female** (SMF 3550), Jaffa-Rehoboth, J. Aharoni leg. 23.VIII.1913, Strand det. SYRIA. **1 female** (SMF 4839), Haissa (Haysah?), H. Simon leg. 1891, Strand det. **4 females** (SMF 3549), Haissa (Haysah?), H. Simon leg. 1880, Strand det. IRAN. **1 female** (SMF, RII 10726), Salzarwan, Löffler leg., Roewer det. 1953. **3 females [1 female: 1 right embolus]** (SMF, RII 10725), Niri-See, Schiras, Löffler leg., Roewer det. 1953. **2 females, 1 subadult female** (SMF, RII 10727), Maharlu Lake, Schiras, Löffler leg., Roewer det. 1953. **1 female** (SMF, RII 10728), Kuh-i-Labzar, Löffler leg., Roewer det. 1953. INDIA. **1 female [1 left embolus], 1 subadult female** (SMF, RII 4515), Dekkan, Nilgiris, Levi det. 1981. SENEGAL. **1 male, 2 females [1 female: 2 emboli]** (SMF 61149, www), Lompoul, H. Nickel leg. 13.XI.1999. TANZANIA. **1 female [2 emboli]** (SMF 61141), Arusha, Lake Eyasi, Mumba rockshelter, Kohl-Larsen leg. 18.VII.1938. NAMIBIA. **2 females [1 right embolus]** (SMF 61145, RII 5952), Khomas, Windhoek, ex Coll. Roewer. Senckenberg collections contain further 26 series, which are not included in this study.

Emboli were easy to remove from epigynes. The variability of basal embolic thorns (T in Figs 44, 46–47) was smaller than in *A. australis* (T in Figs 49–50). However, in one female two emboli of *A. australis* were found and, vice versa, in females of *A. australis* two emboli of *A. lobata* (e.g., SMF 31849) were observed. Another female (SMF 61145) showed considerable variation when compared with illustrations by Levi (1983: figs 87–91).

Nessler *et al.* (2009) showed for *A. lobata* that males which were cannibalised during their first copulation damaged their pedipalps with a higher probability (74%) than those which escaped. Only a low plugging rate was observed in females (14 %), which can be confirmed from the present study for preserved specimens (12.7 %). Nessler *et al.* (2009: figs 2 A–D) show photos of differently damaged pedipalps (entire embolus or tip of embolus broken).

**Note.** The distribution shown in Levi (1983: map 3, Indonesia, Australia, New Caledonia) may be affected by wrong labels (see note in *A. bruenrichi* on localities in Java and Mexico).

***Argiope australis* (Walckenaer 1805)** (Figs 49–53)

**Material examined (1 male, 18 females, 11 emboli).** CAPE VERDE ISLANDS. **1 female [2 emboli of lobata-type]** (SMF 31849, www), Fogo, Curral Grande, K. Groh leg. 30.X.1979, Groh & Assmuth det. 1981 sub *A. clarki*. GABOON. **2 females** (SMF 61072, RII 5483), Kama. TANZANIA. **1 male, 1 subadult female [epigyne fully developed under cuticle]** (SMF 39400, www), T. Russell-Smith leg. 17.I.1996, Grasshoff det. sub *A. suavissima*. **1 female [without emboli]** (SMF 40098), Dindeia Mkomazi, *Dichrostachys*, T. Russell-Smith leg. 09.IV.1995, T. Russell-Smith det. 1997 sub *A. suavissima*. **1 female [2 emboli]** (SMF 61071), Tabora, S. Schablitzki & W. Sattler leg. 1913. **1 female [1 embolus]** (SMF 61083), Dodoma, Kondoa District, headwater of Bubo river, 1000 m altitude, L. Kohl-Larsen leg. 1935. **1 female [1 right embolus]** (SMF 61147), Arusha, Lake Eyasi, Mumba Rockshelter, Kohl-Larsen leg. 18.VII.1938. NAMIBIA. **1 female [2 emboli], 2 juvenile females** (SMF 61078, RII 8190), Omath-eke, Gobabis. **1 female, 1 subadult female** (SMF, RII 4414, www), Windhoek, Roewer det. 1934, sub *A. nigrovittata*. SOUTH AFRICA. **1 female** (SMF 3553), Cape of Good Hope, Dreyer leg. 1915, sub *A. nigrovittata*. **2 females [1 female: 2 emboli]** (SMF 61124), Nordkap, Namaqualand, S. Vogel leg. 1952. **1 female [1 right embolus]** (SMF 61148), Nordkap, Namaqualand, R. Braun leg. 1952. **1 female** (SMF 61127), Nordkap, Namaqualand. **1 female [2 emboli]** (SMF 61123, RII 5226), Mpumalanga, N of Drakensberge, near Long Tom Pass, Mashishing [Leydenburg]. DOUBTFUL LOCALITIES. **1 female** (SMF 3541), Africa, Strand det. sub *A. flavipalpis*. **1 female** (SMF 61095, RII 510), Africa. **1 female** (SMF 61096, RII 2785), Africa.

Emboli were easy to remove from epigynes. In most cases the long embolic apophysis was visible in the epigynal depression and made a removal unnecessary. There was a great variability especially of the basal thorn (H in Figs 49–50; see also Bjørn 1997). There was also a strong variation in epigyne shape (Figs 51–53; partly covered by illustrations in Bjørn 1997). See also comments for *A. lobata* above and in the discussion.

***Argiope sector* (Forsskål 1775)** (Figs 54–58)

**Material examined (12 males, 20 females, 20 emboli).** SAUDI ARABIA. **1 female** (SMF 61139), Eastern Province, Dauhat Salwa, Jazirat Judhaym / Judaim (cormorant island), 25°28'42"N 50°25'27"E, #907, VO 1992, R. Kinzelbach & M. Werner leg. 9.–19. XII.1992. TUNISIA. **1 female [4 right + 3 left emboli]** (SMF 37082), G. Schmidt det. sub *A. lobata*. **1 female [without embolus]** (SMF 61406), southcoast, El Marsa [N 33°12', E 11°13'], semidesert, 50 m from coast line, in dry herbal vegetation, ca. 1 m above ground, H. Nickel leg. 28.VIII.1996, P. Jäger det. 1996 sub *A. lobata*. EGYPT. **2 females [1 female: 3 emboli, 1 female: 2? emboli]** (SMF 61126), Al Fayyum, E. Bannwarth leg. 10.I.1913. **2 females, 2 juvenile females** (SMF, RII 1776), Gizeh, Roewer det. 1930 sub *A. lobata*. SENEGAL. **1 female** (SMF 61088), Thies, Lompoul,

H. Nickel leg. 13.XI.1999. CAPE VERDE ISLANDS. **1 male, 3 females [1 female: 2 emboli, 1 female: 1 left embolus, 1 female without emboli]** (SMF 31853, www), Antao, Ribeira Grande, K. Groh leg. 20.–21.XII.1978, Groh & Assmuth det. 1981 sub *A. clarki*. **1 male** (SMF 31854), Tiago, Tarrafal, Friebe & Groh leg. 19.X.1978, Groh & Assmuth det. 1981 sub *A. clarki*. **1 female** (SMF 31851, www), Nicolau, Vila Brava, K. Groh leg. 26.XII.1978, Groh & Assmuth det. 1981 sub *A. clarki*. **9 males, 1 subadult male** (SMF 31880), Vincente, Serra W Mindelo, H. Hölzel, W. Lobin & P. Ohm leg. 9.XI.1980, Groh & Assmuth det. 1981 sub *A. clarki*. **4 females [2 females: 2 emboli, 2 females: 1 right embolus]** (SMF 31850), Fogo, 5 km SW San Filipe, B. Friebe leg. 27.X.1979, Groh & Assmuth det. 1981 sub *A. clarki*. **3 females [2 females: 2 emboli, 1 female without embolus]** (SMF 31895), Sal, Groh & Assmuth det. 1981 sub *A. clarki*. **1 male** (SMF 37515), Santiago, Tarrafal, reared from egg-sac, G. Schmidt leg. + det. II.1992. **1 female** (SMF 37547), Santiago, Tarrafal, G. Schmidt leg. 10.II.1992, G. Schmidt det.

The male embolus of this species can be deformed in different ways, when stuck in an epigyne, i.e. the tip can be bent more or less strongly (Figs 56–58; cf. Fig. 54 for an embolus in situ), in some cases it was coiled 3-dimensionally (Fig. 56). The embolus in situ (Fig. 54: SMF 31853, 31854, 31880) showed no basal thorn in spiders from Cape Verde Islands as illustrated and proposed as diagnostic by Bjørn (1997: 225, fig. 67). Probably this character is also variable as in other species of this group.

### ***Argiope ahngeri* Spassky 1932**

No material was found in the Senckenberg collection. Judging from illustrations in the original publication and from illustrations made by Marusik (unpubl.), the species belongs clearly to the *lobata*-group, and is most similar to *A. sector*. Beside the three female syntypes from the type locality Akhal-Teke [old name of an oasis in S Turkmenistan: N foothills of Kopetdagh {=Kopetdag} Mts., environments of Geok-Tepe {=Gök-depe}, c. 38°09'N, 57°57'E] (Spassky 1932), the species was recorded from Kyrgyzstan (Bakhvalov 1974), Tajikistan (Andreeva 1976) and Uzbekistan (Karaul-Bazar: Marusik 1989) (Mikhailov, in litt.).

### ***Argiope* sp. cf. *tapinobata* Bjørn 1997** (Figs 59–60, Photos 22–24)

**Material examined (1 female, 1 embolus).** NAMIBIA. **1 female [1 embolus]** (SMF 61122, RII 5953, www), Khomas, Windhoek.

The female from Namibia shows distinctly stronger lateral opisthosomal lobes (Photos 22–23) than the holotype of *A. tapinobata* illustrated by Bjørn (1997: fig. 80). Moreo-

ver, the Namibian specimen exhibits thinner black transversal lines. The broken embolus (Fig. 59) and the posterior view of the epigyne (Fig. 60) showed distinct differences in comparison with Bjørn (1997: figs 83, 85). It might represent a new species, but more material and males are necessary to finalise a species diagnosis.

***Argiope coquereli* (Vinson 1863)** (Figs 61, Photos 25–27)

**Material examined (7 females, 6 emboli):** MADAGASCAR. **2 females [1 female: 2 emboli, one on each side]** (SMF 3526), Nossi Bé, A. Stumpff leg. 18.XII.1885, Strand det. **2 females [1 female: 2 emboli, one on each side; 1 female: 1 right embolus], 1 subadult female, 1 juvenile female** (SMF 3524), Nossi Bé, A. Stumpff leg. 1881, Strand rev. **2 females** (SMF 3525, www), Nossi Bé, A. Stumpff leg. 1883, Strand det. **1 female [1 right embolus]** (SMF 3523), C. Ebenau leg. 1875, Strand det.

The broken embolus has a distinctly broader base than the preceding species. Moreover it is armed with strong and numerous proximad teeth (Fig. 61). In comparison, the embolus shown in Bjørn (1997: fig. 48) exhibits less teeth. The median sternal band is narrower in one female (SMF 3525: Photo 26) than that illustrated by Bjørn (1997: fig. 44). All females could be unambiguously identified as *A. coquereli* by the broad bright epigynal rim and the lateral depressions as well the opisthosomal colour pattern (Photos 25–27).

Representatives of the following species (*A. flavipalpis*, *A. ranomafanensis*) are characterised by a rather short and only slightly curved embolus without basal apophysis or distal pendant in males and the epigynal roof wider than long and sub-triangular. Additional species: *Argiope levii* Bjørn 1997 from Kenya and Tanzania, *Argiope aurocincta* Pocock 1898 from Central, East, and Southern Africa.

***Argiope flavipalpis* (Lucas 1858)** (Figs 62–64, Photos 28–33)

**Material examined (1 male, 34 females, 3 emboli).** IVORY COAST. **3 females [1 female: 1 left embolus]** (SMF 61132), Comoé National Park, Research Station University of Würzburg, S. Otto leg. VII–IX.2002. **3 females** (SMF 58820, www), Northeast Region, Bouna and Ferkessedougou Prefectures, Comoé National Park, S. Otto leg. 30.VIII.2002. **1 female, 1 subadult female** (SMF 61108), Abidjan, D. Sattler leg. CAMEROON. **1 female** (SMF 61082, RII 12863), Centre, Yaounde. **1 female** (SMF 61079, RII 1842), Sud, Bipindi. **7 females** (SMF 61077, RII 7258), no further data. **7 females**

(SMF 61097, RII 7257), no further data. **3 females [1 female: 2 emboli]** (SMF 61144, RII 6793), no further data. CONGO. **1 male** (SMF 61133, www), Kasango, 580 m altitude, 4°38.2'N, 26°20.667'E. **3 females, 1 subadult female, 1 juvenile female** (SMF 61085), Orientale Ituri Region, Epulu, M. Grzimek leg. KENIA. **1 female** (SMF 31735) Gedi, Grasshoff leg. 30.X.1979, Grasshoff det. 1982 sub *A. cuspidata*. RUANDA. **1 female, 1 subadult female** (SMF 61073, RII 7891). TANZANIA. **1 female** (SMF 61103), Morogoro, at Mfizigo river, near Matombo, H. Knipper leg. 12.VII.1952. DOUBTFUL LOCALITIES. **1 female** (SMF 61069), Africa. **1 female** (SMF 61093), Africa, Berlin Zoo ded.

In contrast to the embolus in situ (Fig. 62; Bjørn 1997: fig. 53) the embolus tip might be regularly bent strongly in broken emboli (Fig. 64). Male and female are illustrated by means of photos for the first time (Photos 28–33).

### ***Argiope ranomafanensis* Bjørn 1997** (Photos 34–37)

**Material examined (6 females):** MADAGASCAR. **1 female** (RMCA 200.453), Foulpointe, forêt sur argile, tamisage litiere, A. Pauly leg. 7.XII.1993. **1 female** (RMCA 200.195), Foulpointe, forêt sur sable, marais à Pandanus, dans toiles, A. Pauly leg. 10.XI.1993. **1 female** (RMCA 177.178), Foulpointe, forêt sur sable, A. Pauly leg. 17.XI.1993. **1 female** (RMCA 207.101), Tamatave, Foulpointe, forêt Analalava, A. Pauly leg. I.1995. **2 females** (SMF 61325), Foulpointe, forêt sur argile, tamisage litiere, A. Pauly leg. XII.1993, ex RMCA 200.202.

Since only the male and female type was known from the literature, the present series were included from the RMCA collections. Variation in colour pattern is recognisable from Photos 34–37. No broken emboli could be found in the epigynes, although it cannot be excluded that as in other species another more distal breaking zone exists and only a distal tiny tip breaks in this species which is not visible in the epigynal depression without maceration (cf. *A. bruennichi*).

The ten species listed below were grouped by Levi (1983) as trifasciata-group. One additional South American species, *Argiope legionis* Motta & Levi 2009 from Brazil, is close to *A. ericae* Levi 2004, but distinguished by characters of copulatory organs and colouration pattern (Motta & Levi 2009). Further (Australian) species assigned by Levi (1983: 260) to this group: *A. probata* Rainbow 1916 from Queensland, *A. bullocki* Rainbow 1908 from New South Wales, *A. ocyaloides* L. Koch 1871 from Queensland, and *A. dietrichae* Levi 1983 from Western Australia and Northern Territory. *A. katherina* Levi 1983 from Northern Territory, Australia was placed here provisionally (Levi 1983: 260), but was compared also with *A. minuta* to which latter it was placed within the *anasuja* group (Levi 1983: 300).

***Argiope protensa* L. Koch 1872** (Figs 65–67)

**Material examined (1 male, 8 females, 6 emboli):** AUSTRALIA. **1 female [3 emboli, 2 right]** (SMF, RII 4411), Queensland, Roewer det. 1933. **2 females [1 female: 1 right embolus, 1 female: 1 embolus on each side]** (SMF 3587), Central Australia, von Leonhardi leg. 10.IX.1909, E. Strand det. **1 male, 4 females [raised, without emboli]** (SMF 38009, www), Victoria, G. Schmidt leg. + det. 1993 sub *A. syrmatica*. **1 female [with 2 egg-sacs]** (SMF 38027, www), G. Schmidt leg. + det. 1993 sub *A. syrmatica*.

Broken emboli are smooth and strongly bent ( $> 180^\circ$ ) (Figs 66–67), whereas the embolus in situ (Fig. 65) shows a broad U-shaped course. The embolus base is characterized by a distinct V-shaped incision with differently long arms.

***Argiope trifasciata* (Forsskål 1775)** (Fig. 68)

**Material examined (14 males, 21 females, 2 emboli).** USA. **1 male** (SMF 10549), West Virginia, Tomlinson Run State pk, 3 miles to New Cumberland, K.W. Haller leg. 4.IX.1948, Gertsch det. + ded. 1958, Coll. O. Kraus, VIII. 1958. **1 female** (SMF 10553, www), Texas, Nueces County, Corpus Christi, K.W. Haller leg. 7.XII.1954, Gertsch det. 1958, Coll. O. Kraus, VIII. 1958. **2 females** (SMF 61120), USA, Texas. EL SALVADOR. **1 female** (SMF 8718), Dept. Cuscatlan, Cerro de Las Paras, 1000 m altitude, O. Schuster leg. 27.VIII.1952, sub *A. aurantia*. VENEZUELA. **1 female, 1 subadult female** (SMF, RII 1777), Roewer det. 1934. PERU. **3 males, 1 female, 2 subadult females** (SMF 61415), Pisac (nr. Cusco) [S 13°25'21.30", W 71°51'10.39"], grass, VIII., ex. Coll Wunderlich. BRAZIL. **1 female** (SMF 61121), Pernambuco, Rio Branco. ARGENTINA. **1 female** (SMF, RII 5464), Buenos Aires, Roewer det. 1940. HAITI. **2 females [1 female: 2 emboli, not removable]** (SMF, RII 1090), Roewer det. 1928. BALKANS. **1 female** (SMF 16576), former Yugoslavia [?], Grasshoff det. 1964, Zoo Berlin det. 1958. AZORES. **2 males** (SMF 61089), Madeira, Montanha, E. Schindler leg. 12.07.1960. **2 males, 1 female** (SMF 34845, www), Madeira, Grasshoff leg. 25.III.1986, Wunderlich det. 1986. CANARY ISLANDS. **1 female** (SMF 25213), Gran Canaria, Maspalomas, Oasis, G. Schmidt leg., det. + ded. 1970. **1 male** (SMF 25668), Gran Canaria, Maspalomas, G. Schmidt leg., det. + ded. 1971. **1 female, 4 juvenile females** (SMF 61130), Gran Canaria, 27°44.169'N, 15°35.905'E, Faro, 5 m altitude, P. Jäger leg. 3.XII.2003. **1 female** (SMF 61076, RII 2577), Tenerife. **1 female** (SMF 25847), Tenerife, Puerto de la Cruz, G. Schmidt leg. 1961, det. + ded. 1972. **1 male, 1 female** (SMF 40195), Tenerife, Adeje Municipality, Barranco del Infierno, 28°8'N, 16°42.05'W, 450–650 m altitude, P. Jäger leg. 9.VIII.1993, P. Jäger det. **1 male** (SMF 40196), Tenerife, Teno Alto, 28°20.5'N, 16°52.433'W, 750–800 m altitude, P. Jäger leg. 3.VIII.1993. SENEGAL. **1 male** (SMF 61080, RII 13385). EGYPT. **1 female** (SMF, RII 5664), Gizeh, Roewer det. 1940 sub *A. bruennichi*. **1 juvenile female** (SMF 61075, RII 4377), Quahirah, Kairo. RUANDA. **1 female** (SMF 61074, RII 7890). TANZANIA. **1 male** (SMF 61090), Pwani,

near Msala, H. Knipper leg. 16.IV.1952. **1 male** (SMF 61091), Tabora, Serengeti, Klingel leg. 2.I.1963. MADAGASCAR. **2 females** (SMF 3592), Nossi-Bé, Ebenau leg. 1898.

Platnick (2011) lists “Cosmopolitan except for Europe” as distribution range of this species. In fact it is found in the South Iberian peninsula and in the Balearic Islands (Cardoso & Morano 2010). Populations are considered native, i.e. by expansion to the North and not introduced (Cardoso in litt.). It is not clear whether the single female (SMF 16576) is from former Yugoslavia (Southern Europe) or not. The only broken embolus sticking in the epigyne of one female (R11 1090) could not be removed without probably destroying the specimens. Therefore an embolus in situ is illustrated (Fig. 68). This is coiled three-dimensionally.

### ***Argiope florida* Chamberlin & Ivie 1944**

**Material examined.** USA. **1 subadult female** (SMF 10591, www), Florida, Volusia County, leg. 24.VII.1954, Gertsch det. + ded. 1958, Coll. O. Kraus 1958.

Although immature, the present specimen could be identified by its colouration and locality data.

### ***Argiope madang* Levi 1984**

No material examined. According to Levi (1984) the male palp with the twisted embolus is close to *A. trifasciata*, the embolus has a hooked tip (Levi 1984: fig. 7). The epigyne is unique in having wing-shaped rims (Levi 1984: 250). Dorsal opisthosomal colour pattern is similar to that of *A. manila*, but the only found broken embolus of the latter species (Figs 4–5) does not suggest a closer phylogenetic relationship.

### ***Argiope doboensis* Strand 1911**

**Material examined:** INDONESIA. MALUKU ISLANDS. **Holotype juvenile** (SMF 3534, www), Aru Islands, Pulau Warmar, in forest between Dobo and Wangil, H. Merton leg. 30.I.1908, Strand det.

The female illustrated by Levi (1983) does not show the distinct indentations of the median folium as in the holotype (SMF 3534, www). It may occur that this difference is due to ontogenetic development.

***Argiope chloreis* Thorell 1877** (Figs 69–72)

**Material examined (1 female).** LAOS. **1 female, 1 subadult female** (SMF 61143, www), Champasak Province, Xe Pian National Protected Area, Tha Hou (L103), 14°46.16'N, 105°59.575'E, 132 m altitude, rock extending above wetland forests, vegetation, by day, by hand, P. Jäger & S. Bayer leg. 22.XI.2009.

Epigyne differed from that illustrated by Levi (1983) by the considerably wider posterior part of median septum and the concave septum in lateral view (Figs 69–72). Size matches exactly the same as illustrated by Levi (1983; fig. 146, female from Western New Guinea): PL 2.9, PW 2.55, AW 1.15, OL 4.8, OW 3.1. Colouration differed by the dark ventral opisthosoma with white patches (SMF 61143, www). In the live female this dark stripe was dark-green (SMF 61143, www), which appeared in the preserved specimen black (SMF 61143, www). The web was decorated with ca. five circular stabilimenta and an inner plate of seven zigzag-bands (SMF 61143, www). The spiders represent the first record for Laos. So far, this species was known from Sumatra to New Guinea (Platnick 2011), thus the present specimens represent the northernmost record for this species (Fig. 167: 10).

