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Jörg Wunderlich



FOSSIL SPIDERS IN AMBER AND COPAL

FOSSILE SPINNEN
IN BERNSTEIN
UND KOPAL



Photos of the book cover:

Above: Male of a Dictynid spider in Baltic amber, see photo 289. The spider is less than 3mm long and is placed on a layer in the fossil resin.

Below: Male of the Archaeid spider *Archaea paradoxa* in Baltic amber, see photo 63. The spider is about 3mm long and lived about 50 million years ago in Northern Europe.

The background: Part of a spider's capture web (of the superfamily Araneoidea) in Baltic amber, see the photos 577-578. The threads bear numerous remains of sticky droplets.

Fotos auf dem Buchdeckel:

Oben: Männliche Kräuselspinne im Baltischen Bernstein, siehe Foto 289. Die Spinne ist knapp 3mm lang und befindet sich auf einer Schicht innerhalb des Baltischen Bernsteinstückes.

Unten: Männliche Urspinne (*Archaea paradoxa*) im Baltischen Bernstein, siehe Foto 63. Die Spinne ist etwa 3mm lang und lebte vor etwa 50 Millionen Jahren im Norden Europas.

Im Hintergrund: Teil des Fangnetzes einer Spinne (Vertreter einer Radnetzspinnen-Verwandten) im Baltischen Bernstein, siehe die Fotos 577-578. Die Spinnfäden tragen zahlreiche Reste von Klebtröpfchen.

During printing of these volumes the address of the editor – JOERG WUNDERLICH – and the Publishing House Joerg Wunderlich changed from 75334 Straubenhardt to 69493 Hirschberg-Leutershausen, Oberer Häuselbergweg 24 in Germany.

Orders for these volumes please directly to the editor, J. Wunderlich!

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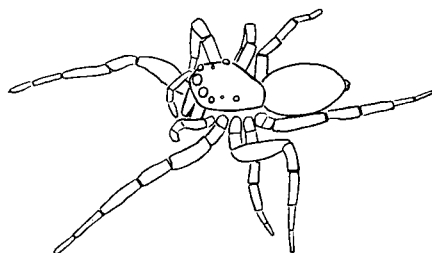
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FOSSIL SPIDERS IN AMBER AND COPAL. Conclusions, revisions, new taxa and family diagnoses of fossil and extant taxa

FOSSILE SPINNEN IN BERNSTEIN UND KOPAL. Rückschlüsse, Revisionen, Neubeschreibungen und Familien-Diagnosen fossiler und heutiger Spinnen

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by JOERG WUNDERLICH, 69643 Hirschberg-Leutershausen, Germany.

Key words: Aeronautic behaviour, amber (Baltic, Bitterfeld, Chinese, Dominican, Lebanese, Rovno, Ukrainian), amputation of legs, ant mimicry, Araneae, autotomy, Bacteria, ballooning, (palaeo-)biogeography, blood, camouflage, capture web, (palaeo-)climatology, chronocladogram, copal (Columbian, Dominican, Madagascan), cribellate threads, courtship behaviour, decomposition, determination, (palaeo-) biodiversity, digestive fluid, dragline, (palaeo-)ecology, egg sac, enemies of spiders, excrements, extinction, evolution, exuviae, fakes of inclusions, fossils, Formicidae, Fungi, haemolymph, handiness, healing of wounds in fossil spiders, hyphae, imitations of inclusions, inclusions, identification keys, laterality, moulting, myrmecomorphy, myrmecophily, new/revised taxa (species, genera, subfamilies families and superfamilies) of spiders, palaeontology, parasites, parasitoids, parthenogenesis, pathogenetic fungi, phylogenetics, plug, pollen grains, phoresy, poison, predators, prey of spiders, regeneration of legs, saprobionts, sperm and sperm web, spiders, spors, teratological structures, spiders' threads.

INCLUSEN

Bernstein in seiner schönsten Form



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Other books on fossil spiders in amber, in German (Weitere Bücher über fossile Spinnen im Bernstein, auf Deutsch):

J. WUNDERLICH (1986): Spinnenfauna gestern und heute - On extinct and extant spider faunas. 283pp. Publishing House Joerg Wunderlich. 65 Euro.

In this volume the fossil spiders in amber - including the descriptions of new species and revisions - are compared with their extant relatives in detail. - In diesem Band werden fossile Spinnen im Bernstein - einschließlich Beschreibungen bisher unbekannter Arten und Revisionen - eingehend mit ihren heutigen Verwandten verglichen.

J. WUNDERLICH (1988): Die fossilen Spinnen im Dominikanischen Bernstein. - The fossil Spiders in Dominican amber. 378pp. Publishing House Joerg Wunderlich. 65 Euro.

In this volume the fossil spiders in Dominican amber - including 143 new species - are described and compared with extant spiders of Hispaniola and with fossil spiders in Mexican amber. (Few books are still available).

A "classical book" on Baltic amber (in German) - Ein "Klassiker" über Baltischen Bernstein (auf Deutsch):

A. BACHOFEN-ECHE (1949): Der Bernstein und seine Einschlüsse. - The < Baltic > amber and its inclusions. Reprint with supplements and an index by J. Wunderlich (1996). 230pp. In German. Publishing House Joerg Wunderlich. 39 Euro.

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PART I: INTRODUCTION, GENERAL FINDINGS AND CONCLUSIONS (TEIL I: EINLEITUNG, ALLGEMEINE BEFUNDE UND RÜCKSCHLÜSSE)

by J. WUNDERLICH

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PREFACE OF THE AUTHOR, EDITOR AND PUBLISHER

This set of two volumes contains **(a)** the third part of a trilogy on fossil spiders in amber (mainly in Baltic amber) and copal by the present author; revisions of higher extant taxa are also treated as well as very few descriptions of new extant spider genera (Dictynidae s. l.: Hahniinae). For the previous two parts see WUNDERLICH (1986) and (1988). These volumes also contain **(b)** six short papers on arachnids by different (co)authors: HOFFEINS, LOURENCO, POINAR, POINAR & BROWN and WUNDERLICH & MILKI.

I have kept the price low for these volumes, not taking into account all the work I put in: The work on one diverse family of fossil spiders (e.g. Anapidae s.l. and Synotaxidae) each took more than one year. Not least using my own publishing house has made this achievement possible.

Jörg Wunderlich, in April 2004

VORWORT DES VERFASSERS, HERAUSGEBERS UND VERLEGERS

Der vorliegende Doppelband beinhaltet **(a)** den dritten Teil einer Trilogie über fossile Spinnen im Bernstein (überwiegend erhalten im Baltischen Bernstein) und Kopal durch den Verfasser dieser Zeilen; ebenso behandelt werden Revisionen höherer Taxa und sehr wenige Beschreibungen heutiger bisher unbekannter Gattungen (Dictynidae s. l.: Hahniinae). Zu den beiden früher publizierten Teilen: Siehe WUNDERLICH (1986) und (1988). Der Band beinhaltet weiterhin **(b)** sechs kurze Arbeiten über Spinnentiere verschiedener Autoren: HOFFEINS, LOURENCO, POINAR, POINAR & BROWN und WUNDERLICH & MILKI.

Nicht zuletzt durch die Veröffentlichung in meinem eigenen Verlag konnte der Preis dieser Bände gering gehalten werden, wobei im Wesentlichen lediglich die Kosten für Drucken, Binden und die Farbfotos einfließen. Die Bearbeitung der Spinnen einer einzigen fossilen Familie (z. B. der Zwerg-Kugelspinnen oder der Kugel-Höhlenspinnen) beanspruchte jeweils mehr als ein Jahr.