***Argiope argentata* (Fabricius 1775)** (Figs 73–79)

**Material examined (14 males, 73 females, 109 emboli).** USA. **1 female [2 emboli, 1 on each side]** (SMF 10593), Florida, Key Largo, Gertsch and R.R. Forster leg. 1.IV.1957, Gertsch det. + ded. 1958, Coll. O. Kraus 1958. MEXICO. **4 females [all: at least 1 embolus]** (SMF 10579), Tamaulipas, Padilla, Cazier, Gertsch & Schrammel leg. 17.V.1952, Gertsch det., Coll. O. Kraus VIII.1958. PANAMA. **1 male** (SMF 10588), Barro Colorado Island, S.J. Hook Bishop leg. 3.VII.1933, Gertsch det. + ded. 1958, Coll. O. Kraus VIII.1958. CUBA. **1 female [2 emboli, 1 on each side], 1 juvenile female** (SMF 10574), Pinar del Rio, San Vicente, C. + P. Vaurie leg. 26.VII.1956, Gertsch det. + ded. 1958, Coll. O. Kraus VIII.1958. LESSER ANTILLES. **1 male, 1 female [at least 1 left embolus]** (SMF 34058, www), Aruba, Zindler leg. 1983, H.-G. Müller det. 1984. ECUADOR. **1 male, 2 females [1 female: 2 emboli, 1 on each side; 1 female: 3 emboli, 2 left, 1 right]** (SMF 61412), Banos, VIII., ex. Coll. Wunderlich. **1 female [2 emboli, one on each side]** (SMF 61411), Galapagos, Santa Cruz, North Coast, VIII. **1 female [5 right emboli, 1 left embolus]** (SMF 31446), Galapagos, James, Jamesbay,

Eibl leg. 3.VIII.1957, Levi det. 1981. **1 female [at least 1 left embolus]** (SMF 31447, www), Galapagos, Indefatigable, Eibl. leg., Levi det. 1981. **1 female [at least 3 emboli]** (SMF 31445), Galapagos, Narborough, Eibl. leg. 6.–10.IX.1957, Levi det. 1981. **1 female [2 emboli]** (SMF 31448, www), Galapagos, Tower, Eibl. leg. 18.VIII.1957, Levi det. 1981. VENEZUELA. **10 females, 4 juvenile females** (SMF, RII 1741), Roewer det. 1934. **3 females [all: at least 1 embolus], 5 subadult females, 7 juvenile females** (SMF 7878), Puerto la Cruz, A. Zilch leg. 31.III.1951. **4 females [all: at least 1 embolus]** (SMF 7886), Puerto la Cruz, A. Zilch leg. 31.III.1951. **4 males** (SMF 8492), Puerto la Cruz, A. Zilch leg. 31.III.1951. **5 females [4 females: at least 2 emboli]** (SMF 7887), Puerto la Cruz, A. Zilch leg. 31.III.1951. **1 female [1 right embolus]** (SMF 61102, RII 9664). COLOMBIA. **3 females [1 female: 2 emboli, 1 on each side, 1 female: 1 right embolus]** (SMF 3485), Paopayan or Couca [Cauca], Lehmann leg. **4 males, 1 female [2 emboli, 1 on each side]** (SMF 35482), Dept. Magdalena, Cabana “Villa Culebra” close to Bonda, ca. 10 km E Santa Marta, H.-G. Müller leg. X.1986, Levi det. 1986. **1 female [without emboli]** (SMF 35480), Barranquilla, Isla de Salamana, H.-G. Müller leg. 25.VII.1985, Levi det. 1986. **1 female** (SMF 61115), Antioquia, 6°34.45'N, 75°44.333'W, East Cordillera, near Monterredondo, Guyabe valley, rainforest, 1700–2000 m altitude, S. Vogel leg. XII.1955. **1 female [1 embolus]** (SMF 61112), Meta Llanos orientales, Los Salados, at Rio Guatiquia, 250 m altitude, S. Vogel. leg. II.1956. **1 female [4 emboli, 1 embolus: broken apophysis]** (SMF 61107), Putumayo, street L Tagua-Leguizamo, Sturm leg. 1956. HONDURAS. **1 female [2 emboli]** (SMF 61111), Islas de Bahía, Isla de Utila, 16°6'N, 86°56'W, G. Köhler leg. IV.1995. TRINIDAD. **1 female [2 emboli]** (SMF 3484), G. Gerold leg. 1888. MARTINIQUE. **4 females** (SMF 61116), Lesser Antilles, Jaeschke leg. 19.IX.1965. FRENCH GUYANA. **1 female [at least 2 emboli]** (SMF 35513), Acarouany, D. Kock leg. 4.II.1985, Grasshoff det. 1986. PERU. **1 male, 1 female [6 emboli, 3 on each side]** (SMF 61409), Lima, ex. Coll. Wunderlich. **1 male** (SMF 61410), Lima, VIII., ex. Coll. Wunderlich. BRAZIL. **3 females [1 female: 6 emboli, 3 on each side; 1 female: 2 emboli, 1 on each side, 1 female: 1 right embolus]** (SMF 3483), Joinville, Santa Catarina, W. Eberhardt leg. 1906. **1 female [2 emboli, 1 on each side]** (SMF 3486, www), Rio de Janeiro, Bresslau leg. 1913. **2 females [both: at least 1 embolus on each side]** (SMF 40114), Sao Paulo, Usina Hidroelétrica Engenheiro, S. Motta leg. I.–II.2000. **1 male** (SMF 40123), Sao Paulo, Usina Hidroelétrica Engenheiro, S. Motta leg. 1998. **2 females [3 emboli], 3 juvenile females** (SMF 61100, RII 7511), Pernambuco. **1 female [2 emboli]** (SMF 61101). **1 female [3 emboli]** (SMF 61098, RII 5460), Bahia. **8 females [almost all: 2 emboli]** (SMF 61119), Pernambuco. ARGENTINA. **2 females [1 female: 1 embolus, 1 female: 2 emboli]** (SMF 61104, RII 7361), Buenos Aires.

The embolus of this species exhibits a distinct apophysis. This is even recognisable, when the broken embolus is still sticking in the epigyne. Therefore a removal of the embolus is usually not necessary to distinguish between the related *A. blanda*. This species holds the record with five emboli sticking in one half of an epigyne. It appears to be slightly larger and more robust than *A. blanda*. However, small females are mentioned by Levi (1983: 58) as having the dorsal opisthosomal pattern of *A. florida*, being coloured like an immature and having broken emboli in the epigyne, which clearly are *A. argentata*. This can be confirmed from one female (SMF 31448, www) with a body length of 8.2. In some of the females examined the two longitudinal anteriorly converging lines between the epigastric furrow and the transverse white bar were absent. Four males (SMF 35482) showed considerable size variation, one very large and differently

coloured male had as all three others an embolic apophysis (Figs 73–79). The tip of the left palp in the three smaller males has been broken, distal hooks were in general much more pronounced than in *A. blanda*. Colouration of males can be more distinct and darker than shown in SMF 34058 (www).

### ***Argiope blanda* O. Pickard-Cambridge 1898** (Figs 80–82)

**Material examined (9 females, 12 emboli).** MEXICO. **1 female [2 right emboli]** (SMF 61094, RII 1792), Tamaulipas, Vera Cruz. **1 female [1 right embolus]** (SMF 61106), H. Wagner leg. EL SALVADOR. **1 female [1 left embolus], 1 juvenile female** (SMF 7871), Dept. Cabañas, Sensuntepeque, 760 m altitude, A. Zilch leg. 17.X.1951, sub *A. argentata*. **2 females [1 female: 1 left embolus, 1 female: 2 emboli on each side]** (SMF 7876, www), Dept. Santa Ana, Metapan, Laguna, Hacienda Santa Rosa, 450 m altitude, A. Zilch leg. 29.VIII.1951, sub *A. argentata*. **1 female, 1 juvenile female** (SMF 7874), Dept. La Libertad, Santa Tecla (=Nueva San Salvador), Finca El Paraiso, 900 m altitude, A. Zilch leg. 8.XI.1951, sub *A. argentata*. **1 female [1 embolus on each side]** (SMF 7873), Dept. Morazán, Osicala, Cacaguatique (Cordillera Cacahuatique), Finca San Pedro, 1200 m altitude, A. Zilch leg. 13.IX.1951, sub *A. argentata*. **1 female [epigyne missing]** (SMF 7877), Dept. La Union, 200 m before La Union, A. Zilch leg. 11.IX.1951, sub *A. argentata*. **1 female [1 right embolus]** (SMF 7875), Dept. San Vicente, volcano San Vicente, Finca El Carmen, 1300 m altitude, A. Zilch leg. 11–16.VI.1951, sub *A. argentata*.

Broken emboli are rather small, usually breaking at the main breaking point, although sometimes tip broke, too (Figs 80–82). In one female (SMF 7876) the embolus broke at a secondary position and exhibited a sperm duct extending beyond the breaking point distally. Some of the material was misidentified as *A. argentata*, in many cases because it was considered immature (original labels!) due to the generally smaller size of *A. blanda*. Beside the broad transversal band the narrow epigynal septum was also good as a differentiating feature (Levi 2004).

### ***Argiope submaronica* Strand 1916** (Fig. 83)

**Material examined (2 females, 2 emboli).** BRAZIL. **Holotype female** (SMF 3590), Santa Catarina, Joinville, W. Ehrhardt leg. 1906. **1 female [2 emboli]** (SMF 61117, www), Amazonas, km 26 road from Manaus to Itacoatiara, Reserva “Adolfo Ducke”, leg. 2.XII.1964, sub *A. savignyi*.

*Argiope submaronica* Strand 1916 is removed from the synonymy of *A. argentata* (proposed by Bonnet (1955: 673), and *A. savignyi* Levi 1968 **syn. nov.** is placed in the synonymy of *A. submaronica*. The female holotype conforms to all details described in Levi (2004). The broken embolus was consisting of a small tip and long sperm duct (Fig. 83).

### ***Argiope ericae* Levi 2004**

**Material examined.** BRAZIL. **2 juveniles** (SMF 61114, www), Pernambuco.

The two specimens represent the first record for Pernambuco and the northernmost for this species. They have been identified by the black colouration of legs (legs ringed black and white in *A. legionis*) and their colouration pattern especially the distinct longitudinal band on the ventral sternum (SMF 61114, www; margins of that band diffuse in *A. legionis*, Motta & Levi 2009: figs 2, 8; cf. Levi 2004: figs 67, 70).

The following two species (*A. ansuja*, *A. minuta*) have been grouped by Levi (1983) as *anasuja*-group. Additional species included by Levi (1983: 260) are: *A. perforata* Schenkel 1963 from Sichuan China, *A. halmaherensis* Strand 1907 from Halmahera, *A. possoica* Merian 1911 from Sulawesi, *A. mascordi* Levi 1983 from Queensland, *A. keyserlingi* Karsch 1878 from Australia, *A. kochi* Levi 1983 from Queensland, and *A. caledonia* Levi 1983 from New Caledonia. *A. katherina* Levi 1983 was placed provisionally in the *A. trifasciata* group (Levi 1983: 260), but was compared—besides *A. dietrichae*—with *A. minuta* to which latter it was placed in the species account (Levi 1983: 300).

### ***Argiope anasuja* Thorell 1887** (Figs 84–87)

**Material examined (8 males, 54 females).** INDIA. **1 female, 1 subadult female [epigyne recognisable under cuticle]** (SMF, RII 1132), Madras, Roewer det. 1928. **3 females** (SMF 31440), Feroke, Malabar, Levi det. 1981. **1 male, 1 female** (SMF 58817), Lakshadweep (= Laccadive Islands), Krammig leg. 1974. **2 males, 2 females** (SMF 58818), Lakshadweep (=Laccadive Islands), Bangaram Island resort, Krammig leg. 15.X.1974. **4 females, 1 subadult female** (SMF 58819), Lakshadweep (=Laccadive Islands), Agatti, Krammig leg. 12.X.1974. MALDIVES. **1 female** (SMF 31443), Addu Atoll, Hittadi Island, W. Klausewitz leg. 23.I.1958, Levi det. 1981. **6 females, 2 juvenile females** (SMF 31441, www), Ari Atoll, Fusdu Island, W. Klausewitz leg. 18.II.1958, Levi det. 1981. **3 females** (SMF 31429), Matè-Atoll, Levi det. 1981. **1 female** (SMF 31438), Fadiffulu Atoll, Wadewaru Island, S. Gerlach leg. 7.IV.1917, Levi det. 1981. **5 males,**

**1 subadult male, 32 females, 2 subadult females, 7 juvenile females** (SMF 31437, www), Rastu Atoll, W. Klausewitz leg. 8.III.1958, Levi det. 1981.

No embolus has been found in epigynes, although checking carefully and dissecting one vulva. The filamentous structure protruding from the spermathecae is considered from its consistency hardened secretion rather than a sperm duct (Figs 86–87). The embolus in situ illustrated (Fig. 84) is shorter and stouter than that drawn by Levi (1983: fig. 172).

### ***Argiope minuta* Karsch 1879** (Fig. 88)

**Material examined (1 male, 10 females).** JAPAN. **1 male, 9 females, 1 subadult female** (SMF 3551, www), Saga and Nagasaki, W. Dönitz leg. 1882, Strand rev. **1 female [without emboli]** (SMF 56480), Okinawa, Iriomotejima Island, Urauchi, A. Tanikawa leg. 14.VIII.1992, A. Tanikawa det.

The embolus in situ is spirally coiled, the tip is drawn to facilitate comparison to other (broken) emboli (Fig. 88). Some females were considerably smaller (SMF 3551, www).

The following species may be close to *A. vietnamensis* Ono 2010 (Fig. 167: 11). It has a similar colour pattern and shape of opisthosoma, body size and epigynal shape, especially the extending rim in lateral view (see also diagnosis of *A. hinderlich* spec. nov.). The embolus without any modification resembles more that of males from the *reinwardti*-group, colour pattern of *A. hinderlich* females also similar to *reinwardti*-group.

### ***Argiope hinderlich* spec. nov.** (Figs 89–92, 167: 7, Photos 38–45)

**Type material (2 females, 3 emboli):** LAOS. **Holotype female [2 emboli]** (SMF), Luang Prabang Province, NE Luang Prabang, Nam Ou, Nong Khiao, Tham Pathok, L7, N 20°33.082', E 102°37.925', 373 m altitude, in front of limestone rock, vegetation, by hand, by day, P. Jäger & S. Bayer leg. 16.XI.2009. **Paratype.** LAOS. **1 female [1 right embolus]**, Bolikhamsay Province, S of Sayphou Loyang, Ban Na Deua (= Ban Nadua), northern slopes of Phou Samkeng, 7.9 air km WSW of Lak Sao, L88, N 18°11'9.00" E 104°53'55.00", 520 m altitude, limestone forest, vegetation at forest margin, small caves, by hand, by sweepnet, P. Jäger & S. Bayer leg. 8.XI.2009.

**Etymology.** The species is named in honour of Jürgen Hinderlich (Solidaritätsdienst International, SODI e.V., Lak Sao), who cleared bombs in Laos which have been dropped in the so-called “secret war”, and who supported field work of the author in Bolikhamsay Province; name in genitive case.

**Diagnosis.** Males of *A. hinderlich* spec. nov. are only known from the two broken emboli. Potentially diagnostic features are 1. Embolus without pendant, 2. Embolus tip sharply pointed, smooth (Fig. 89). Females of *Argiope hinderlich* spec. nov. similar to *A. vietnamensis* Ono 2010 in having a similar body size and epigyne, but can be distinguished by 1. Colouration of dorsal opisthosoma and legs (distinct transversal bands and uniformly dark legs in *A. hinderlich* spec. nov., Photos 38, 41, 44; without distinct bands and with tibiae I–II with white patch in *A. vietnamensis*: Ono 2010: fig. 10), 2. Epigyne elongate, extending posteriorly distinctly beyond epigastric furrow (Figs 90–92; not elongate, extending slightly beyond epigastric furrow in *A. vietnamensis*, Ono 2010: fig. 26).

**Description.** Female (holotype). PL 8.4, PW 7.3, AW 3.7, OL 12.4, OW 10.3. Eye diameters: AME 0.43, ALE 0.21, PME 0.45, PLE 0.45. Eye interdistances: AME–AME 0.32, AME–ALE 0.68, PME–PME 0.50, PME–PLE 1.02, AME–PME 0.85, ALE–PLE 0.02, clypeus AME 0.35, clypeus ALE 0.32. Leg and pedipalpus measurements: pedipalpus 10.5 (3.6, 1.6, 2.1, –, 3.2); leg I 43.3 (12.5, 3.8, 10.6, 13.5, 2.9), II 42.2 (12.5, 3.9, 9.9, 13.4, 2.5); leg III 25.3 (8.7, 2.7, 5.3, 6.6, 2.0); leg IV 40.1 (13.4, 3.8, 8.7, 12.2, 2.0). Leg formula. 1243.

Cheliceral furrow with 10–15 tiny and partly very indistinct denticles and 4 anterior and 3 posterior teeth. Palpal claw with 7 teeth.

Copulatory organ as in diagnosis. Epigynal field with elongate patch anteriorly and two slit sense organs anterolaterally (SS in Fig. 90). Spermathecae elongate oval, anteriorly concave (Fig. 92). Rim forming small bulge in lateral view. Flange strongly developed. Septum gradually diverging anteriorly (Fig. 91).

Colour in ethanol (Photos 38–43). Dark brown with bright pattern. Dorsal prosoma with reticulate pattern consisting of white hairs and bright and dark cuticular parts. Sternum with pale orange pentalobal patch and one pair of lateral patches at coxae II. Labium and gnathocoxae dark with distal pale orange lip. Ventral coxae II–IV black with one yellow patch each, larger patches posteriorly. Frontal chelicerae with inner parts orange. Palps with irregular pattern. Legs almost uniformly dark brown. Dorsal opisthosoma with three transversal, clearly delimited bands, muscle sigilla reddish brown, dark parts darker posteriorly. Lateral opisthosoma spotted anteriorly, becoming darker posteriorly. Ventral opisthosoma with two white parallel stripes with median extension and three pairs of bright median patches connected to first three pairs of four muscle sigilla pairs. Spinnerets orange. For colouration of live specimen see Figs 298–299. All bright parts of preserved specimens are shiny yellow in live spiders (Photos 44–45).

Male. Unknown (except for embolus; see diagnosis and Fig. 89).

**Variation.** Female paratype with PL 7.5, PW 6.9, AW 3.1, OL 13.2, OW 10.3; cheliceral furrow with c. 15 indistinct denticles. Broken embolus of right half of paratype’s epigyne with pointed tip broken. Left tarsus of holotype has a extraordinary branch, most likely results from a malformation during individual development.

**Distribution.** Known from Laos (Luang Prabang Province: Nong Khiao; Bolikhamsay Province: Lak Sao) (Fig. 167: 7).

The following three species (*A. jinghongensis*, *A. aethereoides*, *A. luzona*) have an embolus with blunt and widened tip, which is well hidden in the conductor in resting position.

***Argiope jinghongensis* Yin, Peng & Wang 1994** (Figs 93–107, 167: 4, 7–9, 12–13)

**Material examined (3 males, 4 females, 2 emboli):** CHINA. **Holotype male** (HNU), Yunnan Province, Jinghong, J.F. Wang leg. 21.–23.X.1987. LAOS. **1 female** (SMF 61735), Bolikhamsay Province, S of Sayphou Loyang, Ban Na Deua (= Ban Nadua), L88, northern slopes of Phou Samkeng, 7.9 air km WSW of Lak Sao, N 18°11'9.00" E 104°53'55.00", 520 m altitude, limestone forest, vegetation at forest margin, small caves, by hand, by sweepnet, P. Jäger & S. Bayer leg. 10.XI.2009. **1 female [without embolij]** (SMF 56331), Khammouan Province, 8.7 air km (9.5 car km) NE Thakek, N 17°26.936', E 104°52.499', 159 m altitude, foot caves and surroundings, by hand, sweeping, P. Jäger & V. Vedel leg. 30.X.2004. **1 female [2 embolij]** (SMF 61734), Champasak Province, Muang Bachiang (=Ban Bachieng), That Paxuam (L92), 22 air km NNE of Pakse, N 15°16'35.50", E 105°55'22.00", 190 m altitude, secondary forest, vegetation, by hand, by day, P. Jäger & S. Bayer leg. 25.XI.2009. THAILAND. **1 male, 1 female** (SMF 61733, www), Trat Province, Ko Chang, Kheeri Phet waterfall, N 12°00'27.6", E 102°21'09.2", 50–150 m altitude, secondary forest, waterfall, by hand, by day, P. Jäger & S. Bayer leg. 02.XI.2009. **1 male** (SKU), Songkhla Province, Tumbon Chalung, Amphoe Hat Yai, edge zone between rubber plantation and forest (Khuan Khao Wang Forest Park) (from N 6°59'43", E 100°19'50" – N 7°1'37", E 100°18'20"), ca 200 m altitude, 3.II.2009, PSUZC-EN-AR 09-94.

**Diagnosis.** Males can be distinguished by 1. Embolus distally widened with two distinct triangular protrusions, hidden by conductor in resting position (Fig. 94), best observed in broken embolus (PT in Fig. 98), 2. Median apophysis toothed and with sabre-toothed spur (95–97). Females of *A. jinghongensis* similar to species of the *aetherea* group in having a similar colouration, but can be distinguished from those of *A. taprobancia*, *A. luzona*, *A. pulchella*, *A. modesta*, *A. aethereoides* and *A. aetherea* by 1. Median septum with parallel margins (M) and abrupt widening to posterior plate (PP) (Figs 100, 103, 106), 2. Long convex anterior margin of epigyne (CM) in lateral view (Figs 101, 104, 107).

**Note.** One male was found at the same locality with a female (Ko Chang). Additional evidence for conspecificity was given by the congruence of the embolus sticking in the female epigyne.

**Redescription.** Male (Koh Chang). PL 2.0, PW 1.8, AW 0.7, [opisthosoma absent]. Eye diametres: AME 0.16, ALE 0.08, PME 0.19, PLE 0.15. Eye interdistances: AME–AME 0.08, AME–ALE 0.07, PME–PME 0.18, PME–PLE 0.15, AME–PME 0.19, ALE–PLE 0.05, clypeus AME 0.07, clypeus ALE 0.09. Leg and pedipalpus measurements: pedipalpus 1.47 (0.40, 0.16, 0.21, -, 0.70); leg I–II [missing]; leg III 4.72 (1.48, 0.52, 0.93,

1.11, 0.68); leg IV 7.01 (2.13, 0.70, 1.46, 1.87, 0.75). Leg formula. 43. Cheliceral furrow with 15–20 tiny denticles and 4 anterior and 3 posterior teeth. Chelicerae length 0.61. Palp as in diagnosis. Broken embolus tip as wide as long, with two triangular processes (one of which containing sperm duct) and semicircular sperm duct attached (Fig. 98). Embolus in situ with membranous part between the two triangular processes, thus one process hidden (Fig. 93). Embolus without distinct kink. Distal conductor with strong ridges distally (Fig. 94). Median apophysis with two equal branches (Fig. 97). Colour in ethanol (SMF 61733, www). Pale yellowish brown. Dorsal PS anterolaterally darkened. fovea slightly marked with fine reddish brown line. Sternum and ventral coxae II pale yellowish brown, ventral coxae I, III–IV, gnathocoxae, labium and legs with irregular black pattern. Leg segments becoming brighter distally. Chelicerae pale yellow with proximal part black.