Jörg Wunderlich, im April 2004

INTRODUCTION TO THE PAPERS ON FOSSIL SPIDERS IN AMBER AND COPAL

"Books are thicker letters to friends."

Jean Paul

They <the fossil insects in amber> imposed at least on me the opposite view: that preferably by studying fossil insects - because of their intimate connection with the surface of the earth and its atmosphere - one can reach the most certain (reliable) and most excellent conclusions on the development and the sequence < ! > of the organic creatures and thus on the physical history of our planet. - (Translated from German).

G. C. BERENDT (1845) in his preface to "Der Bernstein
und die in ihm befindlichen Pflanzenreste der Vorwelt"
by GOEPPERT & BERENDT.

Why study fossils? Initially scientists as well as "amateurs" are simply curious: they want to know all about lost worlds, the diversity of their organisms, their behaviour and their environments. Baltic amber is a fascinating "window to the past": It shows an exciting mixed (spider) fauna which includes "modern" as well as few "Cretaceous taxa" - which in my opinion were relicts already in the Early Tertiary -, taxa which preferred a tropical climate as well as taxa which preferred subtropical or even moderate climates. We probably know one third of the extant spider fauna but much less of the fossil Baltic spider fauna! Learning more and more about the distributional (biogeographical) relationships of the spider fauna of the old Baltic amber forest was most surprising to me. Several families of this fauna are extinct in Europe today - e.g. Plectreuridae, Tetrablemmidae and Deinopidae - or are even extinct in most parts of the whole Northern Hemisphere, e.g. Archaeidae, Cyatholipidae and Synotaxidae; members of these families, however, were frequent and diverse in the subtropical

Baltic amber forest in an era up to 55 million years ago, "only" 10 million years after the extinction of the dinosaurs!

Fossil Araneae in Baltic amber - probably some thousand species, described are more than six hundred - are the most diverse group (order) of arthropods besides Acari (mites), Coleoptera (beetles), Diptera (flies and midges) and Hymenoptera (ants, bees, wasps and their kin). Never before has such a large arthropod order in Baltic amber been studied in detail and published in a single work: Several hundred species of about fifty families in Baltic amber. (The number of extant spider families may be more than one hundred).

Well-founded conclusions on biogeographical relationships of fossil taxa are chiefly possible on the genus level and after knowing their extant relatives. Because of their freely visible genital structures - they are most important for their identification, see the photos 53, 63, 87, 101, 182, 198-199, 239, 287, 303-307, 316, 424 and the drawings - the male spiders are the best objects for finding out their phylogenetical and biogeographical relationships. (In the beetles and most other insects the genital structures are hidden, so the identification of their species- and even genus-relationships are frequently unsure). - Almost all descriptions and most of the drawings of the spider species in this work are based on male genital structures.

The scientific study of fossil spiders in amber began one and a half centuries ago. Only very few authors published large works on fossil spiders: KOCH & BERENDT in BERENDT (1954) (with numerous remarks and descriptions of new species by MENGE in this paper, including nomina nuda), PETRUNKEVITCH (1942, 1946, 1950, 1958), WUNDERLICH (1986) and WUNDERLICH (1988) on spiders in Dominican amber. KOCH, BERENDT, MENGE and PETRUNKEVITCH published important results and the descriptions of numerous new species, but a lot of nomina dubia, too, which are based on juvenile spiders. PETRUNKEVITCH did not know that most types of the collection of KOCH & BERENDT are kept in the Palaeont. Inst. of the Humboldt University in Berlin. This author confused several spider taxa and published for example the genus *Acrometa* PETRUNKEVITCH 1942 even within different families. Almost all fossil species of the family Segestriidae in Baltic amber were based on juveniles, few on females; the important references to male genital structures were wanting, and the number of synonyms is still unknown. This is a fundamental taxonomical problem in fossils (in spiders as well): Conspecific juveniles as well as members of the male and the female sex may have been described under different species and even different generic names. Although my descriptions of fossil spiders are mainly - more than 95% - based on males, the assignment of conspecific females is usually impossible; couples (of both sexes) are rarely preserved, they are occasionally preserved in *Balticoroma*, *Eohahnia* and *Orchestina*. The level of some taxa - (morpho)species, subspecies or only an intra-specific variability? - is uncertain, for example the taxa *Eopopino* PETRUNKEVITCH 1942 (Nesticidae) (the structures of the bulbus; see WUNDERLICH (1986)) and *Eodictyna communis* n. gen. n. sp. (Dictynidae: Dictyninae; the length of the hairs; these volumes).

The diagnostic characters of several families are uncertain or even unknown (e.g. in the Dictynidae, Insecutoridae and in the Miturgidae); the diagnostic characters may be restricted to behavioural patterns as in the Segestriidae: the special resting position of the legs, or in the Pisauridae: the special carrying of the egg sac by the female.

Such a diverse group of fossil animals - leading to a work of 25 years (with interruptions) - may be too much for a single person. The investigation and documentation of inclusions in amber needs much time and patience. When I asked colleagues for a discussion and co-operation, the answer was usually negative: "What about the other side of the spider? It is covered by an emulsion!" "Important structures are hidden or hard to observe" "I am quite unsure about the relationships of this species!" "I prefer to study extant spiders",.....

When I - 16 years ago - finished the volume on fossil spiders in Dominican amber I wanted to publish revisions and new descriptions of selected fossil spiders in Baltic amber only some years later in a small book. (Un)fortunately I got ten thousands of further fossil spiders during the following years, mainly in Baltic amber - altogether more than 100 000 fossil specimens -, more and more undescribed species appeared, about 400 new taxa (about 300 new species in Baltic amber, several new subfamilies, three new families in Baltic amber: Baltsuccinidae, Protheridiidae and Borborobactidae; Borborobactidae are still alive). Hence not only the number of new taxa was growing but also the conclusions on fakes (photos 83, 179, 248, 441-447), on the biogeography and on the biology (see below) of fossil spiders. During my work it became clear to me that numerous higher spider taxa of extant and fossil spiders are ill-diagnosed. I also recognized that I had to compare and revise numerous extant taxa worldwide for a comparison with the fossils. So years and years passed with buying, loaning, polishing, labelling, discussing, describing, drawing and photographing this material as well as making comparisons with and revisions of extant material/taxa. Almost ten years ago I gave up my job to concentrate on the work on fossil spiders. Recent publications of several authors - see the important and very helpful works of DEELEMAN-REINHOLD (2001), DIPPENAAR-SCHOEMAN & JOCQUE (1997) (most family diagnoses in this book are restricted to African spiders), FORSTER, GRISWOLD, LEHTINEN, LEVI, PLATNICK and PLATNICK et al. - gave essential hints at the taxonomical and biogeographical relationships of fossil spider taxa in Baltic amber. Among these revised spiders are "exotic" families like Archaeidae and Cyatholipidae. It is true that my personal view of the phylogenetic relationships of some higher fossil taxa is quite different to some New World's authors and PC-cladists; see my remarks e.g. in the papers on the (super)families Eresoidea s. l., Araneoidea s. l., Araneidae, Mimetidae s. l. and Zoropsidae s. l., as well as the chapters on phylogenetics and palaeofaunistic.

Because of its huge size the present third part on fossil spiders (see the preface) had to be split into two volumes, Beitr. Araneol., 3a and 3b. The first volume (3a) deals with mainly general aspects chiefly of the fauna of the Early Tertiary Baltic amber. It also contains 700 coloured photos with the legends in English and German, as well as new descriptions of (morpho)species of some spider families of the Mygalomorphae, Dysderoidea, Eresoidea s. l. (including the Archaeidae) and Oecobioidea. The second volume - Beitr. Araneol., vol. 3b - mainly contains new descriptions of spider taxa in Baltic amber but also few spiders in Chinese, Dominican and Lebanese amber, in young resins (copal) or extant ones (Dictynidae s. l.: Hahniinae) as well as two fossil arachnids besides the Araneae: a scorpion and a whipscorpion (Amblypygi). It also deals with various general aspects.

This work is aimed at (a) producing a survey (partly an almost complete work) on the known fossil spiders in Baltic amber including general aspects - mainly of their diversity and their biogeography as well as a comparison with their extant relatives.

(Because of the enormous diversity of the spider family Theridiidae in Baltic amber I had to exclude the revision of this family - which is in preparation -, and also had to exclude the identification of numerous juvenile spiders of the type collection of KOCH & BERENDT (1854); the determination of these partly badly preserved and young spiders is very difficult). - It is also aimed at **(b)** making a small step forewards in the taxonomy and phylogeny of spiders in the tradition of SIMONS's "Histoire Naturelle des Araignees" (1892-1903): I want to add some findings on extant and fossil spiders.

Some collectors of amber inclusions and friends asked me to publish in English but others asked for a German edition. As a compromise I have decided to publish this volume in English but I present several parts - e.g. the legends of the coloured photos - in English and in German as well.

The reading of some parts of my works is difficult because of overlappings/cross connections of numerous aspects. For example let's take the events of fossil spiders which are fighting with ants (photos 608-613): this refers to the items "prey" as well as "enemies" besides the taxonomical relationships -, the same spider may be ant-shaped - see the items "myrmecomorphy" and "camouflage", it furthermore may have broken legs with remains of blood and healed cuticular structures - see the items "injuries/amputated legs", "remains of blood" and "healing systems". In my opinion the links are more important than an easier reading and a difficult personal search for links.

Advice to beginners/non-biologists concerning the fossil spiders which are treated in these volumes: you may look at first at the impressive 700 coloured photos in volume 3a (e.g. 63, 76, 82, 150, 438, 459, 578 and 589f) of the fascinating and exotic spiders as well as surprising events, "frozen behaviour" ("action pieces") of "vanished worlds" up to 130 million years ago! This part - a document of selected fossil material - may be called "a book in a book". Especially the coloured photos and the conclusions drawn from this material may stimulate the reader's imagination and incite collectors - amateurs, too - to make investigations themselves - thus my own studies on fossil spiders could be a small step in an "endless story" of new findings and conclusions, a work for numerous generations of students in the future! Some of the excellently preserved specimens show details as today's spiders, and each document of a spider inclusion tells a unique "story"! Examples are events of fights between spiders and ants resp. a mite (photos 606, 608, 614), the geologically oldest known spiders which are parasited by mites (photos 589, 596), the geologically oldest known spiders which imitate ants (ant mimicry, photo 376) or wasps, spiders as the extraordinary members of the family Archaeidae of the Baltic amber forest (photos 56-83) which are extinct in Europe but have extant relatives in South Africa, Madagascar and Australia, remains of poison at the tips of the fangs of fossil spiders (photo 389), remains of prey animals of fossil spiders, some of which are spun in in threads and may hang in the capture web of a spider (e.g. photo 636), remains of sticky droplets (photo 537), a female fossil spider which guards and transports its spiderlings (photo 523), structures which allow conclusions on the courtship-behaviour (e.g. photos 362-363)! - Then a beginner may read the rest of the introduction and the "general" chapters in volume 3a which give hints concerning further reading in volume 3b.

Joerg Wunderlich, April 2004

EINLEITUNG ZU DEN ARBEITEN ÜBER FOSSILE SPINNEN IN BERNSTEIN UND KOPAL (gekürzte Übersetzung)

"Bücher sind umfangreichere Briefe an Freunde."

Jean Paul

Mir wenigstens drang sich aus ihnen <den fossilen Insekten im Bernstein> die entgegengesetzte Meinung auf: daß man vorzugsweise durch das Studium der fossilen Insekten, wegen ihres innigen Zusammenhanges mit der Oberfläche der Erde und deren Atmosphäre, die sichersten und schönsten Folgerungen für die Entwicklung und Aufeinanderfolge < ! > der organischen Geschöpfe und folglich für die physische Geschichte unseres Planeten gewinnen kann.

G. C. BERENDT (1845) in seinem Vorwort zu "Der Bernstein und die in ihm befindlichen Pflanzenreste der Vorwelt" von GOEPPERT & BERENDT.

Woher kommt das Interesse für Fossilien? Wissenschaftler wie "Amateure" sind zunächst einfach neugierig: Sie möchten alles über vergangene Welten erfahren, die Vielfalt ihrer Lebewesen, ihres Verhaltens und ihrer Umwelt. Der Baltische Bernstein ist ein faszinierendes "Fenster zur Vergangenheit". Er umfaßt eine in aufregender Weise gemischte (Spinnen-)Fauna, "moderne" wie auch einige urtümliche "Kreide-Fossilien" (diese waren offenbar bereits im Frühen Tertiär Überbleibsel einer früheren Fauna). Es existierten Gruppen von Lebewesen, die tropisches, subtropisches wie auch gemäßigtes Klima bevorzugten. Wir kennen vielleicht ein Drittel der heutigen Spinnenfauna, aber wesentlich weniger von der Fauna des Baltischen Bernsteinwaldes!

Während meiner Untersuchungen erlebte ich mehr und mehr Überraschendes über die geographischen Beziehungen der Baltischen Spinnenfauna: Verschiedene Familien sind heute in Europa ausgestorben, z. B. die Achtaugen-Fischernetzspinnen (Plectreuridae), die Vieraugenspinnen (Tetrablemmidae) und die Käscherspinnen (Deinopidae), oder sie sind in weitesten Gebieten der Nördlichen Halbkugel sogar ausgestorben, z. B. die Urspinnen (Archaeidae), Becherspinnen (Cyatholipidae) und Kugelhöhlenspinnen (Synotaxidae). Vertreter dieser Familien existierten vielfältig und waren zahlreich im subtropischen Baltischen Bernsteinwald vertreten, in einer Zeit vor bis zu 55 Millionen Jahren, "lediglich" 10 Millionen Jahre nach dem Aussterben der Dinosaurier!

Fossile Spinnen im Baltischen Bernstein - möglicherweise mehrere tausend Arten, von denen bisher mehr als sechshundert beschrieben wurden - sind die vielfältigste Gruppe (Ordnung) der Gliederfüßer nach den Milben, Käfern, Zweiflüglern (Mücken und Fliegen) und Hautflüglern (Ameisen, Bienen, Wespen und Verwandte). Bisher war keine derartig umfangreiche Gruppe von Gliederfüßern des Baltischen Bernsteinwaldes eingehend untersucht und in einem einzigen Werk dokumentiert worden: mehrere hundert Arten aus etwa fünfzig Familien.