**Description.** Female (Ko Chang). PL 5.2, PW 4.5, AW 2.3, OL 8.3, OW 7.6. Eye diameters: AME 0.31, ALE 0.19, PME 0.35, PLE 0.31. Eye interdistances: AME–AME 0.26, AME–ALE 0.42, PME–PME 0.41, PME–PLE 0.74, AME–PME 0.55, ALE–PLE 0.02, clypeus AME 0.18, clypeus ALE 0.24. Leg and pedipalpus measurements: pedipalpus 5.9 (1.9, 0.7, 1.4, -, 1.9); leg I 27.9 (8.3, 2.3, 6.7, 8.5, 2.1), leg II 29.9 (8.9, 2.5, 7.3, 9.1, 2.1); leg III 14.2 (5.6, 1.8, 3.0, 2.7, 1.1); leg IV 27.3 (9.3, 2.5, 5.8, 8.0, 1.7). Leg formula. 2143. Chelicerae length 1.8, with c. 27 denticles in field along entire furrow, and 4 strong anterior and 3 posterior teeth. Palpal claw with 10 teeth.

Copulatory organ as in diagnosis. Epigyne with rectangular patch anteriorly and one to three slit sense organs anterolaterally on each side (Figs 99, 102, 105). Spermathecae elongate oval, anteriorly concave (Figs 101, 107). Lateral margins straight to concave (Figs 100, 103, 106). Rim with white lip. Median septum and posterior plate bright with darker (redbrown) transversal band in between (SMF 61733, www).

Colour in ethanol (SMF 61733, www). Yellowish to reddish brown. Dorsal prosoma with mainly radial and irregular pattern of dark patches and white hairs. Sternum with median white band and 2 pairs of white patches in dark lateral bands. Ventral Coxae with black and white pattern, coxa IV with distinctly more white parts. Chelicerae with bright frontal oval patch and brighter inner sides. Palps almost entirely yellowish pale. Legs (especially femora, but also patellae and tibiae) with dark patches, femora between patches spotted, metatarsi and tarsi reddish brown. Dorsal opisthosoma with three thin transversal lines in front of broad transversal band consisting of black anterior and orange posterior part, anterior band with 5 larger and several smaller white patches. Posterior third behind white transverse band alternating black and orange with transverse rows of white patches. Lateral opisthosoma with irregular pattern. Ventral opisthosoma with two white parallel stripes and three pairs of white median patches with posterior pair largest and fused with lateral stripes. Spinnerets orange.

**Variation.** PL 3.9–5.3, PW 3.6–4.5, AW 1.7–2.1; OL 6.5–6.8, OW 6.2–7.1. Palpal claw with 10–12 teeth.

**Distribution.** Known from China (Yunnan Province; type locality), Laos (Champasak Province: Muang Bachieng; Khammouan Province: Thakek; Bolikhamsay Province: Lak Sao) and Thailand (Trat Province: Ko Chang; Songkhla Province: Hat Yai) (Fig. 1674, 7–9, 12–13). First records for Laos and Thailand.

***Argiope aetheroides* Yin, Wang, Zhang & Peng 1989** (Figs 108–110, 167: 3)

**Material examined (1 male).** CHINA. **1 male, 1 subadult female** (HNU), Hunan Province, Shimen County, Huping Mountain, X.J. Peng & L.P. Xie leg. 25.VI.-5.VII.1992.

A broken embolus was illustrated by Yin *et al.* (1989: fig. 1E). It resembles that of *A. jinghongensis* (Fig. 98). When the embolus tip in situ of the present material is viewed from behind (Fig. 109) it is similar to *A. luzona* (cf. Fig. 113) with its two pointed structures. Males show a distinct pattern of fine transversal lines on their dorsal opisthosoma, which is absent in males of other species of this group.

***Argiope luzona* (Walckenaer 1841)** (Figs 111–114)

**Material examined (1 male, 7 females, 8 emboli).** PHILIPPINES. **7 females [3 females: without embolus, 4 females: 2 emboli, 1 on each side], 6 juvenile females** (SMF 31444, www), Luzon, Mt. Makiling, Baker leg., Levi det. 1981. **1 male** (SMF 61140, RII 4431, www), Laguna, Luzon Island, Mt. Maquiling.

A multiple plugging as in *A. argentata* does not seem to be possible in this species, due to the lack of space in the depression when plugged with one embolus. Beside the shape of the distal part also the acute tip at the breaking zone is characteristic (Figs 111–112).

The following species (*A. pulchella*, *A. pulchelloides*, *A. dang*) and *A. versicolor* (Dole-schall 1859) exhibit an embolus distally split or furcate. *A. dang* may represent a transition to the following group of species (*A. aetherea* and others), i.e. the inner branch of the bifurcate embolus tip would be homologous to the embolic pendant.

***Argiope pulchella* Thorell 1881** (Figs 115–118)

**Material examined (5 males, 67 females, 49 emboli).** BANGLADESH. **3 females [1 female: 1 embolus]** (SMF 61408), Dhaka Province, Matikhola [N 24°38', E 90°31'], in garden behind house, Gazzal Hassan leg. 13.II.1994. BIRMA. **4 females [1 female: 1 embolus]** (SMF, RII 7992), Mt Popa, Chrysanthus det. sub *A. aetherea*, Levi rev. 1981. THAILAND: MAE HONG SON. **1 female [3 emboli]** (SMF 56702), Soppong, D. Kovac leg. 7.VI.2006. **1 female** (SMF 61159), near Ban Nam Rin, D. Kovac leg. 23.IX.2003.

TRAT. **1 male, 2 females** (SMF), Ko Chang, 3km S Hat Sai Kao, at stream bed in forest, by hand, by night, P. Jäger & S. Bayer leg. 2.XI.2009. LAOS: LUANG NAM THA. **1 female [2 emboli, 1 on each side]** (SMF 56308), 5 km N of Luang Nam Tha, N 21° 1.201', E 101° 24.632', 597 m altitude, secondary forest, vegetation, rocks, soil, beside road, by night, by hand, sweeping, P. Jäger & V. Vedel leg. 8.XI.2004. **3 females [3 emboli], 1 juvenile female** (SMF 56350), with same data as for preceding specimen, 7.XI.2004. **1 female [1 right embolus]** (SMF 56339), Muang Sing, N 21°11.422', E 101°9.45', 639 m altitude, agricultural fields, hedge, beside street, by day and night, by hand, P. Jäger & V. Vedel leg. 3.XI.2004. **1 female [without embolus]** (SMF 56365), 7.8 air km ESE Luang Nam Tha, Ban Tavan, N 20° 58.702', E 101° 28.686', 581–657 m altitude, disturbed primary forest, by day, by hand, sieving, sweeping, P. Jäger & V. Vedel leg. 9.XI.2004. OUDOMXAI. **1 female [2 emboli], 1 subadult female** (SMF 60322, www), L54, stupa hill, by night, by hand, P. Jäger & S. Bayer leg. 17.XI.2009. LUANG PRABANG. **1 female [1 embolus]** (SMF 56677), Luang Prabang, Phou Si, N 19° 53.39', E 102° 8.061', 299 m altitude, disturbed forest, by day and night, by hand, P. Jäger & J. Altmann leg. 4.+9.III.2006. **1 female [without emboli]** (SMF 56674), 9.5 air km ESE Luang Prabang, Ban Ean, Nam Khan, That Se, N 19° 50.562', E 102° 13.118', 304 m altitude, waterfall, along stream, secondary forest, by day and night, by hand, sieving, sweeping, P. Jäger & J. Altmann leg. 4.III.2006. **1 subadult female** (SMF 56675), with same data as for preceding specimen, 5.III.2006. **1 female [2 emboli]** (SMF 60414), Muang Phou Khoun, Tham Sua, L82, N 19°26'35.80", E 102°26'19.10", 1240 m altitude, in cave, vegetation along trail, on ground, ground vegetation layer, bushes, bamboo, trees, by hand, day and night, P. Jäger & S. Bayer leg. 13.XI.2009. VIENTIANE. **1 female [1 embolus]** (SMF 58681, www), 10 air km N Vang Vieng, Ban Phoxay, N 19° 0.731', E 102° 26.766', 260 m altitude, shrubs, small trees, herb layer, by day and night, by hand, P. Jäger leg. 14.III.2008. **1 female [without emboli]** (SMF 56384), 5.2 air km W Vang Vieng, Tham Pou Kham, N 18° 55.549', E 102° 23.734', 260 m altitude, outside cave, by hand, sweeping, P. Jäger & V. Vedel leg. 17.XI.2004. **1 female [2 emboli]** (SMF 56383), 1.6 air km SE Vang Vieng, N 18° 54.698', E 102° 27.35', 229 m altitude, river in agricultural fields, gravel banks and vegetation, by hand, P. Jäger & V. Vedel leg. 16.XI.2004. BOLIKHAMSAY. **1 female [2 emboli]** (SMF 60358, www), E end of Sayphou Loyang, W slopes of Pha Hua, L91, N 18°13'9.40", E 104°56'36.90", 580 m, limestone forest, plantation, vegetation, by hand, by day and night, P. Jäger & S. Bayer leg. 8.XI.2009. KHAMMOUAN. **1 female [without embolus]** (SMF 56312), 6.9 air km ENE Thakek, Ban Tham, N 17° 25.799', E 104° 51.906', 161 m altitude, outside cave, by hand, P. Jäger & V. Vedel leg. 31.X.2004. **1 female [without embolus]** (SMF 56329), 16 air km ENE Thakek, Tham En, N 17° 26.672', E 104° 56.921', 171 m altitude, inside and outside cave, by hand, sweeping, P. Jäger leg. 28.II.2003. **2 males** (SMF 56315), Ban Thathot, N 17° 37.471', E 105° 8.797', 180 m altitude, village and surroundings, by hand, sweeping, P. Jäger leg. 18.–19.II.2003. **1 female [1 embolus]** (SMF 56325), same data as for preceding specimen, 23.II.2003. **1 male, 1 subadult male, 1 female [2 emboli], 2 juvenile females** (SMF 56324), same data as for preceding specimen. CHAMPASAK. **1 female [2 emboli]** (SMF 60315), Bolaven plateau, Ban Lak 38, road 16 E, That Fane, 36 air km ENE of Pakse, Dong Hua Sao National Protected Area, L95, N 15°11'3.00", E 106° 7'36.90", 960 m altitude, garden of resort, by hand, by day, P. Jäger & S. Bayer leg. 27.XI.2009. **1 female [1 left embolus]** (SMF 60272), with same data as for preceding specimen, P. Jäger & J. Martens leg. 17.III.2010. **1 male, 1 female [2 emboli]** (SMF 60410, www), Ban Thangbeng, Tha Hou, L103, 1.8 air km S of Ban Thahou, Xe Pian National Protected Area, N 14°46'9.60", E 105°59'34.50", 130 m

altitude, rocks, vegetation, forest, by hand, by day, P. Jäger & S. Bayer leg. 22.XI.2009. INDONESIA: SUMATRA. **1 female** (SMF, RII 827), Roewer det. 1931 sub *A. reinwardti*, Jäger rev. 2010 (1 male = *A. aemula*). **5 females [8 emboli]** (SMF 31429), Fort de Kock (=Bukittinggi), Jacobson leg. 1924, Levi det. 1981. **25 females [several females: at least 1 embolus each], 3 juvenile females** (SMF 31425), Padang, Levi det. 1981. JAVA. **1 female** (SMF 3591), Krakatau, Strubell leg. 29.VI.1889, Strand det. sub *A. succincta*. WEST NUSA TENGGARA. **3 females [1 female: 2 emboli]** (SMF, RII 6614), Sumbawa, Chrysanthus det. 1959 sub *A. aetherea*.

Broken emboli as well as variation of epigynes were illustrated by Jäger & Praxaysombath (2009). Emboli can break in this species exceptionally at three different points (Levi 1983, present study): 1. rarely at the point where also the sperm duct breaks, 2. sometimes at the distal hook, 3. mostly between these positions. When it breaks in the latter position, the sperm duct extending beyond the broken embolus (see 3. above; Figs 116–117) is characteristic beside the shape of the embolus: it describes an extended semicircle, in some cases with straight parts included. The new findings match these descriptions. In all cases broken emboli were easy to remove from epigynes. The characteristic cross-shaped web decorations were observed in female webs in Laos. These might be indistinct to absent (SMF 58681, www). In juveniles and subadult males a circular web decoration as described for *A. chloreis* was found.

#### ***Argiope pulchelloides* Yin, Wang, Zhang & Peng 1989** (Figs 119–120, 167: 1–2)

**Material examined (1 male, 1 female).** CHINA. **1 male paratype** (HNU), Sichuan Province, Miyi County, X. E. Chen leg. **1 female paratype** (HNU), Sichuan Province, X.E. Chen leg. VII. 1988 [year probably mistaken, Peng personal communication].

The male palp was not fully sclerotised, part of the median apophysis was destroyed (Fig. 120: right end). Distinguished from *A. pulchella* by the shorter embolus and its less strongly split tip (Fig. 119). The spur of the median apophysis arises medially on the particular branch (Fig. 120; distally in *A. pulchella*: Fig. 118). Broken emboli are illustrated by Yin *et al.* (1989: fig. 4E, 1997: fig. 18g). These as well as epigynes are similar to those of *A. pulchella*.

#### ***Argiope dang* Jäger & Praxaysombath 2009** (Figs 121–122, 167: 6, 10)

**Material examined (2 males, 6 females, 1 embolus).** LAOS: VIENTIANE. **Holotype male** (SMF 58757, www), Vang Vieng, Nam Song, L22, riverbanks, vegetation, at night, by hand, P. Jäger & F. Steinmetz leg. 12–13.III.2007. **1 male, 2 female paratypes**

(SMF 58758), with same data as for holotype. **2 females [with 1 left embolus], 1 juvenile female** (SMF 56382), with same data as for holotype, vegetation close to river, by hand, by night, P. Jäger & S. Bayer leg. 16.XI.2009. **1 female, 1 immature female** (SMF 60916, www), with same data as for preceding specimens, 12.XI.2009. CHAMPASAK. **1 female** (SMF 60915), SE slopes of Phou Kao, Ban Nongsa, Wat Phou, 11 air km SW of Champasak, N 14°50'53.64", E 105°48'51.92", 110–200 m altitude, rocks, vegetation, by hand, by day, P. Jäger & S. Bayer leg. 28.XI.2009.

From the rounded embolus, the kink and pendant (Fig. 120–121) it is similar and probably close to *A. pulchella* and *A. pulchelloides*.

### ***Argiope mangal* Koh 1991** (Fig. 167: 14)

No material examined. From illustrations of Koh (1991) the species may key out close to *A. pulchella* or the *aetherea* group sensu Levi (1983) due to its embolus with a kink and rounded bent embolus tip and the rounded V-shaped epigynal roof in ventral view. The projection of the rim in lateral view is unique within this species-group but similar to *A. macrochoera*. Koh (1991) compares this species with *A. ocula* and *A. macrochoera*. A closer relationship with the first can be excluded by the distinctly different male palpal conformation. Males are distinguished also by the large basal outgrowth of the conductor.

The following species (*A. cameloides*, *A. modesta*, *A. pictula*, *A. appensa*, *A. brunnescentia*, *A. squallica*, *A. bougainvila*, *A. aetherea*, *A. picta*) possess an embolus with a subdistal membranous pendant. Shape, size and position of this pendant vary between species, but are invariable within species. It might be a good character for further revision of this group.

### ***Argiope cameloides* Zhu & Song 1994** (Figs 123–125, 167: 5)

**Material examined (1 male).** CHINA: HAINAN. **Holotype male** (MHBU), Ledong County, Jianfengling Mountains, N 18°42', E 108°48', Mao-Bin Gu leg. 15.VIII.1989. Description: See Zhu & Song (1994). Measurements [with data from original description if different]: PL 2.1, PW 1.7 [2.0], AW 0.7, OL 2.3 [2.2], OW 1.6 [1.2]. Chelicerae length 0.67, with 4 anterior, 3 [1] tiny posterior teeth and ca. 10 [not mentioned] denticles. The original illustrations showed no embolic pendant (Zhu *et al.* 1994: fig. 8B). In the holotype such an appendage was present in both palps (Figs 123–125), in the left

palp the tip of the pendant was bent (Figs 123–124). The latter condition and the thin membranous structure make it difficult to recognise this outgrowth. However, for future revisions material of this species group should be carefully examined in this respect. According to this feature the species appears related to those species of the *aetherea* group sensu Levi (1983) with an embolic pendant. It can be distinguished from *A. pulchella* and *A. dang* by the embolic pendant arising from the embolus distal portion of the embolus at a right angle (Fig. 125; more or less parallel to embolus tip in *A. dang* and *A. pulchella*), and from *A. modesta* (Figs 126–127), *A. pictula* (Figs, 131–133), *A. squallica* (Fig. 153), *A. appensa* (Fig. 147), *A. aetherea* (Fig. 155) and *A. brunnescentia* (Fig. 152) by its distinctly shorter pendant, and from *A. picta* (Figs 159, 161, 163, 165) by its pendant pointing in a right angle (pointing to embolus tip in *A. picta*). However, with the presence of an embolic pendant and considering the diversity within this species group the status of the species should certainly be approved by a female considering similar emboli in the *aetherea*-group.

### ***Argiope modesta* Thorell 1881** (Figs 126–130)

**Material examined (13 females, 2 emboli).** INDONESIA: JAVA. **2 females** (SMF 31606), Levi det. 1981. WEST NUSA TENGGARA. **3 females** (SMF 3527), Sumbawa, Wawo, B. Rensch leg. 1927, sub *A. crenulata*. SULAWESI. MALUKU ISLANDS. **1 female syntype of *A. aetherea keyensis* Strand 1911 [1 embolus]** (SMF 3467), Great Key, Elat, H. Merton leg. 1908, Strand det. **1 female syntype of *A. aetherea keyensis* Strand 1911** (SMF 3473), Small Key, Langgoer, H. Merton leg. 1908, Strand det. **6 females [1 embolus]** (SMF 3461, www), Key Doelah [Dula, Tual, Kepalan Ewab; Levi 1983], H. Merton leg. 1908, Strand det. sub *A. aetherea*, Levi rev. 1981.

*Argiope aetherea keyensis* Strand 1911 is removed from the synonymy of *A. aetherea* and placed in synonymy of *A. modesta*. The present females have the typical banded pattern of the *aetherea*-group (SMF 3461, www) like in *A. pulchella* or *A. jinghongensis*. They can probably be distinguished by a bright median longitudinal band in the posterior half on the ventral opisthosoma. The male is unknown, but the emboli sticking in epigynes (Figs 126–127) suggest a close relationship with *A. appensa* and *A. aetherea*. Epigyne with converging lateral margins of septum in posterior view (Fig. 129).

### ***Argiope pictula* Strand 1911** (Figs 131–146)

**Material examined (1 male, 11 females, 2 emboli).** INDONESIA: SULAWESI. **2 female syntypes of *A. crenulata pictula* Strand 1911** (SMF 3532, www), SE Sulawesi,

Boeton, SO-Bove, J. Elbert leg. 7.III.1909, 18.V.1910, Strand det. **1 female** (SMF 3533, www), Kabaena, J. Elbert leg. X.1909, Strand det. sub *A. crenulata pictula*. **Male holotype of *A. boetonica* Strand 1915** (SMF 3505, www), SE-Sulawesi, Boeton, SO-Bove, Sunda-Expedition 1909/1910, Johannes Elbert leg. 7.III.1909, 18.V.1910, Strand det., Chrysanthus rev. sub *A. aetherea* 1968, Levi rev. sub *A. appensa* 1981. **7 females [1 female: 1 left embolus], 1 subadult female** (SMF 3529, www), SE Sulawesi, Boeton, SO-Bove, J. Elbert leg. 1909, Strand det. 1910 sub *A. crenulata*. **1 female [1 left embolus]** (ex SMF 3529), SE Sulawesi, Boeton, SO-Bove, J. Elbert leg. 1909, Strand det. 1910 sub *A. crenulata*.

*Argiope boetonica* Strand 1915 is removed from the synonymy of *A. appensa* and recognised as junior synonym of *A. pictula*, since the embolus of the holotype of *A. boetonica* and especially its pendant was congruent with broken emboli in females from the type locality (Boeton = Buton) of *A. crenulata pictula*. Although females show variation in the opisthosomal colour pattern, the shape of opisthosomal margins (lobed or not) and in shape of the epigyne, both names are considered synonyms due to the striking similarity of epigynal lips in ventral and lateral view. There are transitions (SMF 3529, www) between the clear colour pattern of the syntypes of *A. pictula* (SMF 3532, www) and other material from the type locality.

The embolus shows distinct differences to all other known males of the *aetherea*-group: the embolic pendant shows a toothed to serrated distal margin (Figs 131–133) and is intermediate in its strength between the slender shape of the majority of *aetherea*-group males and the broad pendant of *A. brunnescentia*. Moreover, the median apophysis exhibits a different shape. It is therefore removed from the synonymy of *A. modesta*. Broken emboli (Figs 132–133) were found in females identified as *A. crenulata*. Shape and strength of the embolic pendant point to conspecificity with *A. pictula*. However, female copulatory organs (Figs 135–146) and colour pattern show an intermediate position between *A. modesta* and *A. appensa*.

### ***Argiope appensa* (Walckenaer 1841)** (Figs 147–151)

**Material examined (1 male, 11 females, 1 embolus).** PHILIPPINES. **1 female** (SMF, RII 4407), Sulu-Islands, Chrysanthus det. 1959. INDONESIA: SULAWESI. **1 male, 1 female** (SMF, RII 824, www), Roewer det. 1931. PALAU. **2 females** (SMF, RII 4391), Palau Islands, Roewer det. 1934. **1 female** (SMF 3584), Palau, Angaur, E. Wolf leg. 1909, Strand det. sub *A. picta*. MICRONESIA. **2 females** (SMF 3531), W-Caroline Islands, Yap, E. Wolf, leg. 20.IX.1909, Strand det. 1910 sub *A. crenulata*. **1 female** (SMF 3530), W-Caroline Islands, Feis, E. Wolf, leg. 3.X.1909, Strand det. 1910 sub *A. crenulata*. **1 female** (SMF 31424, www), Caroline Islands, Tobi, Levi det. 1981. PAPUA NEW GUINEA. **2 females [1 embolus]** (SMF 61157), Sandaun, Eitape (Aitape), leg. 1912.

Epigynes of some females (SMF 3530, 3531) are similar to those illustrated sub *A. modesta* by Levi (1983), especially in lateral view. However, dorsal and ventral opisthosomal pattern as well as the known distribution range let suggest that they belong to *A. appensa*. Embolus exhibits a long pendant with a blunt tip (Fig. 147).

*Argiope brunnescentia* Strand 1911 (Figs 152)

**Material examined (37 females, 1 embolus).** PAPUA NEW GUINEA. **2 female syntypes** (SMF 3482, www), Squally Island (Emirau Island), E. Wolf leg. 30.IV.1909, Strand det. 1910 sub *A. a. brunnescentia*. **1 female** (SMF 3488), Squally Island (Emirau Island), E. Wolf leg. 1909, Strand det. 1910 sub *A. avara*. **1 female syntype of *Argiope avara tristipes* Strand 1911** (SMF 3500, www), Squally Island, E. Wolf leg. 1909, Strand det. 1910. **5 female, 3 subadult female syntypes of *Argiope avara tristipes* Strand 1911** (SMF 3501), Squally Island, E. Wolf leg. 30.IV.1909, Strand det. 1910. **1 female syntype of *A. aetherea angulicosta* Strand 1911** (SMF 3491), Keule Island [= Koil Island], E. Wolf leg. 17.IV.1909, Strand det. 1910, Levi rev. 1981 sub *A. aetherea*. **8 female syntypes of *A. aetherea angulicosta* Strand 1911** (SMF 3492), Keule Island [= Koil Island], E. Wolf leg. 17.IV.1909, Levi rev. 1981, sub *A. aetherea*. **2 females** (SMF 3493), Keule Island [= Koil Island], E. Wolf leg. 17.IV.1909, Levi rev. 1981 sub *A. aetherea*. **6 female syntypes of *A. aetherea angulicosta* [1 embolus]** (SMF 3494), Keule Island, E. Wolf leg. 17.IV.1909, Levi rev. 1981, sub *A. aetherea*. **1 female** (SMF 3495, www), Keule Island [= Koil Island], E. Wolf leg. 17.IV.1909, Strand det. 1910 sub *A. avara*. **1 female** (SMF 3496, www), Keule Island [= Koil Island], E. Wolf leg. 17.IV.1909, Strand det. 1910 sub *A. avara*. **2 female syntypes of *A. aetherea ocelligera* Strand 1911** (SMF 3497), Keule Island [= Koil Island], E. Wolf leg. 17.IV.1909, Levi rev. 1981 sub *A. aetherea*. **1 female** (SMF 3498), Archipel, E. Wolf leg. IV.–V.1909, Strand det. 1910 sub *A. avara*. **1 female** (SMF 3499), Wogeo [=Voeko, neighbour to Koil Island], Schouten Islands [most likely a mistake], E. Wolf leg. 12.IX.1909, Strand det. 1910 sub *A. avara ocelligera*. **1 female** (SMF 3487), Wogeo [=Voeko, neighbour to Koil Island], Schouten Islands [most likely a mistake], E. Wolf leg. 1909, Strand det. 1910 sub *A. avara*. **1 female syntype of *Argiope avara tristipes* Strand 1911** (SMF 3503), Admiralty Islands, Lo Island, E. Wolf leg. 10.IX.1909, Strand det. 1910. **2 female syntypes of *Argiope avara tristipes* Strand 1911** (SMF 3502), small island close to St. Matthias, E. Wolf leg. 29.IV.1909, Strand det. 1910. **Holotype female of *Argiope lihirica* Strand 1913** (SMF 3546), New Ireland, E. Wolf leg. 3.V.1909, Strand det., Levi rev. sub *A. aetherea*. **1 immature female syntype of *A. aetherea tangana* Strand 1911** (SMF 3470), N of New Ireland, Tanga Islands, E. Wolf leg. 4.V.1909, Strand det.

*Argiope avara angulicosta* Strand 1911, *A. a. ocelligera* Strand 1911, *A. a. tristipes* Strand 1911, *A. aetherea tangana* Strand 1911 and *A. lihirica* Strand 1913 are removed from the synonymy of *A. aetherea* (sensu Levi 1983: 313) and placed in the synonymy of *A. brunnescentia*, as all specimens show clearly opisthosomal shape and colouration characteristic for the latter species. As Levi (1983) assumed the male he illustrated as belonging to *A. brunnescentia* is most likely not conspecific. New evidence for this hypothesis is given by one broken embolus from an *A. brunnescentia* epigyne (SMF 3494) which exhibits a broad and toothed embolic pendant (Fig. 152), distinctly different from all others in the *aetherea*-group. It cannot be determined to which species Levi's male belongs. Females can be recognised by the shape of their epigyne (see Levi 1983: figs 279–281), the shape of the opisthosoma (combination of a rounded pentagonal shape and a pointed posterior tip), colouration of the sternum (black with one central and 5 peripheral orange to pale yellow patches; this pattern may be indistinct in brighter specimens), dorsal opisthosoma with transversal rows of muscle sigilla reaching from

lateral in a marginal zone (these rows may be darkly coloured; sigilla in females after egg laying often indistinct), prosoma dark reddish brown, flat. Opisthosoma may be black (greyish in ethanol) with or without white patches (melanistic forms mentioned by Levi 1983: 314 had been affiliated to *A. aetherea*). Size varies strongly: body length 15.5–28.0 mm. Only one out of 37 females had a broken embolus.

### ***Argiope squallica* Strand 1915** (Figs 153–154)

**Material examined (1 male).** PAPUA NEW GUINEA. **Holotype male** (SMF 3588, www), Squally Island (Emirau Island), E. Wolf leg. 30.IV.1909, Strand det., Levi rev. sub *A. brunnescentia*.

The embolus (in situ) showed a large gap between the embolus tip and the pendant. Within this gap a small tooth-like appendage was present (Fig. 153). According to a comparison with a broken embolus in an *A. brunnescentia* epigyne (SMF 3494, see above; Fig. 152), it is definitely not a synonym of this species. It is removed from the synonymy here and placed as valid species, although it is possible that it belongs to one of the described species from the *aetherea*-group (*A. aetherea*, *A. modesta*). For shape of the median apophysis see Fig. 154.

### ***Argiope bougainvilla* (Walckenaer 1847)**

**Material examined (25 females).** PAPUA NEW GUINEA. **3 female, 3 juvenile female syntypes of *Argiope leopardina clavifemur* Strand 1911** (SMF 3503), Admiralty Islands, Lo Island, E. Wolf leg. 10.IX.1909, Strand det. 1910. **13 females, 1 subadult female, 2 juvenile females** (SMF 3544), Solomon Islands, Duka, E. Wolf leg. 29.VIII.–2. IX.1909, Strand det. sub *A. leopardina*. **8 females, 1 juvenile female** (SMF 31421, www), Madang Province, Madang, Finel Sier, Schauinsland leg. 1906, Levi det. 1981. **1 female** (SMF 61158), Bougainville, W-coast, Taboroi leg. 1908.

Some of the specimens examined have a brighter and more reticulate pattern (SMF 31421, www) in comparison to that shown by Levi (1983: 289). Few specimens exhibited a bright transversal patch on the dorsal opisthosoma anteriorly. In others the bright paraxial bands on the ventral opisthosoma are extended as a bright broad ring around the spinnerets (SMF 31421, www).

***Argiope aetherea* (Walckenaer 1841)** (Figs 155–156)

*Argiope aetherea annulipes* Thorell 1881: 68 (description of female; female holotype from Yule Islands, New Guinea, MCSN, not examined).

**Note.** Levi (1983: 313) examined the holotype and included this subspecies in the synonymy of *A. aetherea* (as proposed by Bonnet 1955: 668), but it was not followed by Platnick (2011).

**Material examined (3 males, 20 females).** INDONESIA: MALUKU ISLANDS. **1 female syntype of *A. udjirica* Strand 1911** (SMF, RII 825), Aru Islands, Roewer det. 1931. **1 female syntype of *A. udjirica* Strand 1911** (SMF 3593), Aru Islands, H. Merton leg. 15.IV.1908. **1 female** (SMF 3475), Aru Islands, Maoenmbai, Kobroor, H. Merton leg. 1908, Levi rev. 1981. **2 males** (SMF 3528, www), Kai Islands (Great Key), between Elat and Ohilim, H. Merton leg. 1908, Chrysanthus det. 1959, Levi rev. 1981. PAPUA PROVINCE. **2 females** (SMF 10545), Merauke, Gertsch det. + ded. III.1958, Coll. O. Kraus. **1 female** (SMF 22249), Merauke, Fr. Monulfus leg. 1956–1957, Chrysanthus det., Coll. Wiehle. PAPUA NEW GUINEA. **1 female, 1 subadult female syntypes of *A. aetherea melanopalpis* Strand 1911** (SMF 3469), New Ireland, Lamassa, E. Wolf leg. 7.IX.1909, Strand det. **2 female, 1 juvenile syntypes of *A. aetherea melanopalpis* Strand 1911** (SMF 3468), New Ireland, Lamassa, E. Wolf leg. VII.1909, Strand det. Levi rev. 1981. **3 female syntypes of *Argiope wolffi* Strand 1911** (SMF 3595), New Ireland, Anir, E. Wolf leg. 4.V.1909, Levi rev. 1981. **Holotype female of *A. novae-pommeraniae* Strand 1915** (SMF 3554), New Britain, Toma, E. Wolf leg. 14.V.1909, Levi rev. 1980. **1 female** (SMF 3465), New Britain, Rabaul, E. Wolf leg. 23.II.1909, 26.X.1909, Strand det. 1909 sub *A. a. deusta*, Levi rev. 1981. **1 female syntype of *A. friedericii* Strand 1911** (SMF 3542), Eitape, G. Friederici leg. XII.1909, Strand det. 1909. **2 female syntypes of *A. friedericii* Strand 1911** (SMF 3543), Eitape, G. Friederici leg. XII.1909, Strand det. 1909. **Holotype female of *A. wogeoncola* Strand 1915** (SMF 3594), Wogeo (Schouten Island), E. Wolf leg. 12.IX.1909, Levi rev. 1980 sub *A. aetherea*. AUSTRALIA. **1 female** (SMF 31420, www), Felten leg., Levi det. 1981. **1 female** (SMF 61413), Cairns, bushes, ex Coll. Wunderlich. **1 male** (SMF 61414), Cairns, bushes, VIII., ex Coll. Wunderlich.

Levi (1983) lumped many species and subspecies (23 in total) within this widely spread species. Some of these synonymies were contradicted by results of the present study (see also notes in *A. modesta* and *A. brunnescentia*). I doubt that *A. aetherea* is in fact that variable in respect to its opisthosomal shape for instance as proposed by Levi. The specimen illustrated by him (Levi 1983: figs 306–307) from the Solomon Islands (New Georgia) appears from the shape of the opisthosoma and the sternal pattern more close to *A. brunnescentia* than to *A. aetherea*. Syntypes of *A. friedericii* Strand 1911 exhibit a far longer epigyne in lateral view as shown for *A. aetherea*. The holotype female of *A. wogeoncola* shows also considerable differences to the *aetherea* epigyne illustrated by Levi (1983). The dorsal opisthosomal colour pattern of the syntypes of

*A. udjirica* and *A. wolffi* varies distinctly from what Levi (1983) illustrated as *aetherea*, sternal pattern of the latter species resembles more *A. brunnescentia*. As the species status cannot be solved here, all species mentioned above are kept in the synonymy as proposed by Levi (1983).

### ***Argiope picta* L. Koch 1871 (Figs 157–166)**

*Argiope papuana* Workman 1900: legend of plate 129 (description of female; subadult female holotype from New Guinea, Port Moresby, NMID, examined). Omitted by Levi 1983. **Syn. nov.**

**Note.** The subadult female holotype showed clearly the characteristic colour pattern (dorsal and ventral opisthosoma and sternum) of *A. picta* as shown in Levi (1983: figs 313–314) and in this paper (SMF 31423, www).

**Material examined (7 males, 85 females, 1 embolus).** INDONESIA: MALUKU. **1 female** (SMF, RII 826), Aru Islands, Roewer det. 1934 sub *A. principalis*. **1 female, 1 subadult female, 4 juvenile females** (SMF 3559), Aru Islands, close to Gomo-Gomo, Berkai, H. Merton leg. 4.IV.1908, Strand det. **1 female, 2 juvenile females** (SMF 3560), Aru Islands, close to Gomo-Gomo, Berkai, H. Merton leg. 4.IV.1908, Strand det. **1 female** (SMF 3556), Aru Islands, Kobroor, Seltoetti, H. Merton leg. 29.IV.1908, Strand det. **1 male** (SMF 3586), Aru Islands, Gomo-Gomo, Barkei, H. Merton leg. 4.IV.1908, E. Strand det. 1910 sub *A. picta*?. **3 female, 1 subadult female** (SMF 3555), Trangan Island, close to Popjetoer, H. Merton leg. 10.II.1908, Strand det. **1 subadult female** (SMF 3558), Trangan Island, Ngaigoeli, H. Merton leg. 6.II.1908, Strand det. PAPUA PROVINCE. **3 females** (SMF 3569), Jappen Island (=Yapen Island), G. Friedrici leg. I.1910, E. Strand det. 1910 sub *A. p. gorgonea*. **1 male** (SMF 3589), Yapen Island, G. Friederici leg. I.1910, Strand det. sub *A. squallica*, Chrysanthus rev. 1966. **1 female** (SMF 3561), District Jayapura, Humboldt bay (=Yos Sudarso Bay), G. Friederici leg. I.1910, E. Strand det. 1910 sub *A. p. gorgonea*. **2 males** (SMF 11399, www), Merauke, Fr. Monulfus leg. 1956–1957, Fr. Chrysanthus det. + ded., Coll. O. Kraus, VIII.1960. **3 females** (SMF 10544), Merauke, Chrysanthus det + ded. III.1958, Coll. O. Kraus. **1 male** (SMF 22248), Mindiptana, Fr. Monulfus leg. 1959, Chrysanthus det. sub *A. aetherea*, Levi rev. sub *A. picta*, Coll. Wiehle. **1 female** (SMF 25252), Merauke, Fr. Monulfus leg. 1956–1957, Chrysanthus det., Coll. Wiehle. **1 male** (SMF 22251), Merauke, Fr. Monulfus leg. 1956–1957, Chrysanthus det., Coll. Wiehle. PAPUA NEW GUINEA. **6 females [1 left embolus], 5 juvenile females** (SMF 3565), Eitape, G. Friederici leg. XII.1909, E. Strand det. 1910 sub *A. p. gorgonea*. **2 females** (SMF 3568), Eitape, E. Wolf leg. 14.IX.1909, E. Strand det. 1910 sub *A. p. gorgonea*. **4 females** (SMF 3581), Eitape, G. Friederici leg. XII.1909, E. Strand det. 1910 sub *A. p. principalis*. **1 female, 1 juvenile female** (SMF 3585), Eitape, G. Friederici leg. XII.1909, Strand det. 1910. **29 females [all without emboli], 6 subadult females** (SMF 61002), Eitape, leg. 1912. **1 female [cf. *A. picta*]** (SMF 61150), Sandaun, Aitape (Berlinhafen), Seleo Island, Rei-

se L.C. 1912, W. Drewcke leg. 1900. **3 females** (SMF 3580), Sandaun Province, Sera, Sissano, G. Friederici leg. I.1910, Strand det. 1910 sub *A. p. principalis*. **2 females [1 without opisthosoma]** (SMF 61056, ex RII 5474), Matupi [=Matupit]. **1 female** (SMF, RII 818), Roewer det. 1934. **1 male [left embolus broken off], 1 subadult female** (SMF, RII 1153), Roewer det. 1934 sub *A. aetherea*, Levi rev. 1981. **1 female** (SMF, RII 6612), Dorey, Chrysanthus det. 1959. **4 females** (SMF 3562), New Britain, Toma, E. Wolf leg. 12.–15.V.1909, E. Strand det. 1910 sub *A. p. gorgonea*. **1 female** (SMF 3574), New Britain, Toma, E. Wolf leg. 12.–15.V.1909, E. Strand det. 1910 sub *A. p. gorgonea*. **2 females, 1 juvenile female** (SMF 3566), New Guinea Archipel, E. Wolf leg. IV.–V.1909, E. Strand det. 1910 sub *A. p. gorgonea*. **1 female** (SMF 3564), Keule Island [= Koil Island], E. Wolf leg. 17.IV.1909, E. Strand det. 1910 sub *A. p. gorgonea*. **1 female** (SMF 3567), New Ireland, Lamassa, E. Wolf leg. 7.IX.1909, E. Strand det. 1910 sub *A. p. gorgonea*. **2 females** (SMF 3572), Admiralty Islands, Pack Islands, E. Wolf leg. 10.IX.1909, E. Strand det. 1910 sub *A. p. gorgonea*. **1 female** (SMF 3577), Admiralty Islands, Lo Island, E. Wolf leg. 10.IX.1909, Strand det. 1910 sub *A. p. principalis*. **1 female** (SMF 3582), Admiralty Islands, Balnen, E. Wolf leg. 10.IX.1910, Strand det. 1910 sub *A. p. principalis*. **1 female** (SMF 3573), Solomon Islands, Buka, E. Wolf leg. 29.VIII–2.IX.1909, E. Strand det. 1910 sub *A. p. gorgonea*. **4 females, 3 juvenile females** (SMF 3571), Bougainville, E. Wolf leg. 28.VIII.1909, E. Strand det. 1910 sub *A. p. gorgonea*. AUSTRALIA. **1 female** (SMF 31423, www), Junisfail (= Innisfail, Queensland?), Felten leg., Levi det. 1981. **1 female** (SMF, RII 5486), Australia, Cap York, Chrysanthus det. 1959.

One male was found with one left embolus broken off. However, in only one of the females examined (n=85) a left broken embolus could be observed. The pendant of this embolus had two tiny apices (Figs 157–158) in contrast to that illustrated by Levi in situ (1983: fig. 315). Another male (SMF 3586) from Aru Islands, showed differences in the pendant as well as in the shape of the median apophysis (Figs 159–160). One feature shared by males examined was the broad and proximally extending base of the stout pendant (Figs 157, 159, 161, 63, 165) in contrast to other species of the *aetherea*-group.

### ***Argiope comorica* Bjørn 1997** (Figs 490–494)

**Material examined (1 female).** COMORES. **1 female** (RMCA 208.322), Mayotte, Coconi [12°50'2.49"S, 45° 8'11.72"E], campus de la DAF, by hand, R. Jocqué leg. 18.VII.1998, M. Grasshoff det.

The female represents the second record in general and the first record from Mayotte Island (type locality is Grande Comore [=Ngazidja] c. 230 air km apart from the new locality). The present female is slightly larger than the holotype (Bjørn 1997: 229, total length 4.6): PL 2.65, PW 2.5, AW 1.3, OL 4.5, OW 3.6. Chelicerae have 4 anterior and 3 left and 4 right posterior teeth with ca. 20 denticles in the cheliceral furrow.

## Misplaced species

### *Nephila clavata* L. Koch 1878

*Argiope maja* Bösenberg & Strand 1906: 201, text-fig. 1 (description of female; female holotype from Yokohama; according to the editorial by Strand material should be deposited in the Senckenberg collection, but the type could not be found, most likely lost).

**Syn. nov.**

**Note.** Levi (1983: 262) suspected that this species indeed represents a female of *N. clavata*. A careful comparison of the original text description (in German) and material from the SMF collection showed several characters, which point definitely to a synonymy of both species names: 1. Triangular labium with median longitudinal yellow-orange band, the same band at sternum interrupted in the centre of the sternum. 2. The colour pattern described especially of the legs fits exactly the specimens examined; opisthosomal pattern and colouration is variable and sometimes faded, therefore not good in this respect. 3. Size of 20 mm body length: there are only few species with this size and similar colouration in Japan: *Argiope amoena*, *A. bruennichi*, *A. boesenbergi* and *A. aemula*, all of which lacking diagnostic characters mentioned. *Nephila pilipes*, another large species, has a different colour pattern. One confusing issue is the epigyne illustrated together with the text description: a median cleft should be surrounded by one dark crescent bulge on each side. One explanation for this discrepancy may be the bad optics at the time of the description. Indeed, there are two dark lateral areas in the epigyne of *N. clavata*, which might be interpreted as bulges. Another explanation could be a confusion of original drawings by Bösenberg, which were compiled together by Strand after Bösenberg died (Bösenberg & Strand 1906: foreword).

### *Cyrtophora moluccensis* (Doleschall 1857)

*Epeira moluccensis* Doleschall 1857: 418 (description of female; type[s] from Amboina, not found according to Tanikawa *et al.* 2010)

*Argiope thai* Levi 1983: 292, figs 152–156, map 4 (description of female; holotype female from Thailand, Chantaburi, Preuw, MCZ, not examined). **Syn. nov.**

Note. Levi (1983) described this species from one female in poor condition. From his illustrations of opisthosomal colouration and female copulatory organ it is clearly a synonym of *C. moluccensis*, as analysed and illustrated by Tanikawa *et al.* (2010). Especially ventral and lateral view of the epigyne differentiates *C. moluccensis* from *C. ikomosanensis* (Bösenberg & Strand 1906) (Tanikawa *et al.* 2010: figs 8–17).

## DISCUSSION

It could be confirmed that males of *Argiope* spp. break regularly their emboli during the copulation. Although in some species no broken emboli could be found it is not clear whether this is an artefact due to preservation in ethanol, or whether only the short tip is broken, which is hardly recognisable without a maceration (cf. Uhl *et al.* 2007). Another explanation could be that the embolus usually breaks during copulation and the shape of the epigyne (widely open depression without distinct rims) impedes retaining of larger parts of emboli (e.g., in *A. picta*). From the results it is not clear whether in all species with broken emboli these structures are good for an effective plugging in respect of sexual competition between males ('first come, first serve'). In species with multiple plugging, e.g. *A. argentata*, with up to 5 emboli sticking in one side of the epigyne, it seemed as if one embolus was really sticking in and plugging the copulatory duct, and additional emboli were more or less loosely attached, although properly fixed in the epigynal depression. This provides evidence that only the hook may represent the efficient plug of the narrow copulatory duct (cf. Uhl *et al.* 2007). Evidences of broken hook parts are seen in various species. However, only paternity experiments can give a clue about functional aspects (cf. Nessler *et al.* 2006, 2007).

In some species no emboli were recorded in epigynes, e.g., *Argiope picta* L. Koch 1871 (with 35 females examined). It cannot be excluded that only the distal tip breaks off in this species as shown for *A. bruennichi* by Nessler *et al.* (2006: figs C–D) with macerated female copulatory organs. Apparently, the construction of epigynes with wide atria or the functional interaction between an epigyne with a wide atrial opening and an embolus does not allow a retaining of a larger embolus tip. In contrast, in some species a rim was found within the epigynal atrium, where the hook of the embolic breaking point (H in Figs 77, 81) was fixed in that way that a removal of a broken tip with micro-pins or forceps was difficult (e.g., *A. bivittigera*). Levi (1983) mentioned that emboli usually are 'wedged into the opening'. An 'exudate' (secretion) mentioned by Levi (1983: 250) could not be observed in any of the species treated (exception: Fig. 43: *A. aurantia*). Some emboli are hidden as for instance in *A. aurantia* or *A. bruennichi*. In *Argiope* species there are usually two breaking zones in male emboli and usage of breaking points differs between populations of the same species (Uhl *et al.* 2007: *A. bruennichi*, Jäger & Praxaysombath 2009: *A. pulchella*, present study). In some species numerous emboli have been found in epigynes, e.g. *A. argentata* with five emboli stuck in the right half of the epigyne (SMF 31446). Another female of the same species had 4 emboli on each side. One *Argiope sector* female from Tunisia (SMF 37082) had 4 right and 3 left emboli. In all cases encountered left emboli were found in the left half of the epigyne and right palps accordingly.

When using emboli as identification aid it became clear that certain restrictions have to be considered. While comparing broken emboli with emboli in situ on an intact palp it was apparent that they change their shape when they were fixed in an epigyne. This is true for specimens freshly collected as well as for material preserved 100 years ago. Emboli coil or bend mostly in direction of their membranous flange at the concave side (F in Figs 34, 44, 59, 68, 127, 157), the degree of coiling or bending varies. It may be that this membranous flange in combination with the rigid antagonistic convex part is

essential for bending and fixing the embolus or its tip in the copulatory opening, thus being a possible morphological precondition for using emboli as plugs. In contrast, emboli without such flanges are known to retain their original shape within seconds after removal from the copulatory ducts due to the elastic properties of the exocuticle (e.g., *Holconia* sp., Sparassidae, with more than 7 distal embolus coils, Jäger unpublished). The present paper cannot trace this question in depth, as a broad comparison between embolus and palp morphology in groups of plugging and non-plugging Araneidae and probably other families would be necessary. Functional aspects would have to be investigated experimentally. However, Grasshoff (1984: figs 11–13) showed such flanges for broken embolis of *Caerostris* species.