Gut begründete Rückschlüsse über geographische und verwandtschaftliche Beziehungen stützen sich überwiegend auf gute Kenntnisse von Gattungen und auf Kenntnisse ihrer heutigen Verwandten. Wegen ihrer frei beobachtbaren Genitalorgane - sie sind für ihre Bestimmung von besonderer Bedeutung (man vergleiche die Fotos 53, 63, 87, 101, 182, 198-199, 239, 287, 303-307, 316, 424 und die Zeichnungen) - sind männliche Spinnen hervorragend geeignete Objekte für die Ermittlung ihrer Beziehungen. Bei den meisten Insekten wie den Käfern sind die männlichen Genitalorgane im Körper verborgen und können erst nach einer Präparation untersucht werden. Fast alle Beschreibungen und die meisten Zeichnungen der fossilen Spinnen in diesen Bänden gründen sich daher auf die männlichen Genitalstrukturen ("Spinnenporno").

Die wissenschaftliche Untersuchung fossiler Spinnen im Bernstein begann vor ein- einhalb Jahrhunderten. Nur wenige Autoren haben umfangreichere Werke über fossile Spinnen im Bernstein veröffentlicht: KOCH & BERENDT in BERENDT (1854) (mit zahlreichen Anmerkungen und Neubeschreibungen durch MENGE in dieser Arbeit), PETRUNKEVITCH (1942, 1946, 1950, 1958), WUNDERLICH (1986) und WUNDERLICH (1988) über Spinnen in Dominikanischem Bernstein. KOCH, BERENDT, MENGE und PETRUNKEVITCH veröffentlichten wichtige Ergebnisse und beschrieben zahlreiche Arten zum ersten Mal; die Beschreibungen nach Jungspinnen führten allerdings zu zahlreichen zweifelhaften Namen. PETRUNKEVITCH wußte nicht, daß die meisten Typen der von KOCH & BERENDT (1854) beschriebenen Spinnen im Paläont. Inst. der Humboldt-Universität deponiert sind. Dieser Autor verwechselte verschiedene Gattungen wie *Acrometa*, die er - unter Verwendung unterschiedlicher Namen - verschiedenen Familien zuordnete. Dies ist ein grundlegendes Problem bei Fossilien einschließlich der Spinnen: Gelegentlich wurden artgleiche Jungspinnen, Männchen und Weibchen unter verschiedenen Namen veröffentlicht (sogar unter unterschiedlichen Gattungsnamen). Obwohl meine Neubeschreibungen zu mehr als 95% auf der Beschreibung geschlechtsreifer Männchen und den Strukturen ihrer Genitalien (der Pedipalpen) basieren, ist die Zuordnung artgleicher Weibchen gewöhnlich unmöglich; artgleiche Paare beiderlei Geschlechts sind gelegentlich bei Vertretern der Gattungen *Balticoroma*, *Eohahnia* und *Orchestina* im Baltischen Bernstein konserviert.

Die Untersuchung und Dokumentation der Fossilien einer derartig vielfältigen Tiergruppe mag für einen einzigen Bearbeiter zu umfangreich sein. Deshalb dauerte sie einschließlich mehrjähriger Unterbrechungen 25 Jahre lang und erforderte viel Zeit und Geduld. Meine Anfragen zu Diskussionen und Zusammenarbeit wurden von Kollegen gewöhnlich negativ beantwortet: "Wie sieht die andere Seite der Spinne aus? Sie ist mit einer Emulsion bedeckt!" "Wichtige Strukturen sind verdeckt oder kaum erkennbar!" "Die Beziehungen dieser Art sind mir schleierhaft!" "Ich ziehe es vor rezente Spinnen zu bearbeiten."...

Als ich vor 16 Jahren den Band über fossile Spinnen im Dominikanischen Bernstein beendet hatte, hatte ich vor, wenige Jahre später ein kleines Buch über ausgewählte Spinnen im Baltischen Bernstein (Revisionen und Neubeschreibungen) zu schreiben. (Un)glücklicherweise erhielt ich in den folgenden Jahren Zehntausende weiterer fossiler Spinnen - insgesamt mehr als 100 000 Stücke -, mehr und mehr unbeschriebene Arten tauchten auf, etwa 300 im Baltischen Bernstein, darunter Vertreter mehrerer neuer Unterfamilien und Familien (Baltsuccinidae, Protheridiidae und Borboropactidae; letztere haben bis heute überlebt). So wuchs nicht nur die Anzahl der neu zu beschreibenden Arten, sondern auch die Rückschlüsse über Fälschungen (Fotos 83, 179, 248, 441-447), zur Verbreitung (Biogeographie) und zur Biologie (siehe unten) fossiler Spinnen. Im Verlaufe meiner Arbeit wurde die unzureichende Kennzeichnung verschiedener heutiger und ausgestorbener Gruppen von Spinnen deutlich. Ich mußte weiterhin feststellen, daß zahlreiche fossile Spinnen mit heutigen weltweit zu vergleichen waren. So vergingen die Jahre mit dem Erwerben, Ausleihen, Schleifen/Polieren, Etikettieren, Diskutieren, Beschreiben, Zeichnen und Fotografieren des Materials sowie dem Vergleichen mit Revisionen heutigen Materials. Vor nahezu zehn Jahren gab ich meinen Beruf auf, um mich ganz auf die Arbeit über die Fossilien zu konzentrieren. Kürzlich veröffentlichte Werke - siehe die wichtigen und sehr hilfreichen Arbeiten von DEELEMANN-REINHOLD (2001), DIPPENAAR-SCHOEMAN & JOCQUE (1997) (in diesem Buch sind die meisten Familien-Kennzeichnungen auf afrikanische Spinnen beschränkt), FORSTER, GRISWOLD, LEVI, PLATNICK, PLATNICK et al. - gaben wichtige Hinweise auf verwandtschaftliche und geographische Beziehungen der fossilen Spinnen im Baltischen Bernstein. Unter diesen befanden sich "exotische" Familien wie die Urspinnen (Archaeidae) und die Becherspinnen (Cyatholipidae). Allerdings sind meine persönlichen Auffassungen der verwandtschaftlichen Beziehungen mancher Gruppen von Spinnen teilweise von denjenigen einiger Autoren und PC-Kladisten der Neuen Welt recht verschieden; siehe meine Anmerkungen in meinen Arbeiten über die (Über)familien Eresoidea, Araneoidea, Araneidae, Mimetidae und Zoropsidae sowie in den Kapiteln über Phylogenie und Palaeofaunistik.

Wegen seines enormen Umfangs mußte der gegenwärtige dritte Teil über fossile Spinnen (siehe das Vorwort) auf zwei Bände verteilt werden, Beitr. Araneol., 3a and 3b. Im ersten Band (3a) werden hauptsächlich allgemeine Themen behandelt. Sie betreffen ganz überwiegend die Spinnen im Baltischen Bernstein, die mit 700 Farbbildern dokumentiert werden, sowie Beschreibungen der Längskieferspinnen und Verwandten der Sechsaugenspinnen, der Urspinnen und der Scheibennetz-Spinnen. Im zweiten Band (3b) werden - neben weiteren allgemeinen Aspekten - überwiegend die Spinnen weiterer Familien im Baltischen Bernstein beschrieben, aber auch einige im Chinesischen, Dominikanischen, Libanesischen Bernstein und in jungem Kopal, wenige heutige (Bodenspinnen) sowie ein fossiler Skorpion im Baltischen Bernstein und eine fossile Geißelspinne im Mexikanischen Bernstein.