Finally, few ambiguous cases of African species occurred in the present study, where broken emboli and epigynes did not match at least when using diagnostic characters listed in the key of Bjørn (1997) (see illustrations of *A. lobata* and *A. australis* in the present paper). Four options are possible: 1. Males mate with females of other species, 2. Females have a much higher variability than shown in Bjørn (1997), 3. Males have a higher variability, 4. Both forms belong to one species with a high degree of variability. It may occur that among these four possibilities the last one is true, i.e. that both forms represent in fact one species with a wide distribution and a strong variability (Bjørn, in litt., present study). Larger sample sizes may be help in finding answers.

In general, not all species could be distinguished by emboli, especially in cases of simple emboli without any special outgrowths. In these cases a thorough analysis of the base of the broken embolus may help to find diagnostic characters.

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## LEGENDS

**FIGURES 1–28. *Argiope* spp.**, copulatory organs (1–2, 4–7, 10–11, 15–20 Broken embolus; 3, 8 Embolus in situ; 9 Internal duct system, dorsal; 12, 21, 28 Epigyne ventral view; 13, 22, 24, 26–27 Epigyne posterior view; 14, 23, 25 Epigyne lateral view). **1–2 *Argiope manila* Levi 1983** from Luzon, Philippines, female paratype (SMF 31439). **3–7 *Argiope aemula* (Walckenaer 1841)** (3 Luzon, Philippines, R II 4452; 4–7 females from Indonesia, W Sumatra, SMF 31433). **8–9 *Argiope catenulata* (Doleschall 1859)** (8 Laos, SMF 61298; 9 Indonesia, Sulawesi, SMF R II 4192). **10–14 *Argiope bivittigera* Strand 1911** from Indonesia, Maluku Islands, Kai Islands (10–11 SMF 3535; 12–14 SMF 3538). **15–28 *Argiope reinwardti* (Doleschall 1859)** from Indonesia, Java (15, 21–23 SMF 61730; 16–17, 24–25 SMF 61731; 18, 26 SMF 31600; 19–20, 27–28 Syn-type, NMNH). A — Apophysis with opening of sperm duct, B — Distal bulge of embolus, ET — Embolus tip, O — Outgrowth, SD — Sperm duct. Arrow pointing to spherical spermathecae in lateral view.

**FIGURES 29–43. *Argiope* spp.**, copulatory organs (29, 32–38, 42–43 Broken embolus [35 same embolus as in Fig. 34, but in different view]; 30, 40 Epigyne ventral view; 31 Epigyne posterior view; 39 Tip of embolus in situ; 41 Epigyne lateral view). **29–31 *Argiope doleschalli* Thorell 1873**, female holotype from Indonesia, Maluku Islands, Ambon (NMNH). **32 *Argiope* sp.**, female from Indonesia, Maluku Islands, Aru Islands (SMF 3520). **33 *Argiope boesenbergi* Levi 1983** from Japan (SMF 3464). **34–35 *Argiope amoena* L. Koch 1878** from Japan (34 SMF 3481; 35 SMF 31417). **36 *Argiope magnifica* L. Koch 1871** from Papua New Guinea (SMF 3460). **37–41 *Argiope bruennichi* Scopoli 1772** (37 from Greece, Crete, RII 815; 38 from female holotype of *Argiope bruennichi orientalis* Strand 1907 from W-Europe [see remark in text], SMF 31604; 39–41 from Japan, SMF 3509). **42–43 *Argiope aurantia* Lucas 1833** from USA, Texas (SMF 61099). F — Membranous flange at concave side of embolus.

**FIGURES 44–58. *Argiope* spp.**, copulatory organs (44–47, 49–50, 56–58 Broken embolus; 48, 51 Epigyne, ventral view; 52 Epigyne, posterior view; 53 Epigyne lateral view; 54 Embolus in situ; 55 median apophysis). **44–48 *Argiope lobata* Pallas 1872** (44 from Italy, SMF 61146; 45–46 from Spain, SMF 61055; 47–48 Namibia, Windhoek, SMF 61145). **49–53 *Argiope australis* (Walckenaer 1805)** (49 from South Africa, Namaqualand, SMF 61124; 50–53 from South Africa, Transvaal, SMF 61123). **54–58 *Argiope sector* (Forsskål 1775)** (54–56 from Cape Verde Islands, SMF 31853; 57–58 from Egypt, SMF 61126). F — Membranous flange at concave side of embolus. T — Embolic thorn.

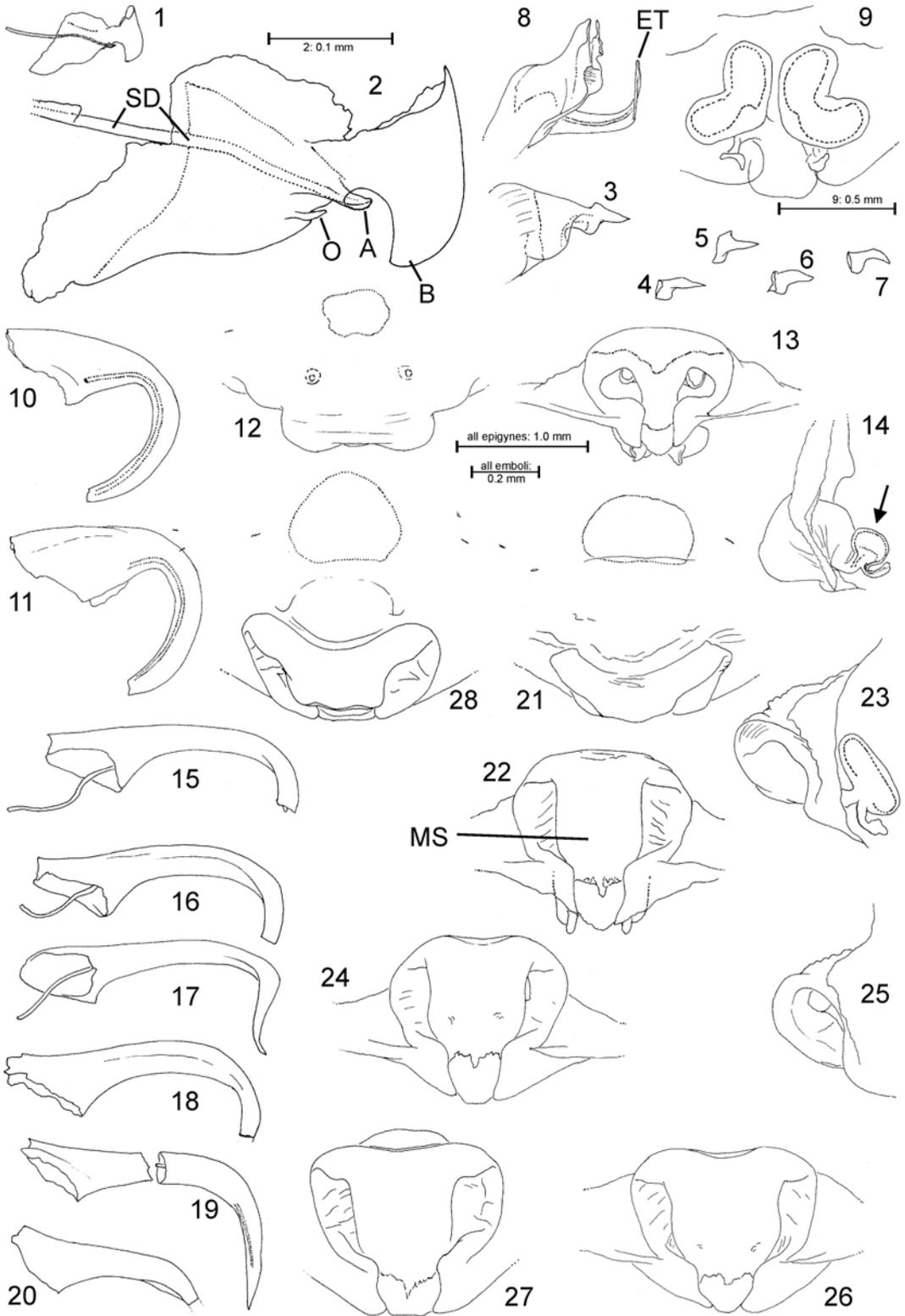
**FIGURES 59–92. *Argiope* spp.**, copulatory organs (62, 65, 68, 84, 88 Embolus in situ; 59, 63–64, 66–67, 74–83, Broken embolus; 60, 72 Epigyne, posterior view; 69 Epigyne, ventral posterior view; 70–71 Epigyne, between ventral and posterior view; 72 Epigyne, lateral view; 85 Median apophysis; 86 Internal duct system, lateral view; 87 Internal duct system, dorsal view). **59–60 *Argiope* sp. cf. *tapinlobata* Bjørn 1997** from Namibia (SMF 61122). **61 *Argiope coquereli* (Vinson 1863)** from Madagascar (SMF 3526). **62–64 *Argiope flavipalpis* (Lucas 1858)** (62 from Congo, SMF 61133; 63 from Ivory

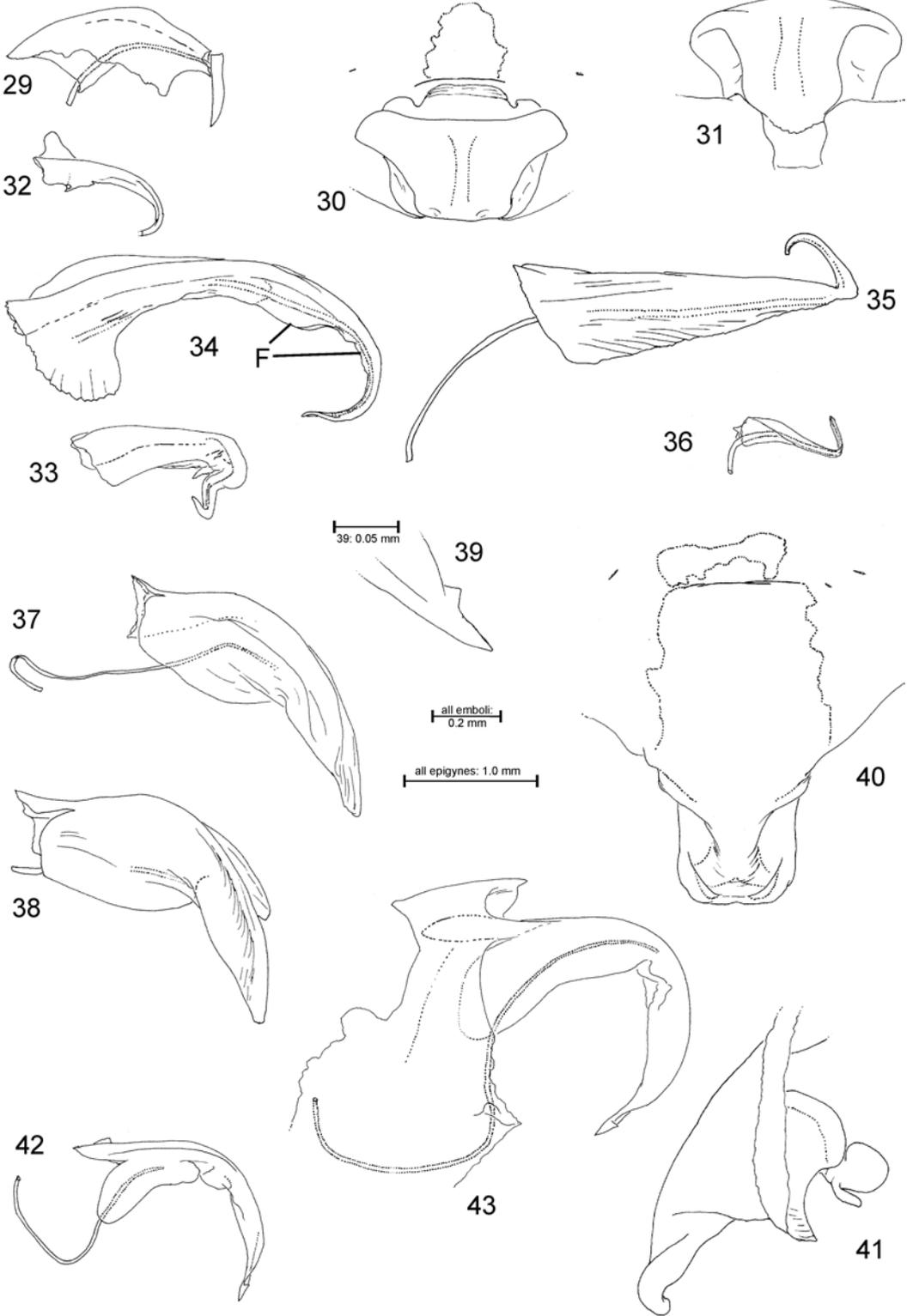
coast, SMF 61132, 64 from Cameroon, SMF 61144). **65–67 *Argiope protensa* L. Koch 1872** from Australia (65 SMF 38009; 66 RII 4411; 67 SMF 3587). **68 *Argiope trifasciata* (Forsskål 1775)** from Portugal, Madeira (SMF 61089). **69–72 *Argiope chloreis* Thorell 1877**, female from Laos (SMF 61143). **73–79 *Argiope argentata* (Fabricius 1775)** 73 Brazil (SMF 61101). 74 Honduras (SMF 61111). 75 Brazil, Pernambuco (SMF 61100). 76–77 Colombia (SMF 61107: 76 with broken apophysis). 78–79 Brazil, Bahia (SMF 61098). **80–82 *Argiope blanda* O. Pickard-Cambridge 1898**. 80 El Salvador (SMF 7876). 81–82 Mexico (SMF 61094). **83 *Argiope submaronica* Strand 1916**, Brazil (SMF 61117). **84–87 *Argiope anasuja* Thorell 1887**, male and female from Maldives (SMF 31437). **88 *Argiope minuta* Karsch 1879**, male from Japan (SMF 3551). **89–92 *Argiope hinderlichi* spec. nov.**, holotype female from Laos, copulatory organs (89 Broken embolus; 90 Epigyne, ventral view; 91 Epigyne, posterior view; 92 Epigyne, lateral view) (SMF) (86–87 Not so scale). F — Membranous flange at concave side of embolus, H — Hook at base of embolus tip, S — Secretion, SS — Slit sense organ, T — Tip of embolus.

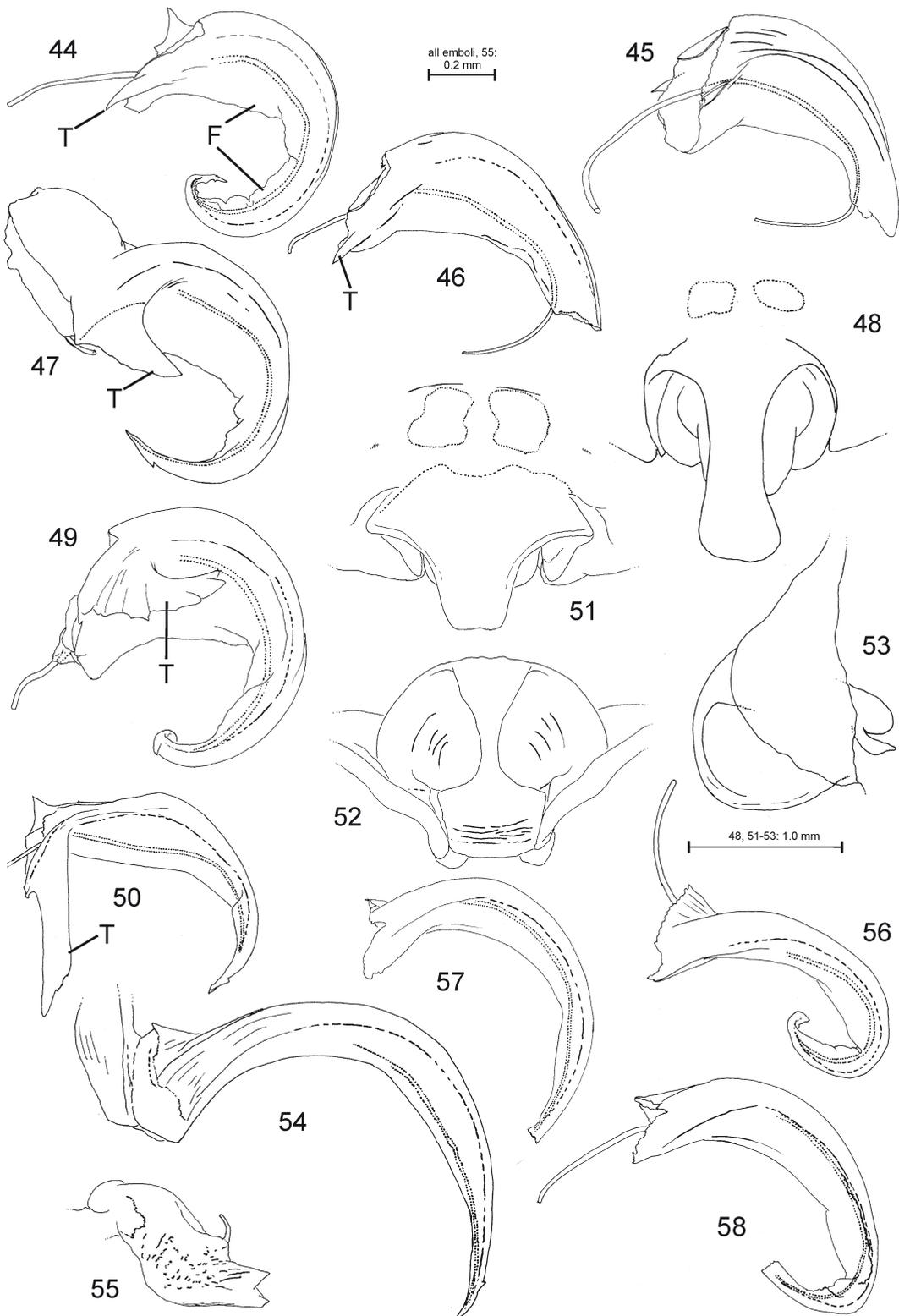
**FIGURES 93–114. *Argiope* spp.**, copulatory organs (93, 108–109, 113 Embolus in situ; 94 Right male palp, mesal view, mirrored; 98, 111–112 Broken embolus; 95–97, 110, 114 Median apophysis; 99, 102, 105 Epigyne, ventral view; 100, 103, 106 Epigyne, posterior view; 101, 104, 107 Epigyne lateral view). **93–107 *Argiope jinghongensis* Yin, Peng & Wang 1994**. 93 Holotype male from China, Yunnan Province (HNU). 94–97 Male from Thailand, Koh Chang (SMF 61733). 95–101 Female from Thailand, Koh Chang (SMF 61733). 102–104 Female from Laos, Bolikhamsay Province (SMF 61735). 105–107 Female from Laos, Champasak Province (SMF 61734). **108–110 *Argiope aetheroideis* Yin, Wang, Zhang & Peng 1989**, male from China, Hunan Province (HNU). **111–114 *Argiope luzona* (Walckenaer 1841)**. 111–112 Females from Philippines, Luzon (SMF 31444). 113–114 Male from Philippines, Luzon (SMF 61140). C — Conductor, CM — Convex anterior margin of epigyne, M — Parallel margin of epigynal septum, PP — Posterior plate of epigynal septum, PT — Protrusions of embolus tip, SD — Sperm duct.

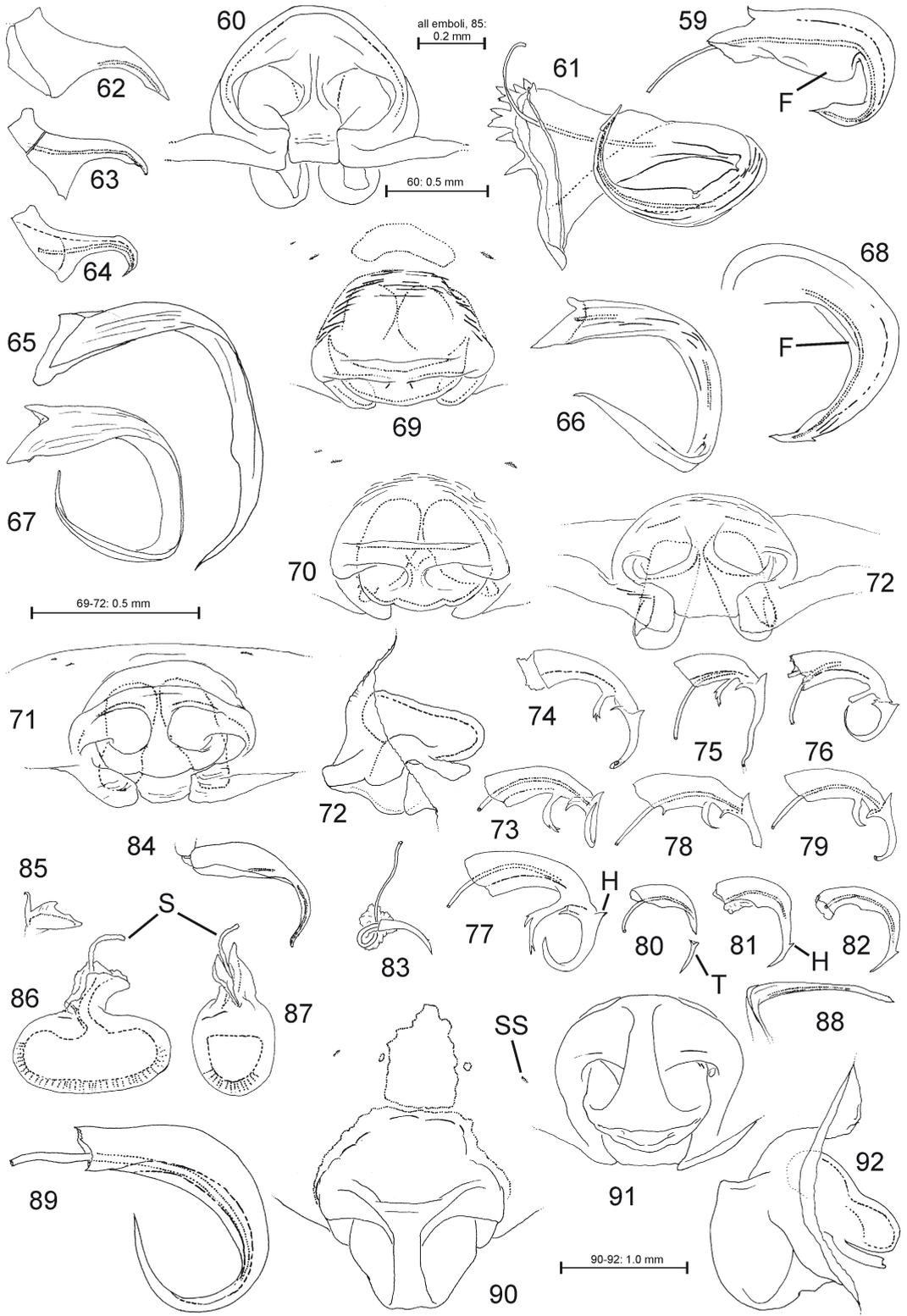
**FIGURES 115–140 *Argiope* spp.**, male copulatory organs (115, 121 Palp, mesal view; 116–117, 122, 126–127, 132–133 Broken embolus; 118, 120, 134 Median apophysis; 119, 123–125, 131 Embolus in situ; 128, 135, 139 Epigyne, ventral view; 129, 136 Epigyne, posterior view; 130, 138, 140 Epigyne, lateral view; 137 Epigyne, posterior-ventral view). **115–118 *Argiope pulchella* Thorell 1881**. 115, 118 from Laos, Luang Prabang Province (SMF 56367); 116 from Laos, Khammouan Province (SMF 56325); 117 from Indonesia, West Nusa Tenggara (RII 6614). **119–120 *Argiope pulchelloides* Yin, Wang, Zhang & Peng 1989** paratype from China, Hunan Province (HNU). **121–122 *Argiope dang* Jäger & Praxaysombath 2009** from Laos, Vientiane Province. 121 Holotype (SMF 58757); 122 Female (SMF 56382). (115–116, 121 modified from Jäger & Praxaysombath 2009). **123–125 *Argiope cameloides* Zhu & Song 1994**, holotype from China, Hainan Province (MHBU). **126–130 *Argiope modesta* Thorell 1881**. 126 Female from Indonesia, Maluku Islands (SMF 3461); 127–130 Female syntype of *A. aetherea keyensis* Strand 1911 from Indonesia, Maluku Islands (SMF 3467). **131–140 *Argiope pictula* Strand 1911** from Indonesia, SE Sulawesi. 131, 134 Male holotype of *A. boetonica* Strand 1915 (SMF 3505); 132–133, 135–140 Females (SMF 3529). F — Membranous flange at concave side of embolus, K — Embolic kink, MA — Median apophysis, P — Embolic pendant.