Die Zielsetzung dieser Bände ist **(a)** eine Übersicht (teilweise eine fast vollständige Bearbeitung) der bis jetzt im Baltischen Bernstein bekannten fossilen Spinnen zu geben, einschließlich allgemeiner Gesichtspunkte - vor allem ihrer Vielfalt (Diversität) und ihrer Verbreitung (Biogeographie) sowie einem Vergleich mit heutigen Verwandten. (Wegen des enormen Artenreichtums der Kugelspinnen im Baltischen Bernstein mußte die Bearbeitung dieser Familie - sie ist in Vorbereitung - aufgeschoben werden. Ebenfalls ausgeschlossen wurde die schwierige Bearbeitung zahlreicher als Jungspinnen beschriebener Fossilien der Typussammlung von KOCH &

BERENDT (1854)). - Weiterhin beabsichtigt ist **(b)** - in der Tradition von SIMON's "Histoire Naturelle des Araignees" (1892-1903) - unsere Kenntnisse (Diagnosen) höherer Gruppen (Taxa) der Spinnen und ihrer verwandtschaftlichen Beziehungen zu erweitern.

Verschiedene Sammler von Bernstein-Einschlüssen und Freunde fragten nach einer Ausgabe in Englisch, andere nach einer Ausgabe in deutscher Sprache. Als Kompromiß habe ich mich für eine englisch-sprachige Ausgabe mit verschiedenen deutsch-sprachigen Abschnitten entschieden; so sind alle Legenden zu den Farbfotos zweisprachig (gelegentlich gekürzt und populärer in Deutsch).

Zahlreiche Hinweise auf Verknüpfungen erschweren die Lesbarkeit mancher Abschnitte meiner Arbeiten. Die Ursache dafür liegt in zahlreichen thematischen Überlappungen. Als Beispiel führe ich mit Ameisen kämpfende Spinnen an (Fotos 608-613): Neben den Beschreibungen der Spinnen selbst beziehen sich die Fotos auf die Themen "Beute" und "Feinde"; sofern die Spinne ameisen-ähnlich ist auch auf "Ameisen-Ähnlichkeit" ("Mimikry") und "Tarnung"; sofern ein Bein der Spinne gebrochen/ "geheilt" ist und Blut ausgetreten ist, kann auf die Abschnitte über "Erhaltung von Blutresten", "Verletzungen", "amputierte Beine" und "Heilungssysteme" verwiesen werden. - Solche Verweise halte ich für wichtiger als eine einfachere Lesbarkeit.

Hinweise für Anfänger/Nicht-Biologen zu den in diesen Bänder behandelten fossilen Spinnen: Man betrachte zunächst die eindrucksvollen 700 Farbfotos (z. B. die Fotos 63, 76, 82, 150, 438, 459, 589f) der faszinierenden exotischen Spinnen und das eindrucksvolle "eingefrorene Verhalten" der "Aktions-Stücke" "verschwundener Welten" aus bis zu 130 Millionen Jahre zurückreichenden Zeiten. Dieser farbig bebilderte Teil - ein Dokument ausgewählten Materials - mag als "Buch im Buch" gelten. Die deutschsprachigen Legenden bieten mehr allgemein-verständliche Beschreibungen. Insbesondere diese Farbbilder und die aus diesem Material gewonnenen Rückschlüsse mögen die Vorstellungskraft des Lesers entfachen und Sammler (auch Amateure) zu eigenen Untersuchungen anregen - so könnte meine Bearbeitung der fossilen Spinnen ein kleiner Schritt in einer "endlosen Geschichte" der Erforschung der Bernstein-Einschlüsse sein, die noch zahlreiche Generationen künftiger Untersucher beschäftigen mag! Einige der hervorragend erhaltenen Stücke zeigen Einzelheiten, wie sie auch bei heutigen Spinnen zu sehen sind, und jedes Fossil dokumentiert eine einzigartige "Geschichte"! Beispiele sind Kampfszenen zwischen Spinnen und Ameisen bzw. einer Milbe (Fotos 606, 608, 614), die geologisch ältesten Spinnen, die Ameisen nachahmen (Ameisen-Mimikry) (Foto 376), Fossilien wie die außergewöhnlichen Ursinnen des Baltischen Bernsteinwaldes, die heute in Europa ausgestorben sind, und deren überlebende Verwandte in Südafrika, Madagaskar und Australien anzutreffen sind (Fotos 56-83), Reste von Gift an der Spitze von Giftklauen fossiler Spinnen (Foto 389), Reste von Beutetieren fossiler Spinnen, die eingesponnen oder in fossilen Fangnetzen hängen geblieben sein können (z. B. Foto 636), Reste klebriger Fäden eines Fangnetzes (Foto 537), eine weibliche fossile Spinne, die ihren Nachwuchs in einem Ballen bewacht und umherträgt (Foto 523), Merkmale, die Rückschlüsse zum Fortpflanzungs-Verhalten erlauben (z. B. Fotos 362-363)! - Anschließend mag ein Anfänger den restlichen Teil der Einleitung und die allgemeinen Kapitel in Band 3a lesen, in denen sich Hinweise auf Kapitel in Band 3b finden.

Jörg Wunderlich, im April 2004

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J. Urban in 09661 Hainichen sold me interesting fossil spiders, from the Bitterfeld deposit, too, and from him one can get numerous inclusions in Baltic/Bitterfeld amber.

MATERIAL and selected INSTITUTIONS cited / MATERIAL und ausgewählte aufgeführte INSTITUTIONEN

Most inclusions are preserved in Baltic amber (BB, BA) and - if not otherwise noted - in the private collection of the author (CJW). Most inclusions of my private collection got numbers which start with an "F" for "fossil".

Recently the following amber inclusions were presented to

(a) the the SMF: *Mastigusa acuminata* MENGE, neotype; *Menneus* sp. indet. 1 (F959/CJW), 1 juv. ♀ and the part of a web; *Balticoblemma unicornis* n. sp., paratype b); *Balticoroma serafinorum* n. gen. n. sp., paratype c) as well as 6 pieces with paratypes: 4 ♂, 2 ♂, 1 ♂, 1 ♂, 1 ♂, 1 ♀; *Balticoroma* sp. indet. (CJW); 2 ♀, *Cornuanandrus maior* WUNDERLICH 1986, holotype; *Eometa calefacta* n. sp., holotype; *Succiniopsis kutscheri* n. gen. n. sp., holotype; *Balticonopsis bitterfeldensis* n. gen. n. sp., holotype; *Lasius* sp. indet. as a prey in a spiders' capture web (WUNDERLICH (1986: Fig. 28)); 21 specimens of *Adorator hispidus* (KOCH & BERENDT 1854); 6 juv. *Syphax megacephalus* KOCH & BERENDT 1854; a capture web of a questionable *Nephila* sp. indet. in Dominican amber; *Grammonota deformans* WUNDERLICH 1998 (= *Ceratinopsis d.*) in copal from Madagascara (a fake); as well as the holotype of the mite *Zachardia flexipes* JUDSON & WUNDERLICH 2003 and

(b) the GPIUH: *Ariadna hintzei* n. sp., holotype in copal from Madagascar (gift of A. HINTZE); *Eotrechalea kruegeri* n. gen. n. sp., holotype + 4 pieces of amber; most of the following inclusions are a gift of R. SCHÖNEICH: Paratype h) of *Balticoroma reschi* n. gen. n. sp.; *Balticoroma* sp. indet., 1 ♂; a piece with 1 ♀ of *Balticoroma* sp. indet., 4 ?juv. Hahnidae indet. and an exuvia; two egg sacs (F122, F1142); the holotype of *Ephalmator ruthildae* n. sp.; the paratype of *Ephalmator distinctus* n. sp. (F592/CJW); a juvenile of ?*Menneus* sp. indet. from Bitterfeld (F964/CJW); the paratype of *Protoorthobula bifida* n. gen. n. sp.; the paratype of *Protoorthobula deelemani* n. gen. n. sp. (F673/CJW); the paratype a) of *Balticoroma ernstorum* n. gen. n. sp.; a juvenile *Trionycha* indet. in its web (F1216); *Custodela* sp. indet. (F1219); an exuvia of *Segestria* indet. (F1109); an exuvia of a questionable Araneidae indet. (F1172); and a paratype ♂ of ?*Telema moritzi* n. sp., from Bitterfeld (F485/CJW).

Probably most of the material which is treated in these volumes will be deposited later in the GPIUH, the SMNHS and the GPIUH.

Important material from the Bitterfeld deposit is preserved in private collections of H. GRABENHORST, JW, H. KRÜMMER, M. KUTSCHER, W. LUDWIG, M. SCHIPPLICK and the PIHUB.

CJW = private collection of J. WUNDERLICH,

IMPGP = Institute and Museum of Geology and Palaeontology of the Georg-August-University Göttingen (H. JAHNKE),

MZ = Museum Ziemi in Warsaw (B. CERANOWICZ, R. KULICKA in former times),

GPIUH = Geological-Palaeontological Institute of the University Hamburg (W. WEITSCHAT),

PIHUB = Palaeontological Institute of the Humboldt University, Berlin (C. NEUMANN and E. PIETRZENIUK previously),

SMNHS = State Museum of Natural History Stuttgart (G. BECHLY and D. SCHLEE previously),

SMF = Senckenberg-Museum Frankfurt a. M. (P. JÄGER and M. GRASSHOFF previously),

ZMUK = Zoological Museum, University of Copenhagen (V. NICOLAI and H. ENGHOFF previously).

WANTED!!! 1000 Euro reward!!

Dead, not alive!

A **fossil spider** in Baltic amber (σ) of the (underlined)...

Oecobiidae: Oecobiinae,
Linyphiidae: Erigoninae,
Tetragnathidae: Tetragnathinae,
Lycosidae (Wolf Spiders),
Salticidae (Jumping Spiders):
 Euophryinae,
 Lyssomaninae,
 Salticinae.

GESUCHT!!! 1000 Euro Belohnung!!

Tot, nicht lebendig!

Eine **fossile Spinne** im Baltischen Bernstein (σ) der (unterstrichen)...

Oecobiidae: Oecobiinae (Eigentliche Scheibennetzspinnen),
Linyphiidae: Erigoninae (Zwergspinnen),
Tetragnathidae: Tetragnathinae (Eigentl. Streckerspinnen),
Lycosidae (Wolfspinnen),
Salticidae (Springspinnen):
 Euophryinae,
 Lyssomaninae,
 Salticinae.

The spiders are to be **sent to** Jörg Wunderlich, Hindenburgstr. 94, 75334 Straubenhardt, Germany.

PART I (TEIL I) - General findings and conclusions

REMARKS ON THE PREPARATION AND THE PRESERVATION OF FOSSILS IN AMBER AND COPAL (ANMERKUNGEN ZU PRÄPARATION UND KONSERVIERUNG VON FOSSILIEN IN BERNSTEIN UND KOPAL)

See SCHLEE & GLÖCKNER (1978: 46-51), WUNDERLICH (1983: 11-12).

(1) Handling, preparation (Bearbeitung)

At first an important advise to entomologists: Never put a piece of a fossil resin in alcohol! (An arachnologist put a spiders' holotype in alcohol and thus destroyed parts of the surface of the amber piece!).

It may be useful to fix a piece of amber under the microscope in the desired position on a piece of soft plastic which is not sticky.

Cutting and polishing of pieces of fossil resins need some experiences: A piece may break along a layer, cooling by water may prevent heating. During the heating by cutting and polishing a piece of copal (and even of young amber) may melt.

A white emulsion on a fossil in Baltic amber may disappear by heating in an autoclave, but parts of the amber and of the inclusion may be more or less deformed and darkened after this procedure, certain structures will be hard to recognize, see the photos 83, 179, 412, 473, and dark stripes may be typical for this handling.

Reflecting borders between different layers of the amber may disappear after using bencoeacidbenzylester, $C_{14}H_{12}O_2$ (in German Benzoessäurebenzylester), but organic structures may be more or less darkened and structures of a spider's male pedipalpus may be hard to recognize after this procedure. From the only known fossil member of the order Solifugae in Baltic amber a photo exists before using bencoeacidbenzylester (photo 688) and after using this material (photo 689). In fig. 688 one can clearly recognize the darkened parts of the specimen.

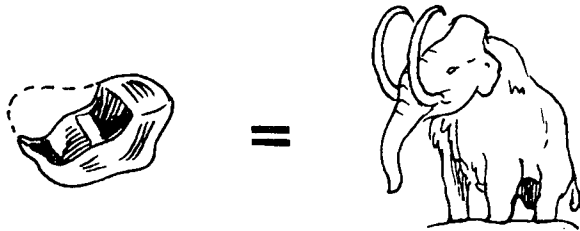
(2) Preservation (Konservierung)

Fossil organisms in amber can outlive hundreds of million years in an optimal condition but can be destroyed e.g. by sun light, oxidation and drying up in few decades. Some investigators put amber pieces into water, oil or glycerine. The best way of preservation is an embedding in artificial resin, e.g. polyester, see HOFFEINS (2001: 215): "This mode of conservation stabilises the amber and protects from breakage and from oxidation and also provides better viewing surfaces for the study and determination of the inclusions."

Paläontologen sind Wissenschaftler, die ausgestorbene Tiere erforschen. Man erkennt einen Paläontologen daran, daß er auf dem Boden umherkriecht. Dort sucht er nach Fossilien oder nach seiner Kontaktlinse

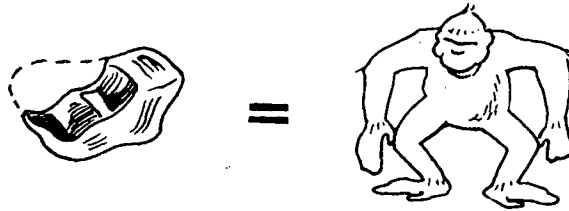
Fossilien sind Spuren früheren Lebens, meistens versteinerte Knochen, Zähne, Fußspuren oder unbezahlte Rechnungen

Rekonstruktion ist die Kunst, aus Fossilien auf deren ursprüngliche Eigentümer zu schließen (siehe Abbildung)



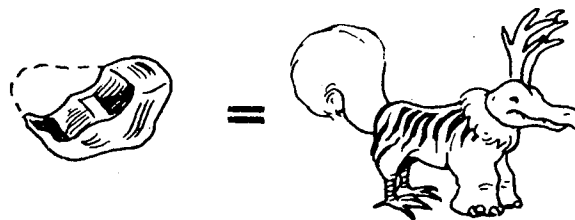
Zahnfossil

Rekonstruiertes Tier



Zahnfossil

Rekonstruiertes Tier



Zahnfossil

Rekonstruiertes Tier

Aus: Tom Weller, Science made stupid; 1985 erschienen im Verlag Houghton & Mifflin (weitere Informationen unter: <http://www.14.pair.com/~kmac/sms>)

REMARKS ON FOSSIL RESINS, AMBERS AND COPALS (ÜBER FOSSILE HÄRZE, BERNSTEINE UND KOPALE)

See the papers of SCHLEE and the book of WEITSCHAT & WICHARD.