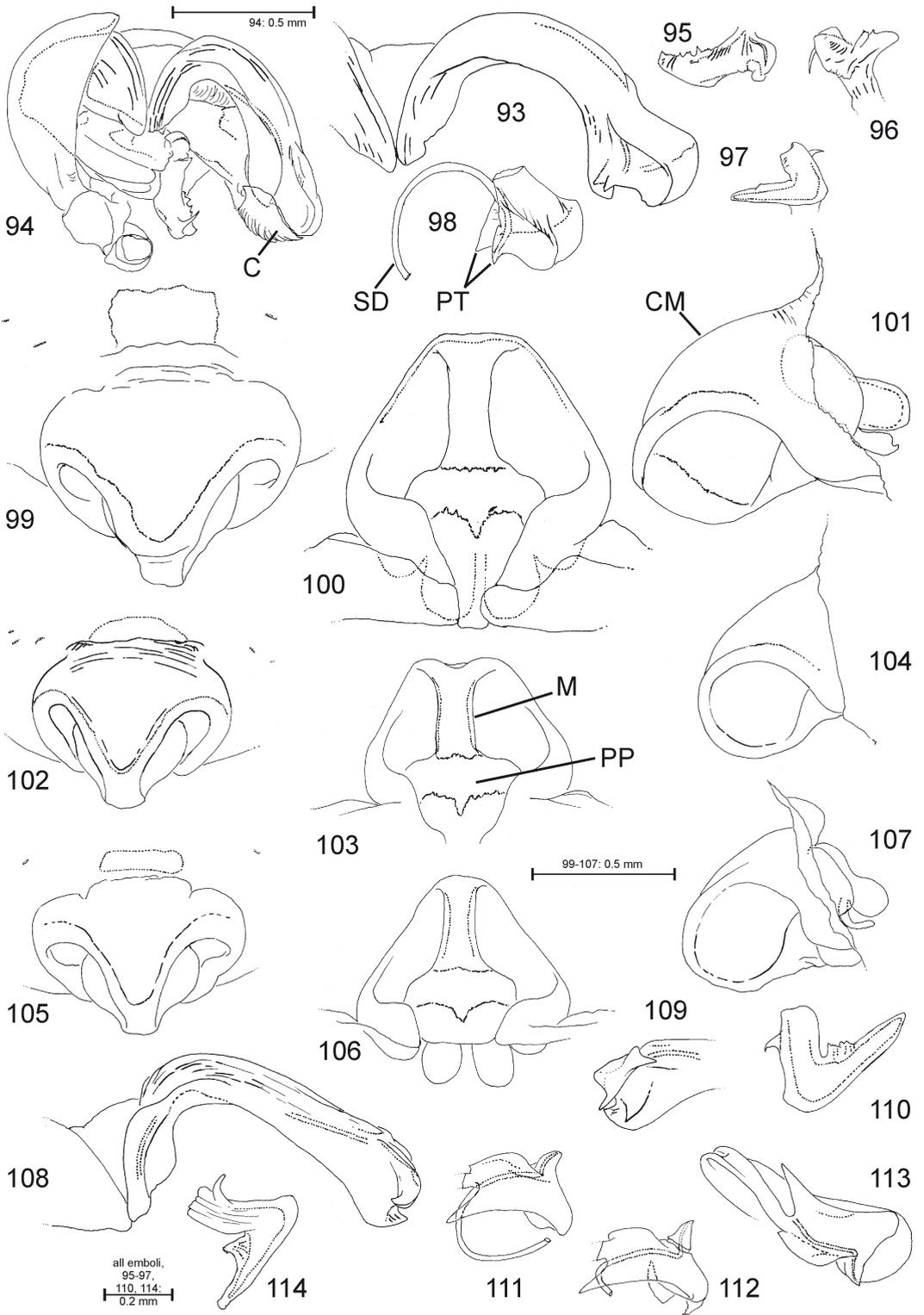
**FIGURES 141–166 *Argiope* spp.**, copulatory organs (141–142, 146, 149 Epigyne, ventral view; 143, 150 Epigyne, posterior view; 144 Epigyne, posterior-ventral view; 145, 151 Epigyne, lateral view; 147–148, 152, 157–158 Broken embolus [148 detail of tip] ; 153, 155, 159, 161, 163, 165 Embolus, in situ; 154, 156, 160, 162, 164, 166 Median apophysis). **141–146 *Argiope pictula* Strand 1911** from Indonesia, SE Sulawesi. 141–145 Female syntypes of *A. crenulata pictula* Strand 1911 (SMF 3532); 146 Female from Kabaena (SMF 3533). **147–151 *Argiope appensa* (Walckenaer 1841)** from Papua New Guinea, Eitape (SMF 61157). **152 *Argiope brunnescentia* Strand 1911**, female syntype of *A. aetherea angulicosta* Strand 1911 from Papua New Guinea, Keule Island (SMF 3494). **153–154 *Argiope squallica* Strand 1915**, holotype male from Papua New Guinea, Squally Island (SMF 3588). **155–156 *Argiope aetherea* (Walckenaer 1841)**, male from Indonesia, Maluku Islands (SMF 3528). **157–166 *Argiope picta* L. Koch 1871**. 157–158 Female from Papua New Guinea, Eitape (SMF 3565); 159–160 Male from Indonesia, Maluku Islands (SMF 3586). 161–166 Males from Indonesia, Papua Province (161–162 SMF 3589; 163–164 SMF 22251; 165–166 SMF 22248). F — Membranous flange at concave side of embolus, P — Embolic pendant.

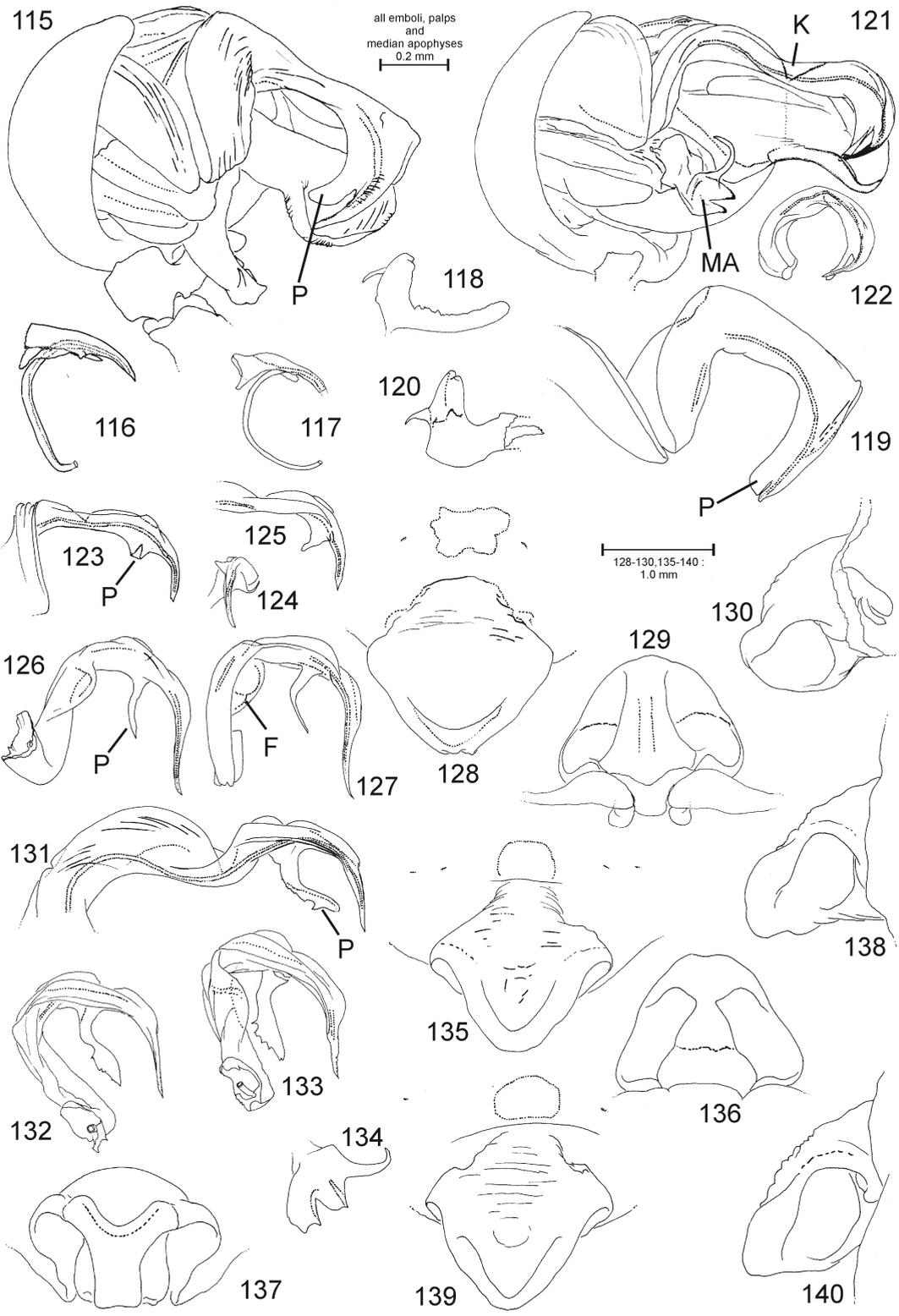


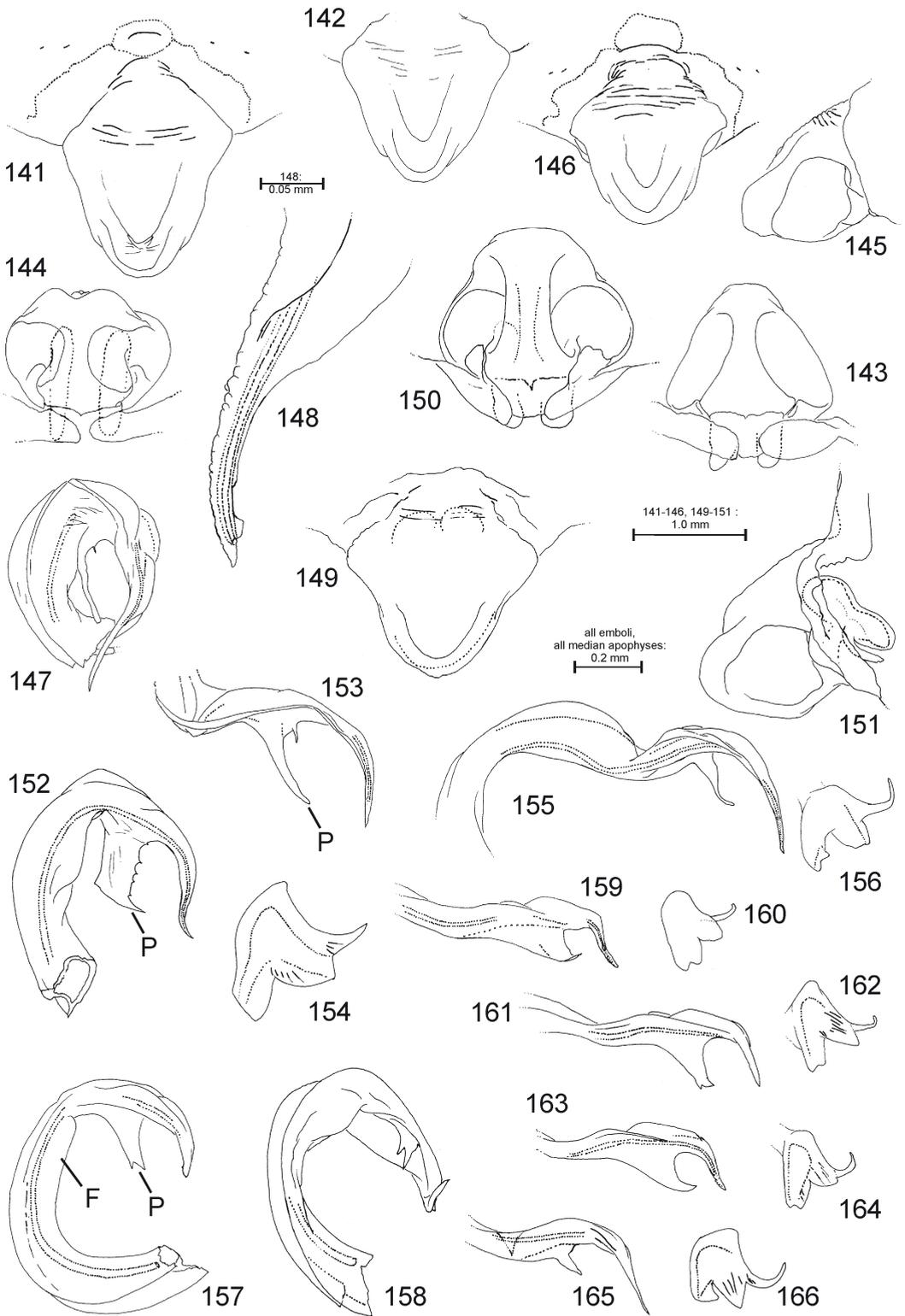


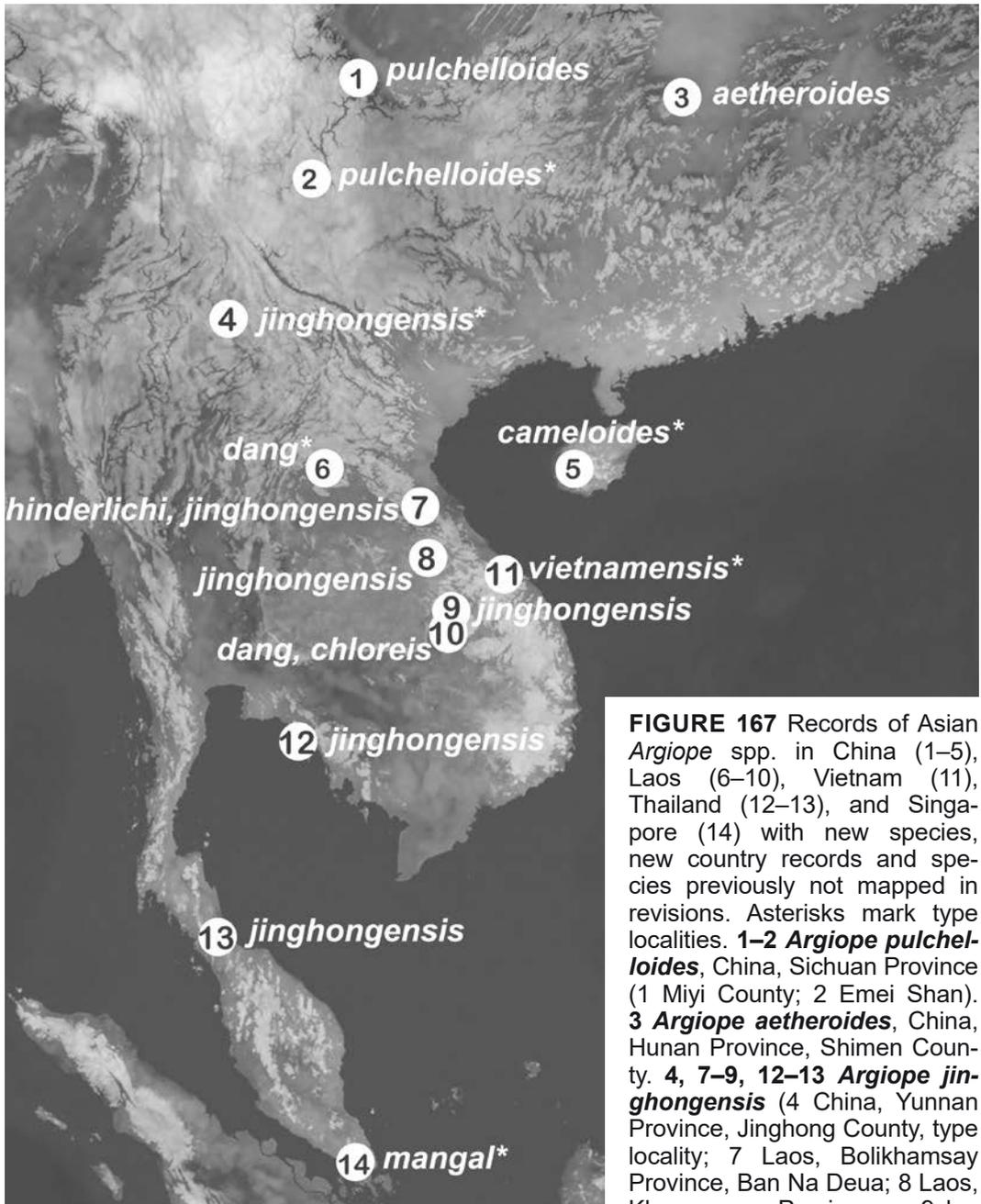












**FIGURE 167** Records of Asian *Argiope* spp. in China (1–5), Laos (6–10), Vietnam (11), Thailand (12–13), and Singapore (14) with new species, new country records and species previously not mapped in revisions. Asterisks mark type localities. **1–2 *Argiope pulchelloides***, China, Sichuan Province (1 Miyi County; 2 Emei Shan). **3 *Argiope aetherooides***, China, Hunan Province, Shimen County. **4, 7–9, 12–13 *Argiope jinghongensis*** (4 China, Yunnan Province, Jinghong County, type locality; 7 Laos, Bolikhamsay Province, Ban Na Deua; 8 Laos, Khammouan Province, c. 9 km

NE Thakek; 9 Laos, Champasak Province, Tad Paxuam; 12 Thailand, Trat Province, Koh Chang; 13 Thailand, Song Khla Province). **5 *Argiope cameloides***, China, Hainan Province, Mt. Jianfengling. **6, 10 *Argiope dang***, Laos (1 Champasak Province, Wat Phou; 13 Champasak Province, Wat Phou). **7 *Argiope hinderlichi spec. nov.***, Laos, Bolikhamsay Province, Lak Sao, type locality. **10 *Argiope chloreis***, Laos, Champasak Province, Tha Hou, first country record, most northern record. **11 *Argiope vietnamensis***, Vietnam, Thua Hien-Hue Province, close to Bach Ma National Park, type locality. **14 *Argiope mangal***, Singapore.



## THE COLOURED PHOTOS

### LEGENDS TO THE PHOTOS, I A: SPIDERS IN COPAL FROM MADAGASCAR

1) *Mysmena* (s. l.) sp. indet. (Mysmenidae), ♂, body length 0.65 mm, lateral aspect, F2371/CM/AR/ CJW.

2) *Madagascarphantes vomerans* n. gen. n. sp. (Linyphiidae), ♂, body length 1.4 mm, lateroventral aspect, F2358/CM/AR/CJW.

3-4) *Lasaeola (Phycosoma) inclinata* n. sp. (Theridiidae), ♂ holotype, body length 1.7 mm, lateral and lateral-dorsal aspects. The arrows point to the anterior prosomal inclination. Note the preservation of the original colouration of body and legs, F2359/CM/AR/CJW.

5) *Platnickina duosetae* n. sp. (Theridiidae), ♂, body length 1.35 mm, anterior-right aspect, F2360/CM/AR/CJW.

6) *Flagellidictyna copalis* n. gen. n. sp. (Dictynidae), ♂, body length 1 mm, dorsal aspect, F2370/CM/ AR/CJW.

7-10) *Dictyna rufa* n. sp. (Dictynidae), ♂ holotype, body length 1.65 mm. Dorsal, dorsal-anterior and ventral aspects. The arrow in photo 7) points to the amputated right tibia I. Note the preservation of the original colouration. 8 and 10: F2372/CM/AR/CJW, 7 and 9: F2373/CM/CJW.

11-12) *Copaldictyna madagascariensis* WUNDERLICH 2004 (?Titanoeceidae), ♂, body length 3 mm, lateral aspects of body and left pedipalpus, F2342/CM/AR/CJW.

## LEGENDS TO THE PHOTOS, I B: SPIDERS IN BALTIC AMBER

- 1) *Segestria flexio* WUNDERLICH 2004 (Segestriidae), ♂, body length 3.5 mm, lateral aspect, F2286/BB/AR/CJW. pedipalpus (note the large paracymbium) with anterior part of the prosoma. F2321/BB/AR/CJW.
- 2-4) *Samlandicmeta mutila* n. gen. n. sp. (Tetragnathidae), ♂, body length 2.6 mm, dorsal and ventral aspects, F2354/BB/AR/CJW. 19-20) *Praetheridion fleissneri* WUNDERLICH 2004 (Praetheridiidae), ♂, body length 4.2 mm, dorsal aspect of the body and prolateral aspect of the left pedipalpus. F2273/BB/AR/CJW.
- 5-6) *Baltleucauge propinqua* n. sp. (Tetragnathidae), ♂, body length 4 mm, dorsal aspects, F2355/BB/AR/CJW. 21-22) *Eoprychia ?succini* PETRUNKEVITCH 1958 (Zoropsidae s. l.: Eoprychini), ♀, body length 10 mm, ventral aspect of the posterior part of the opisthosoma with some leg articles and the spinnerets; the arrow points to the cribellum. Coll. F. KERNEGGER.
- 7-8) *Graea magnocoli* n. sp. (Zygiellidae), ♂, body length 3.5 mm, anterior and ventral aspects, F2322/BB/AR/CJW. 23) *Succiniropsis runcinata* n. sp. (Zoropsidae s. l.: Eomatachiini), ♂, body length 2.6 mm, ventral aspect. F2357/BB/AR/CJW.
- 9) ?*Araneus* sp. (Araneidae), inad. ♀, body length 10.5 mm, dorsal aspect. Body and legs are covered with a white emulsion, the arrow points to the anterior prosomal margin. Note the wide eye field and the wide opisthosoma. F2323/BB/AR/CJW. 24-27) ?*Succinomus gibbosus* n. sp. (Succinomidae), ♂, body length 3 mm, dorsal, lateral (photo 25) and ventral aspects. The arrow in photo 25 points to the deep furrow on the high thoracic part. F2327/BB/AR/CJW.
- 10) *Ero (Succinero) clunis* n. sp. (Mimetidae), ♂, body length ca. 3 mm, anterior aspect of prosoma, pedipalpi and some leg articles. F2029/BB/AR/CJW. 28-29) *Eohalinobius patina* n. sp. (Succinomidae), ♂, body length 3.4 mm, retroventral aspect of the left pedipalpus and eye field. F2328/BB/AR/CJW.
- 11-13) *Ero (Succinero) gracilitibialis* n. sp. (Mimetidae), ♂, body length 3.2 mm, anterior and lateral aspects, ventral aspect of the left pedipalpus (12). F2352/BB/AR/CJW. 30-32) *Eohalinobius hiddenseensis* n. sp. (Succinomidae), ♂, body length 3.5 mm, dorsal, ventral and anterior aspects. The spider is strongly covered with a white emulsion. The arrows in photo 32 point to the small anterior median eyes. Coll. F. EICHMANN Ar 88.
- 14-16) *Ero (Succinero) veta* n. sp. (Mimetidae), ♂, body length ca. 3.5 mm, anterior aspect, left pedipalpus and spinnerets. F2353/BB/AR/CJW. 17-18) ?*Eophantes seorsum* n. sp. (Linyphiidae), ♂, body length 1.8 mm, dorsal aspect of body and legs, and left

33-34) *Ephalmator tredecim* n. sp. (Ephalmatoridae), ♂, body length 2.15 mm, dorsal aspects, enlarged in photo 34. F2206/BB/AR/CJW.

35-37) *Eodoter longimammillae* n. sp. (Clubionidae), ♂, body length 5.2 mm; 35) lateral aspect of the body with two parasitic larvae of Neuroptera: Mantispinae on the anterior part of the opisthosoma (arrow); 36) larvae enlarged; 37) retrolateral aspect of the left pedipalpus. F2275/BB/AR/CJW.

38-40) „*Zachria*“ *desiderabilis* PETRUNKEVITCH 1950 (Sparassidae), ♂, body length 7.5 mm, dorsal aspect of the body and right pedipalpus. F2341/BB/AR/CJW.

41-42) *Syphax ?megacephalus* KOCH & BERENDT 1854 (Thomisidae), juv., body length 3.5 mm, dorsal and ventral aspects of the body. F2204/BB/AR/CJW.

## LEGENDS TO THE PHOTOS, I C: SPIDERS IN CRETACEOUS AMBERS

Remarks: (1) Most inclusions in this kind of amber are more or less deformed.

(2) Besides spiders (order Araneae) only *Poliochera cretacea* and Ricinulei indet. – photos 35 and 36 – are members of the order Ricinulei.

1) *Dipluridae* indet., ?juv., ?anterior leg, length of the femur 4.2 mm, F2278/BU/AR/CJW.

2) Part of a web and remains of prey with *Dipluridae* indet., F2278/BU/AR/CJW.

3) *Dipluridae* indet., juv., body length 1.8 mm, coll. A. BEIGEL BU-42/CAB.

4) *Saetosoma filiembolus* n. gen. n. sp. (Tetrablemmidae), ♂, body length 0.9 mm, F2347/BU/AR/CJW.

5-6) ?*Psilodermes filiformis* n. sp. (Psilodermidae), ♂, body length 1.7 mm, dorsal aspect and anterior part with pedipalpi enlarged. The arrow in photo 6 points to the comb of the pedipalpal femur. F2267/BU/AR/CJW.

7-8) *Eogamasomorpha nubila* WUNDERLICH 2008 (Tetrablemmidae), ♂, prosomal length 0.5 mm, ventral and dorsal aspects. F2362/BU/AR/CJW.

## LEGENDS TO THE PHOTOS, I C: SPIDERS IN CRETACEOUS AMBERS (*cont.*)

9-10) *Leclercera longissipes* **n. sp.** (Psilodercidae), ♂, body length 1.55 mm, dorsal aspects of the spider, enlarged in 10). F2349/BU/AR/CJW.

11-13) *Leclercera spicula* **n. sp.** (Psilodercidae), ♂, body length 1.9 mm, lateral aspect of body and legs, retrolateral aspect of the left pedipalpus (photo 13). F2340/BU/AR/CJW.

14-15) *Palaeoleptoneta calcar* **n. sp.** (Palaeoleptonetidae), ♂, body length 1.8 mm, spider and pedipalpi enlarged. F2350/BU/AR/CJW.

16-18) *Pholcochyrocer pecten* **n. sp.** (Pholcochyroceridae), 16) the piece of amber before cutting, with the fossil spider in the abdomen of the insect jewellery 17-18) the spider. F2268/BU/AR/CJW.

19-21) ?*Pholcochyrocer baculum* **n. sp.** (Pholcochyroceridae), ♂, body length 2.5 mm, lateral aspect and anterior part with pedipalpi enlarged. F2339/BU/AR/CJW.

22-23) *Lagonoburmops plumosus* **n. gen. n. sp.** (Lagonomegopidae), ♀, body length 8 mm, dorsal aspect of the body and the hairy right tibiae I-II. F2270/BU/AR/CJW.

24) *Myanlagonops gracilipes* **n. gen. n. sp.** (Lagonomegopidae), ♂, body length 4 mm, prosoma and legs. F2269/BU/AR/CJW.

25) *Archaelagonops salticoides* **n. gen. n. sp.** (Lagonomegopidae), ♂, body length 4 mm, anterior aspect. F2364/BU/AR/CJW.

26) *Micropalpimanus* **sp. indet.** (Micropalpimanidae), ♀, body length 2 mm, dorsal-lateral aspect. F2285/BU/AR/CJW.

27-29) *Ocululoborus curvatus* **n. gen. n. sp.** (Uloboridae), ♀, body length ca. 2.2 mm, 27) decomposed/dissected body and legs with the peltidium just above the centre left of the distinctly bent posterior metatarsus; 28) threads with remains of a beetle's elythrum; 29) decomposed questionable eggs of a spider, diameter of the clump up to 3 mm. F2278/BU/AR/CJW.

30-31) *Leviunguis bruckschi* **n. gen. n. sp.** (Theridiosomatidae), ♂, body length 1 mm, dorsal aspect of the body and dorsal aspect of the right pedipalpus. The arrow points to an eye lense. F2266/BU/AR/CJW.

32-33) *Hypotheridiosoma paracymbium* **n. gen. n. sp.** (Theridiosomatidae), ♂, body length 0.9 mm, lateral aspects of the body. F2348/BU/AR/CJW.

34-35) ?*Poliochera cretacea* **n. sp.** (order Ricinulei: Poliocheridae), female nymph, body length 2.3 mm, dorsal aspects. Insert in photo 35: Anterior aspect of the right pedipalpus. F2336/BU/CJW.

36) Ricinulei **indet.**, exuvia of a nymph, length of the remains of the body almost 3.5 mm. F2345/BU/CJW.

## A. Spiders in Copal from Madagascar



Photo 1: *Mysmena* (s. l.) sp. indet. (Mysmenidae), F2371/CM/AR/CJW



Photo 2: *Madagascarchantes vomerans* (Linyphiidae), F2358/CM/AR/CJW



Photo 3: *Lasaeola* (Phycosoma) *inclinata* (Theridiidae), holotype, F2359/CM/AR/CJW



Photo 4: *Lasaeola* (Phycosoma) *inclinata* (Theridiidae), holotype, F2359/CM/AR/CJW



Photo 5: *Platnickina duosetae* (Theridiidae), F2360/CM/AR/CJW



Photo 6: *Flagellidictyna copalis* (Dictynidae), F2370/CM/AR/CJW

## A. Spiders in Copal from Madagascar (cont.)



Photo 7: *Dictyna rufa* (Dictynidae),  
F2373/CM/AR/CJW



Photo 8: *Dictyna rufa* (Dictynidae),  
F2372/CM/AR/CJW



Photo 9: *Dictyna rufa* (Dictynidae),  
F2373/CM/AR/CJW



Photo 10: *Dictyna rufa* (Dictynidae),  
F2372/CM/AR/CJW



Photo 11: *Copaldictyna madagascariensis*  
(?Titanoeidae), F2342/CM/AR/CJW

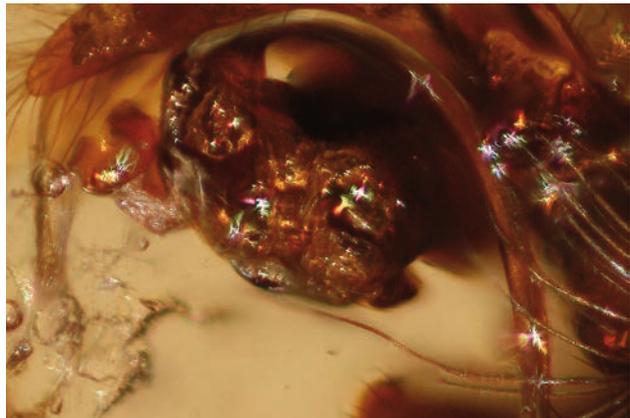


Photo 12: *Copaldictyna madagascariensis*  
(?Titanoeidae), F2342/CM/AR/CJW

## B. Spiders in Baltic amber



Photo 1: *Segestria flexio* (Segestriidae), F2286/BB/AR/CJW



Photo 2: *Samlandicmeta mutila* (Tetragnathidae), F2354/BB/AR/CJW

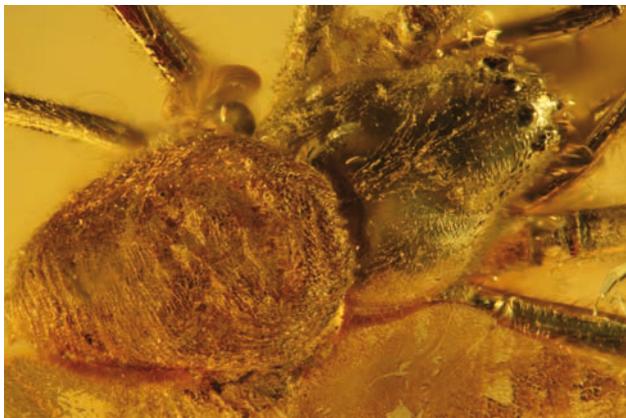


Photo 3: *Samlandicmeta mutila* (Tetragnathidae), F2354/BB/AR/CJW

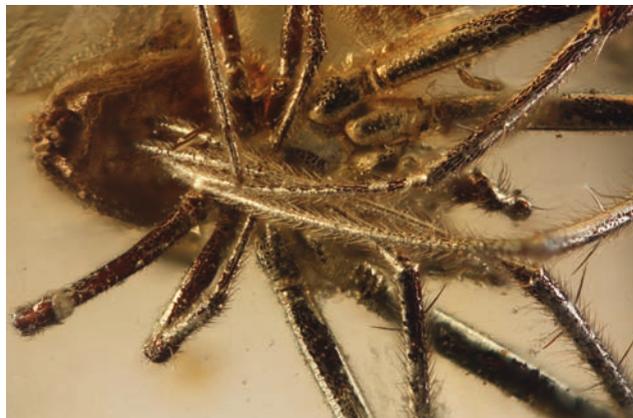


Photo 4: *Samlandicmeta mutila* (Tetragnathidae), F2354/BB/AR/CJW



Photo 5: *Baltleucauge propinqua* (Tetragnathidae), F2355/BB/AR/CJW



Photo 6: *Baltleucauge propinqua* (Tetragnathidae), F2355/BB/AR/CJW

## B. Spiders in Baltic amber (cont.)



Photo 7: *Graea magnocoli* (Zygiellidae), F2322/BB/AR/CJW



Photo 8: *Graea magnocoli* (Zygiellidae), F2322/BB/AR/CJW

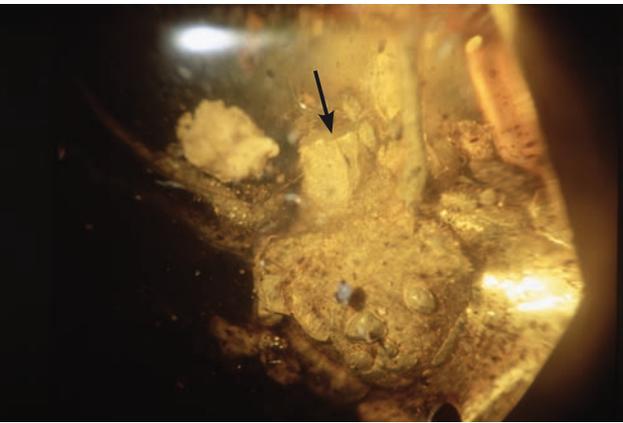


Photo 9: ?*Araneus* sp. indet (Araneidae), F2323/BB/AR/CJW



Photo 10: *Ero* (*Succinero*) *clunis* (Mimetidae), F2029/BB/AR/CJW

Photo 11: *Ero* (*Succinero*) *gracilitibialis* (Mimetidae), F2352/BB/AR/CJW



Photo 12: *Ero* (*Succinero*) *gracilitibialis* (Mimetidae), F2352/BB/AR/CJW

## B. Spiders in Baltic amber (cont.)



Photo 13: *Ero (Succinero) gracilitibialis* (Mimetidae), F2352/BB/AR/CJW



Photo 14: *Ero (Succinero) veta* (Mimetidae), F2353/BB/AR/CJW



Photo 15: *Ero (Succinero) veta* (Mimetidae), F2353/BB/AR/CJW



Photo 16: *Ero (Succinero) veta* (Mimetidae), F2353/BB/AR/CJW



Photo 17: ?*Eophantes seorsum* (Linyphiidae), F2321/BB/AR/CJW

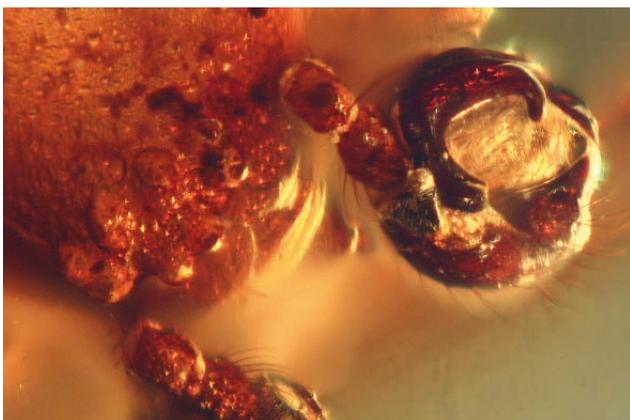


Photo 18: ?*Eophantes seorsum* (Linyphiidae), F2321/BB/AR/CJW

## B. Spiders in Baltic amber (cont.)

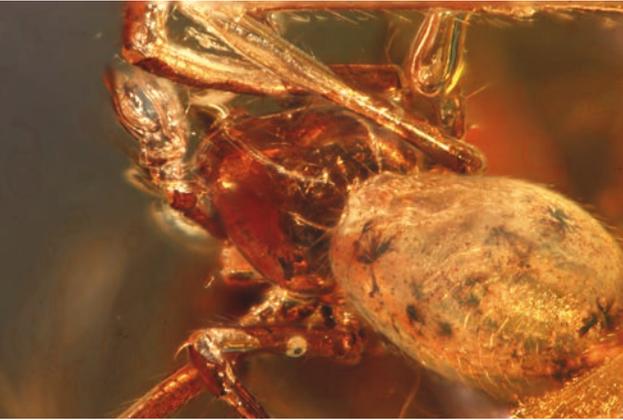


Photo 19: *Praetheridion fleissneri*  
(Praetheridiidae), F2273/BB/AR/CJW



Photo 20: *Praetheridion fleissneri*  
(Praetheridiidae), F2273/BB/AR/CJW

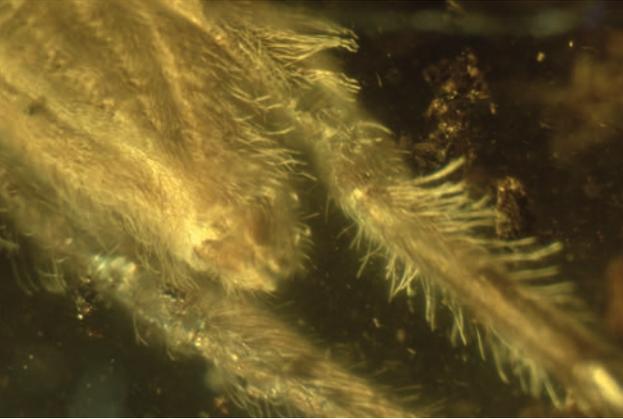


Photo 21: *Eoprychia ?succini* (Zoropsidae s. l.:  
Eoprychiini), coll. F. KERNEGGER

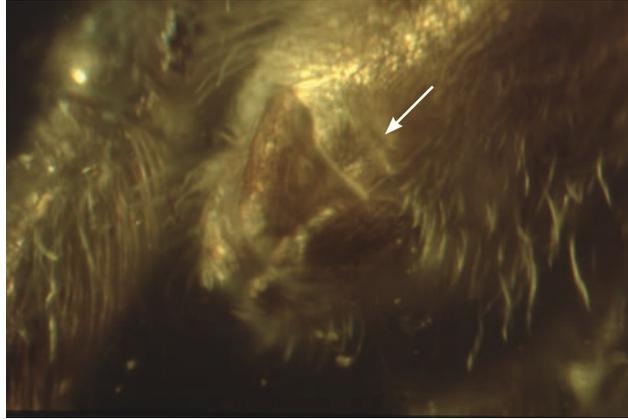


Photo 22: *Eoprychia ?succini* (Zoropsidae s. l.:  
Eoprychiini), coll. F. KERNEGGER

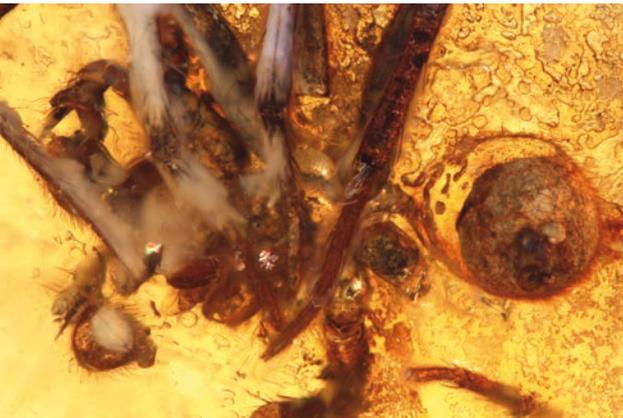


Photo 23: *Succiniropsis runcinata* (Zoropsidae s.l.:  
Eomatichiini), F2357/BB/AR/CJW



Photo 24: *?Succinomus gibbosus* (Succinomidae),  
F2327/BB/AR/CJW

## B. Spiders in Baltic amber (cont.)

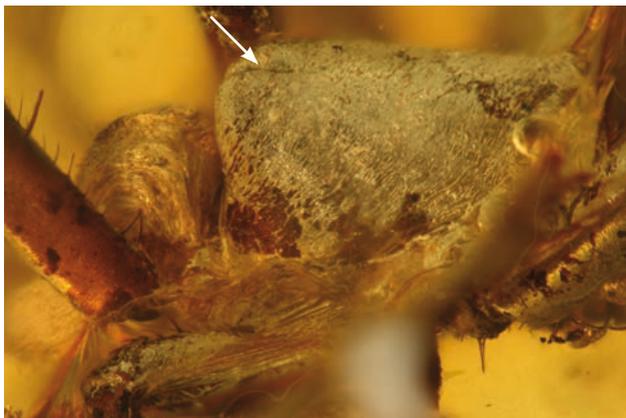


Photo 25: ?*Succinomus gibbosus* (Succinomidae), F2327/BB/AR/CJW



Photo 26: ?*Succinomus gibbosus* (Succinomidae), F2327/BB/AR/CJW

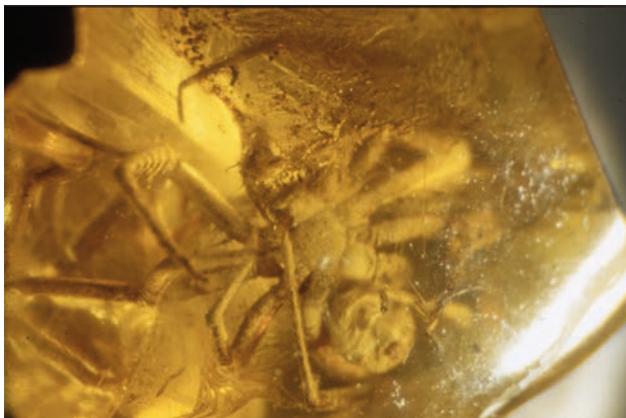


Photo 27: ?*Succinomus gibbosus* (Succinomidae), F2327/BB/AR/CJW

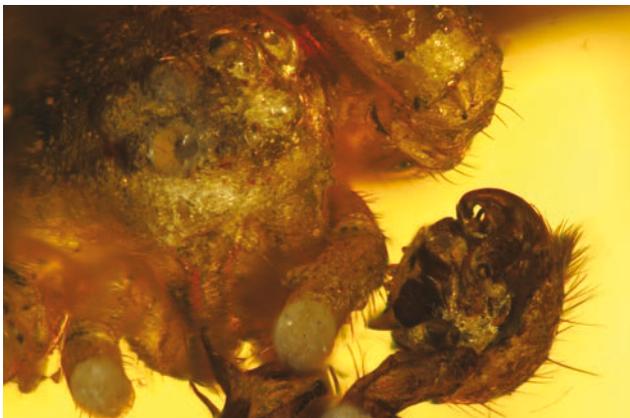


Photo 28: *Eohalinobius patina* (Succinomidae), F2328/BB/AR/CJW



Photo 29: *Eohalinobius patina* (Succinomidae), F2328/BB/AR/CJW

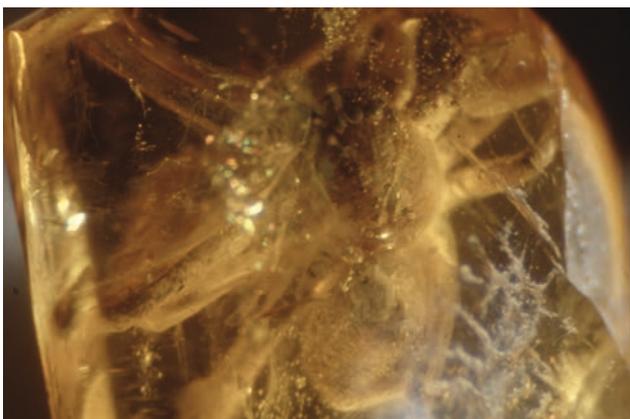


Photo 30: *Eohalinobius hiddenseensis* (Succinomidae), coll. F. EICHMANN AR 88

## B. Spiders in Baltic amber (cont.)



Photo 31: *Eohalinobius hiddenseensis* (Succinomidae), coll. F. EICHMANN AR 88

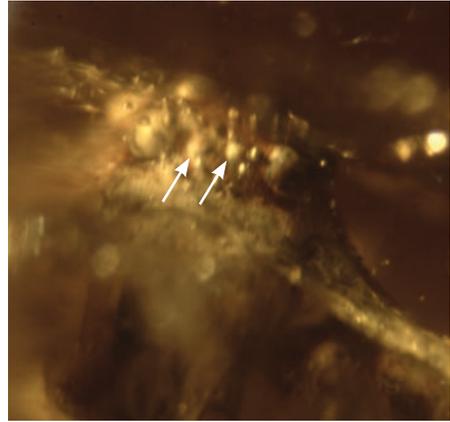


Photo 32: *Eohalinobius hiddenseensis* (Succinomidae), coll.F. EICHMANN AR 88



Photo 33: *Ephalmator tredecim* (Ephalmatoridae), F2206/BB/AR/CJW

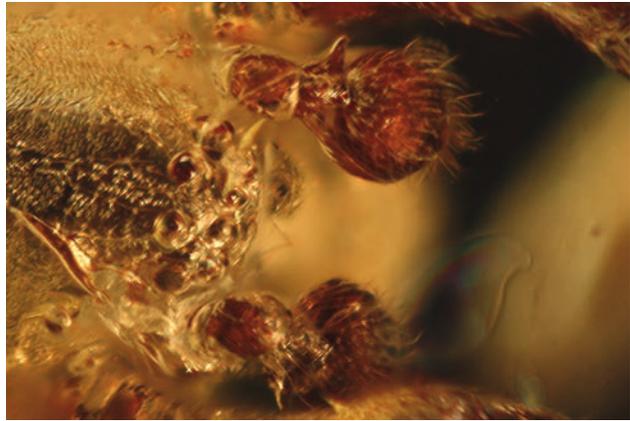


Photo 34: *Ephalmator tredecim* (Ephalmatoridae), F2206/BB/AR/CJW



Photo 35: *Eodoter longimammillae* (Clubionidae), F2275/BB/AR/CJW



Photo 36: *Eodoter longimammillae* (Clubionidae), F2275/BB/AR/CJW – parasitic larvae