Producers of resins are various plants, e.g. palmae, Gymnospermae/needle trees and Angiospermae/deciduous trees. Most probably pines are the main producers of Baltic amber, but several other plants are discussed. Dominican amber and certain copals (e.g. from the Dominican Republic, East Africa and Madagascar) originate from a Leguminosae, the genus *Hymenaea*; other copals originate from needle trees. See the papers on fakes and on spiders in copal from Madagascar in these volumes.

The age of fossil resins, the terms "amber" and "copal": Resins were produced for more than three hundred million years. Young resins are called copal - but what is "young"? Ambers are - according to SCHLEE & GLÖCKNER (1978: 4) - "distinctly" older than one million years, younger resins are called copals. This distinction is not generally accepted. The age of various ambers is shown in fig. 1.

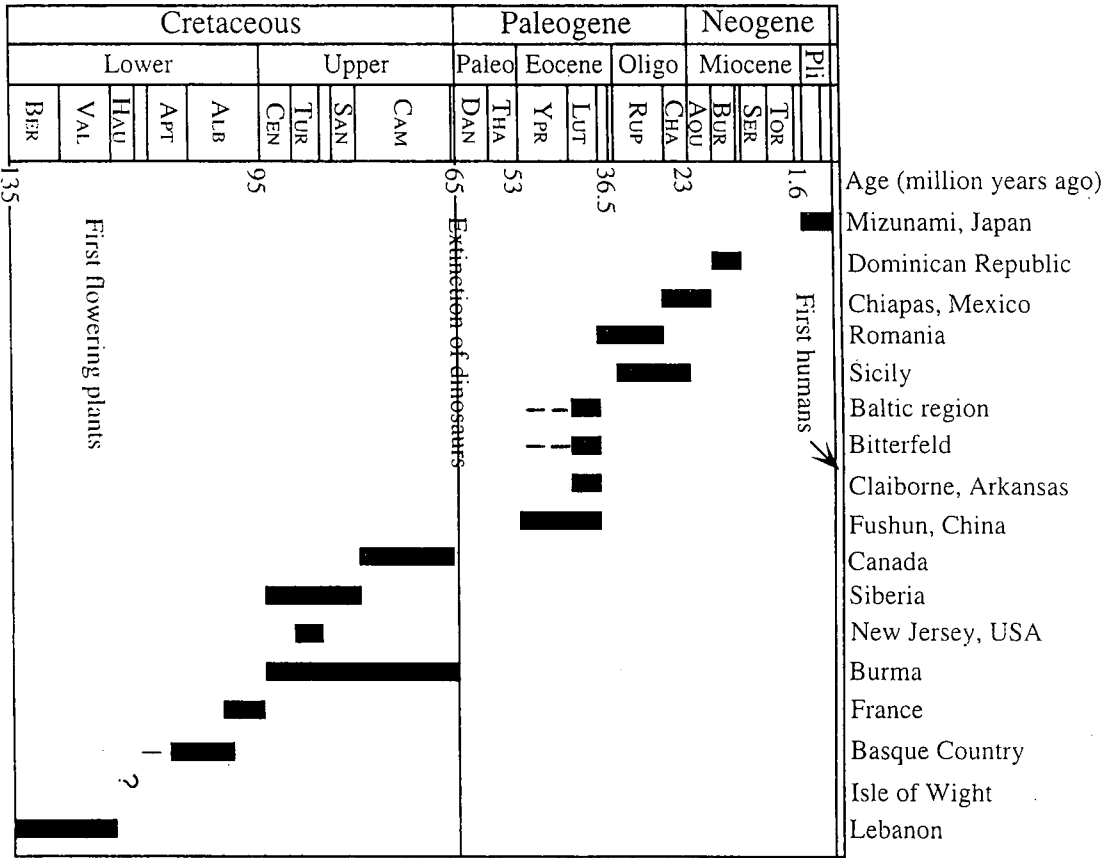


Fig. 1. Localities and stratigraphy of amber deposits known to contain spider inclusions. - Taken from PENNEY (2002: Fig. 1), slightly modified.

Remarks to fig. 1: According to most authors - see e.g. RITZKOWSKI (1997) - the Baltic (and Ukrainian) ambers may be about 10 million years older than shown in this figure. (2) Amber "from France" may be younger (Early Tertiary), e.g. amber from Oise near Paris (W. WEITSCHAT, pers. commun.). (3) The oldest amber of this list comes from the Lebanon and from the time of the first flowering plants. At that time the radiation of several winged insect groups and several spider taxa started, which depended directly or indirectly on flowering/pollinating plants. (4) Also of special interest may be the ambers from Canada and from Burma because they contain inclusions just before the Cretaceous-Tertiary event. Here we will probably still find taxa which became extinct during the Early Tertiary and are rare or even absent in the Early Tertiary European ambers; see the new spider families Balduccinidae and Protheridiidae.

The dating: Most copals are not older than few thousand years; their age can be determined with the help of the carbon-14 dating. Unfortunately this method has a limit of about 50 000 years; this is much too less for dating amber but useful for most kinds of copal. - It is rare that the amber-bearing sediment is the original (autochthonous) layer, but usually it is the second, third,... layer. No method is known to determine the age of amber directly, but the amber-bearing sediments may be determined, e.g. by the K-Ar dating, see RITZKOWSKI (1997).

I am grateful to Prof. M. A. GEYH, Niedersächsisches Landesamt für Bodenforschung in Hannover, who dated two pieces of Dominican copal (from Cotui) as 10 820 (+3530/-2445) and 1170 (+/- 130) years old, see WUNDERLICH (1986: 15-16). Other pieces of copal from Cotui were dated as "younger than 280 years"; SCHLEE (1984). - In 1999 four pieces of copal from N-Madagascar and one piece from Columbia (Pena Blanca, Prov. Santander) were dated in Hannover as not earlier produced than 1958 resp. 1955. - (Remark: Although young ("subfossil" or "subrecent"), such copals may be of great scientific interest because large parts of the resin-producing forests are now destroyed, and numerous species are extinct but still preserved in copal).

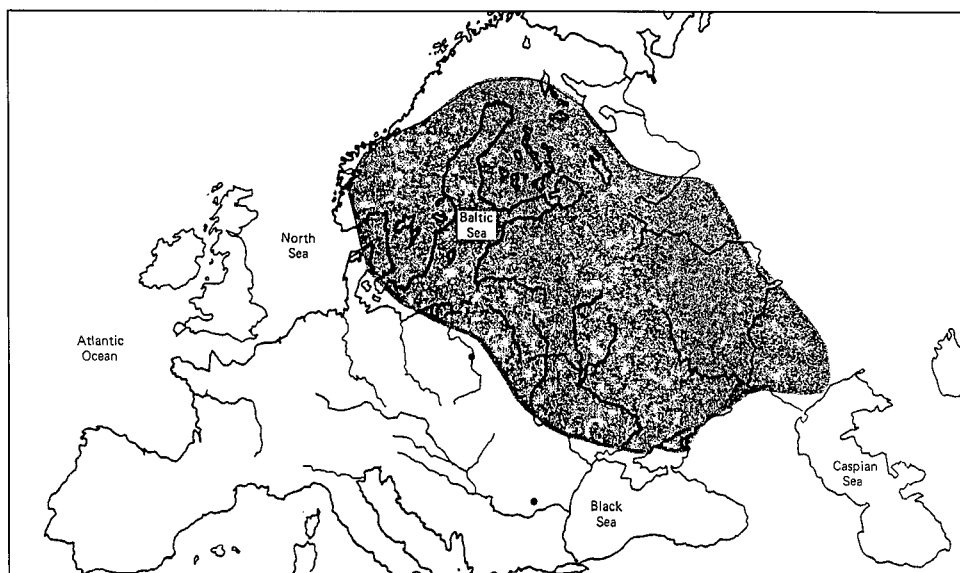


Fig. 2. Distribution of the Early Tertiary European amber forests, taken from RICE (1993: Fig. 6-6).