## B. Spiders in Baltic amber (cont.)



Photo 37: *Eodoter longimammillae* (Clubionidae), F2275/BB/AR/CJW



Photo 38: "*Zachria*" *desiderabilis* (Sparassidae), F2341/BB/AR/CJW



Photo 39: "*Zachria*" *desiderabilis* (Sparassidae), F2341/BB/AR/CJW



Photo 40: "*Zachria*" *desiderabilis* (Sparassidae), F2341/BB/AR/CJW



Photo 41: *Syphax* ?*megacephalus* (Thomisidae), F2204/BB/AR/CJW



Photo 42: *Syphax* ?*megacephalus* (Thomisidae), F2204/BB/AR/CJW

## C. Spiders in Cretaceous ambers

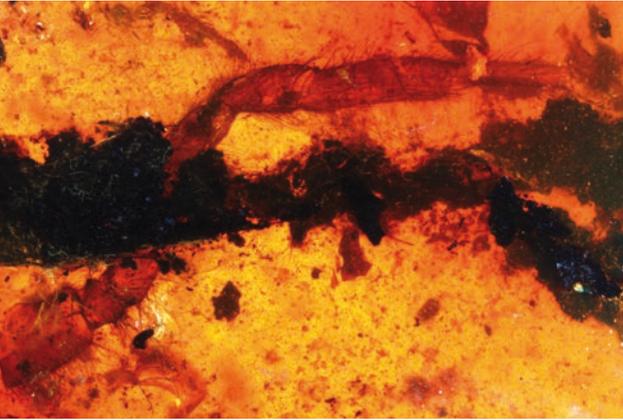


Photo 1: *Dipluridae* indet., F2278/BU/AR/CJW

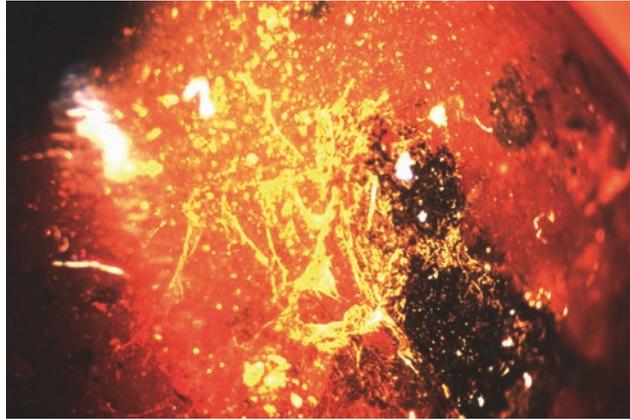


Photo 2: *Dipluridae* indet., juv.: Web, prey, F2278/BU/AR/CJW



Photo 3: *Dipluridae* indet., coll. BEIGEL BU-42/CAB



Photo 4: *Saetosoma filiembolus* (Tetrablemmidae), F2347/BU/AR/CJW



Photo 5: ?*Psilodermes filiformis* (Psilodercidae), F2267/BU/AR/CJW



Photo 6: ?*Psilodermes filiformis* (Psilodercidae), F2267/BU/AR/CJW

## C. Spiders in Cretaceous ambers (cont.)



Photo 7: *Eogamasomorpha nubila*  
(Tetrablemmidae), F2362/BU/AR/CJW

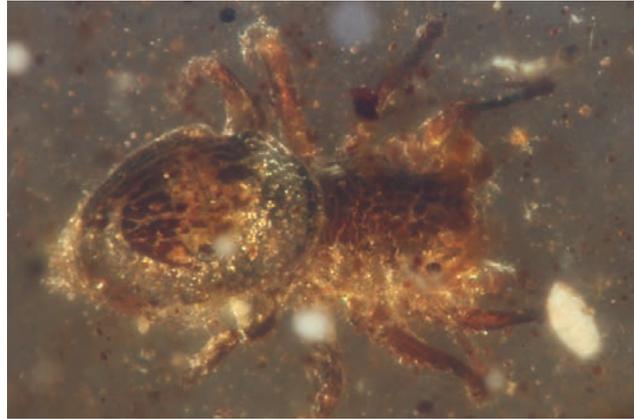


Photo 8: *Eogamasomorpha nubila*  
(Tetrablemmidae), F2362/BU/AR/CJW



Photo 9: *Leclercera longissipes* (Psilodercidae),  
F2349/BU/AR/CJW

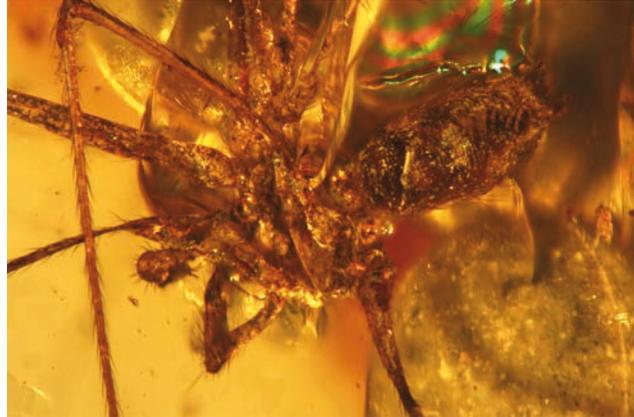


Photo 10: *Leclercera longissipes*  
(Psilodercidae), F2349/BU/AR/CJW

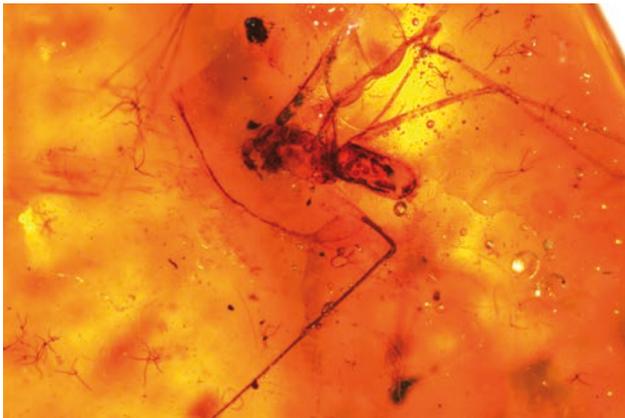


Photo 11: *Leclercera spicula* (Psilodercidae),  
F2340/BU/AR/CJW

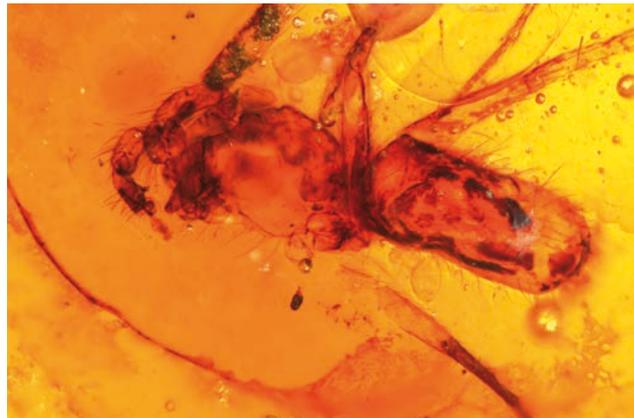


Photo 12: *Leclercera spicula*  
(Psilodercidae), F2340/BU/AR/CJW

## C. Spiders in Cretaceous ambers (cont.)



Photo 13: *Leclercera spicula* (Psilodercidae), F2340/BU/AR/CJW



Photo 14: *Palaeoleptoneta calcar* (Palaeoleptonetidae), F2350/BU/AR/CJW

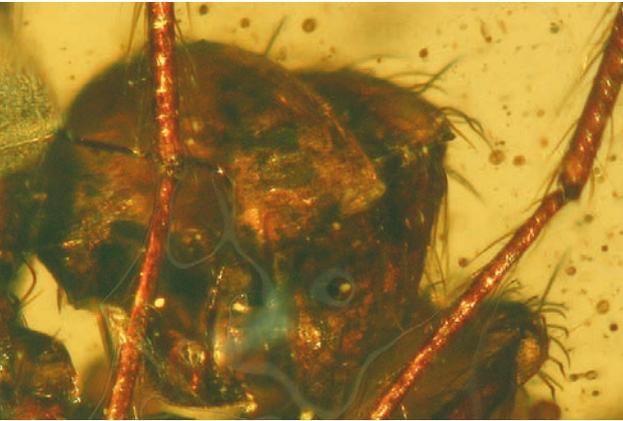


Photo 15: *Palaeoleptoneta calcar* (Palaeoleptonetidae), F2350/BU/AR/CJW



Photo 16: *Pholcochyrocer pecten n.n.p.* (Pholcochyroceridae), F2268/BU/CJW



Photo 17: *Pholcochyrocer pecten n.n.p.* (Pholcochyroceridae), F2268/BU/CJW



Photo 18: *Pholcochyrocer pecten n.n.p.* (Pholcochyroceridae), F2268/BU/CJW

## C. Spiders in Cretaceous ambers (cont.)



Photo 19: ?*Pholcochyrocer baculum*  
(Pholcochyroceridae), F2339/BU/AR/CJW



Photo 20: ?*Pholcochyrocer baculum*  
(Pholcochyroceridae), F2339/BU/AR/CJW

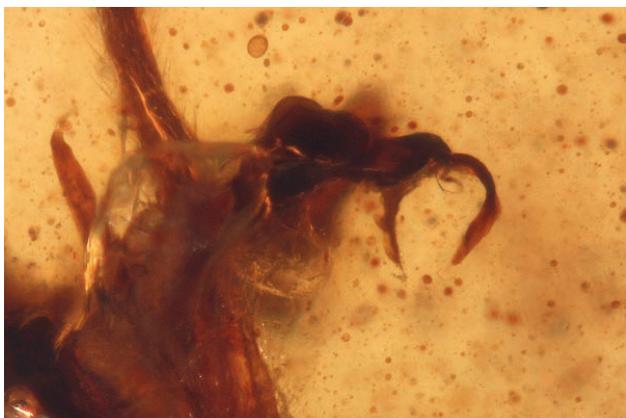


Photo 21: ?*Pholcochyrocer baculum*  
(Pholcochyroceridae), F2339/BU/AR/CJW



Photo 22: *Lagonoburmops plumosus*  
(Lagonomegopidae), F2270/BU/AR/CJW

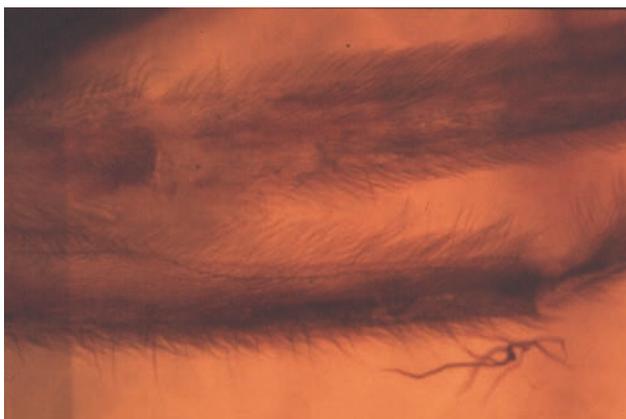


Photo 23: *Lagonoburmops plumosus*  
(Lagonomegopidae), F2270/BU/AR/CJW

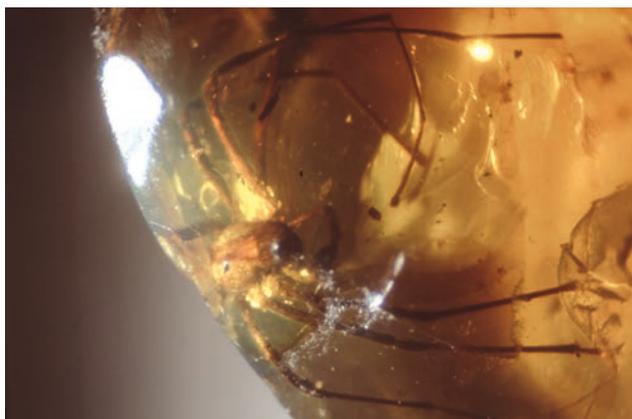


Photo 24: *Myanlagonops gracilipes*  
(Lagonomegopidae), F2269/BU/AR/CJW

## C. Spiders in Cretaceous ambers (*cont.*)



Photo 25: *Archaelagonops salticoides* (Lagonomegopidae), F2364/BU/AR/CJW



Photo 26: *Micropalpimanus* sp. indet. (Micropalpimanidae), F2285/BU/AR/CJW



Photo 27: *Ocululoborus curvatus* (Uloboridae), F2278/BU/AR/CJW

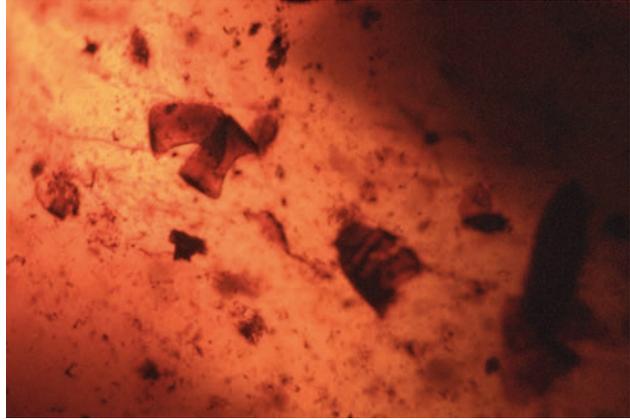


Photo 28: *Ocululoborus curvatus* (Uloboridae), F2278/BU/AR/CJW

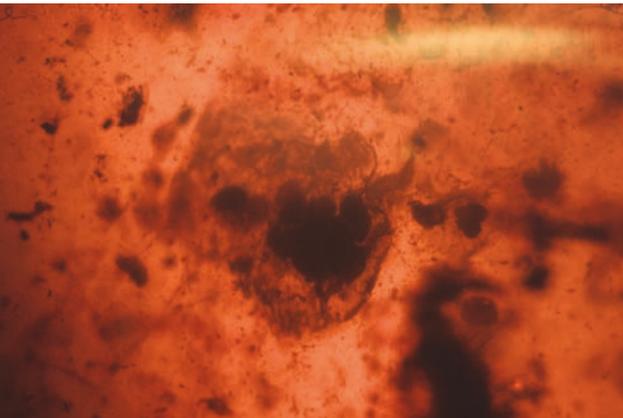


Photo 29: *Ocululoborus curvatus* (Uloboridae), F2278/BU/AR/CJW



Photo 30: *Leviunguis bruckschi* (Theridiosomatidae), F2266/BU/AR/CJW

## C. Spiders in Cretaceous ambers (cont.)

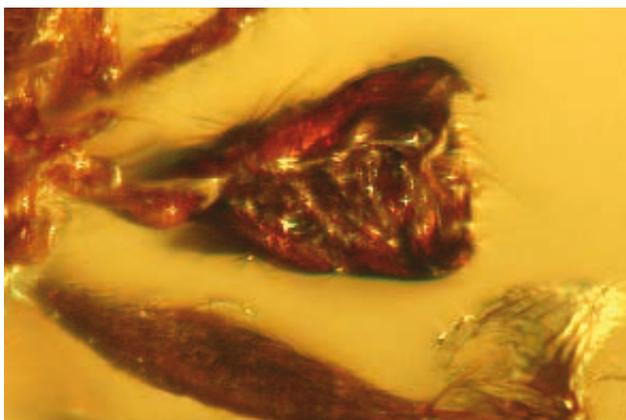


Photo 31: *Leviunguis bruckschi* (Theridiosomatidae), F2266/BU/AR/CJW



Photo 32: *Hypotheridiosoma paracymbium* (Theridiosomatidae), F2348/BU/AR/CJW



Photo 33: *Hypotheridiosoma paracymbium* (Theridiosomatidae), F2348/BU/AR/CJW



Photo 34: ?*Poliochera cretacea* (Ricinulei: Poliocheridae), F2336/BU/CJW



Photo 35: ?*Poliochera cretacea* (Ricinulei: Poliocheridae), F2336/BU/CJW



Photo 36: *Ricinulei* indet., F2345/BU/CJW

# Otacilia

## Photo Legends

**Photos 1–6.** *Otacilia bicolor* n. sp. (1–3 holotype male; 4–6 paratype female; from Laos, That Fane). 1, 3 Dorsal habitus. 2, 4 Frontal view. 3 Opisthosoma, caudal. 6 Epigyne, ventral view.

**Photos 7–11.** *Otacilia namkhan* sp. n. (7–9 holotype male, 10–11 paratype female; from Laos, Ban Keng Koung). Habitus (7, 10, dorsal; 8, 11 ventral; 9 lateral)

**Photos 12–16.** *Otacilia loriot* n. sp. (holotype male from Laos, Houay Kho), habitus (12 dorsal, 13 ventral, 14 lateral, 15 frontal, 16 caudal).

**Photos 17–20.** *Otacilia vangvieng* n. sp. (holotype male from Laos, Tham Pou Kham), habitus (17 dorsal, 18 ventral, 19 frontal, 20 caudal).

**Photos 21–29.** *Otacilia kao* n. sp. (21–24 holotype male; 25–29 paratype female; from Thailand, Koh Chang). 21, 26 Dorsal habitus. 22–23, 27 Lateral habitus. 24, 28 Traceal spiracle, ventral. 25 Frontal habitus. 29 Epigyne, ventral.

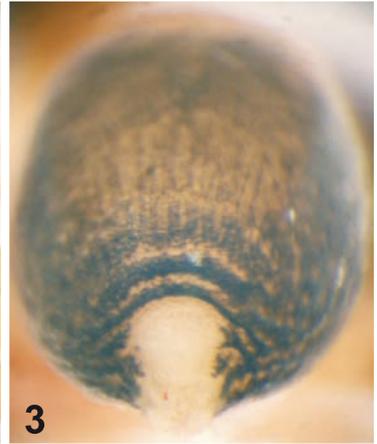
**Photos 30–33.** *Otacilia paracymbium* n. sp. (holotype male from China, Emei Shan). 30–32 Habitus (30 dorsal, 31 lateral, 32 frontal). 33 Palp, retrolateral.

**Photos 34–40.** *Otacilia* sp. indet. B (female from Laos, Tad Vang Fong). 34–39 Habitus (34, 37 dorsal, 35 ventral, 36 lateral, 38 frontal, 39 caudal). 40 Right leg II, prolateral, showing ventral spines.

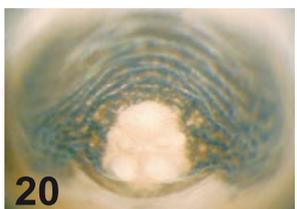
**Photos 41–44.** *Otacilia christae* n. sp. (holotype male from Laos, Ban Keng Koung), habitus (41 dorsal, 42 ventral, 43 frontal, 44 lateral).

**Photos 45–49.** *Otacilia* sp. indet. A (female from Laos, Ban Keng Koung), habitus (45 lateral, 46 dorsal, 47 ventral, 48 frontal, 49 caudal).

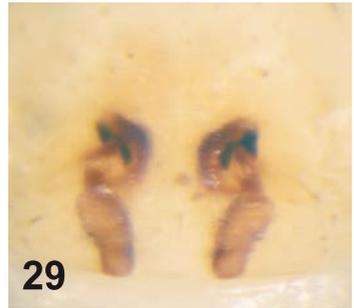
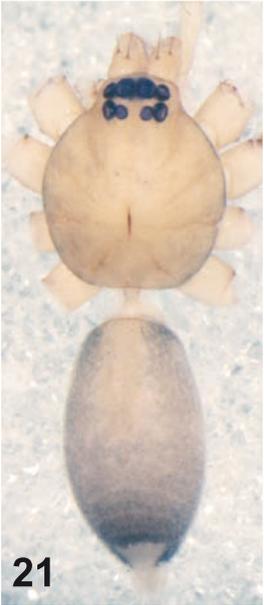
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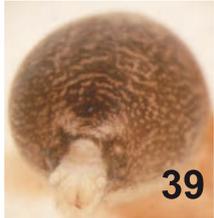
*Otacilia* (cont.)



*Otacilia* (cont.)



*Otacilia* (cont.)



*Otacilia* (cont.)



# *Argiope* spp.

## Photo Legends

**Photos 1–11.** *Argiope* spp., habitus (1, 3, 6, 9 dorsal; 2, 4, 7, 10 ventral; 5, 8, 11 lateral). **1–5** *Argiope bivittigera* Strand 1911, females from Indonesia, Maluku Islands, Kai Islands (1–2 SMF 3535; 3–4 Syntype, SMF 3538; 5 Syntype SMF 3539). **6–11** *Argiope reinwardti* (Doleschall 1859), females from Indonesia, Java (6–8 SMF 61732, 9–11 Syntype, NMNH).

**Photos 12–21.** *Argiope* spp., habitus (12, 15, 19 dorsal; 13, 16, 20 ventral; 14, 17–18, 21 lateral). **12–14** *Argiope reinwardti* (Doleschall 1859), female syntype from Indonesia, Java (NMNH). **15–18** *Argiope doleschalli* Thorell 1873, female holotype from Indonesia, Maluku Islands, Ambon (NMNH). **19–21** *Argiope* sp., female from Indonesia, Maluku Islands, Aru Islands (SMF 3520).

**Photos 22–33.** *Argiope* spp., females, habitus (22, 25, 28, 31 dorsal; 23, 26, 29, 32 ventral; 24, 27, 30, 33 lateral). **22–24** *Argiope* sp. cf. *tapinlobata* Bjørn 1997, from Namibia (SMF 61122). **25–27** *Argiope coquereli* (Vinson 1863), from Madagascar (SMF 3525). **28–33** *Argiope flavipalpis* (Lucas 1858), 28–30 Male from Congo, SMF 61133. 31–33 Female from Ivory Coast, SMF 58820.

**Photos 34–45.** *Argiope* spp., females, habitus (34, 36, 38, 41, 44 dorsal; 35, 37, 39, 42, 45 ventral; 40, 43 lateral). **34–37** *Argiope ranomafanensis* Bjørn 1997, females from Madagascar. 34–35 RMCA 200.453. 36–37 RMCA 200.195. **38–45** *Argiope hinderlichi* spec. nov., females from Laos (44–45 alive in original habitat). 38–40, 44–45 Paratype from Bolikhamsay Province, Lak Sao, 41–43 Holotype from Luang Prabang Province, Nong Khiao (all SMF).

*Argiope* spp.



*Argiope* spp. (cont.)



*Argiope* spp. (cont.)



22



23



24



25



26



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31



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33

*Argiope* spp. (cont.)



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