The "Tertiary European amber forests"

According to LARSSON (1978: 52) "The European amber forests have had a very great geographical cover from west to east, penetrating deep into the Asiatic continent, even possibly as far as the Pacific coast." According to RICE these large primeval forests covered large parts of Europe including the Ukraine but not Southern and Western as well as the whole Central Europe (fig. 2). KATINAS (1971) showed a small range of the "primary deposits of amber" (fig. 3). The actual range of these old Tertiary amber forests is unknown.

LARSSON (1978: 52) used the term "European amber forests". I would like to introduce the term "Eocene European amber forests" or "Early Tertiary European amber forests" for these subtropical forests, which include the Baltic (= Samlandic, Kalinin-grad) amber, the Bitterfeld amber (which may be called "Baltic amber from the Bitterfeld deposit", see the chapter on the palaeofauna in this volume), the Ukrainian ambers (e.g. from Rovno), the amber from Oise near Paris and probably some other European ambers from the Early Tertiary. According to SCHLEE & GLÖCKNER (1978) the Ukrainian ambers are "part of the large Baltic amber forest", but - because of the different origin, deposit and the partly different fauna - I do not want to include the Ukrainian amber in a widened term "Baltic amber".

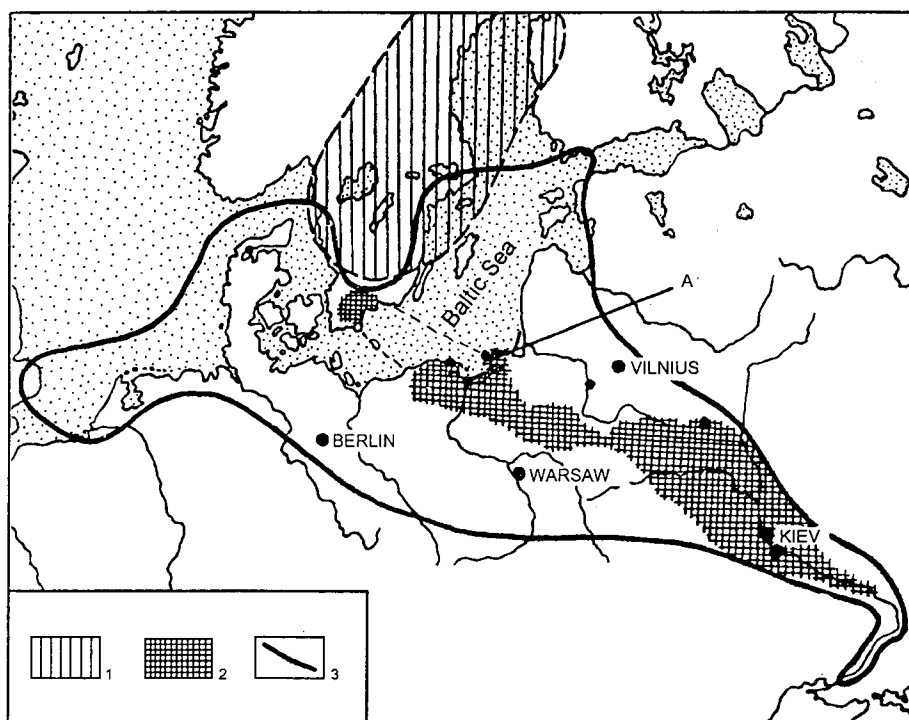


Fig. 3. Distribution of some Tertiary European amber-bearing sediments; taken from KATINAS (1971), modified. 1 = primary deposits of Baltic amber; 2 = amber of Palaeogene deposits; 3 = boundary of distribution of redeposited amber; A = Kaliningrad region.

Remark: According to HELM "succinite" contains 3-6% succinic acid. Succinite is not a useful term for the Baltic (or other European) amber, because other resins may contain a similar percentage of succinic acid, see WEITSCHAT & WICHARD (2002: 9).

The Ukrainian ambers: According to VASSILISHIN & PANTSCHENKO (1997) the age of the Ukrainian ambers is about 38-42 million years (Eocene). There exist several deposits, and some ambers may be older than 42 million years. Climate and Arthropod fauna are not identical but very similar to Baltic ambers. The Ukrainian amber forest was probably united with the Baltic amber forest. See the paper on spiders in Ukrainian amber in these volumes.

The "**Oligocene European amber forests**" - from Sicily and probably from Romania - existed after the Eocene/Oligocene cooling. Their relationships to the Baltic amber fauna are not well-studied: The descriptions of spiders in Romanian amber were mainly based on weakly determinable juveniles - see PROTESCU (1937) -, and a revision is necessary. Spiders and other arthropods in amber from Sicily are waiting for descriptions.

The "Lower Cretaceous Mediterranean ambers"

The age of the ambers from Lebanon, Jordan and Alava (Spain) is about 110 to 135 million years, that is almost two and a half times the age of the Baltic amber. Probably in the Early Cretaceous existed a large "amber forest" in wide parts of the Mediterranean, which climate was tropical to subtropical. The investigation of the inclusions of these ambers just started - see the papers of PENNEY & SELDEN (2002), POINAR & MILKI (2001) and my paper on the new subfamily Microsegestriidae in these volumes. These ambers will surely be of greatest value regarding the evolution of the ancestors of various higher insect and spider taxa; e.g. members of the spider family Salticidae - which are frequent in Baltic amber - have not (yet?) been discovered in these ambers, and did probably not yet exist at that time, and the search of their origin and their ancestors is an exciting matter.

Upper Cretaceous amber from New Jersey, USA

The investigation of this ambers has just started, see GRIMALDI (ed.) (2000), PENNEY (2002).

Oligocene neotropical Dominican and Mexican ambers

These ambers are only half as old as Baltic amber (Oligocene), see above. The spider fauna of the Dominican amber forest has been studied by PENNEY (1999ff) and WUNDERLICH (1988).

ON THE PRESERVATION OF SELECTED STRUCTURES OF SPIDERS IN FOS- SIL RESINS (ZUR ERHALTUNG AUSGEWÄHLTER STRUKTUREN VON SPIN- NEN IN FOSSILEN HARZEN)

Introductory remarks

The three-dimensionally preserved organic inclusions in fossil resins offer tremendous possibilities for various palaeontological conclusions. Fine structures such as spinules of spinnerets, sense organs, genital structures, threads and even cells are recognizable. Surprisingly also microstructures e.g. of muscles and probably spermatozoa are preserved in amber fossils, see KOHRING (1998), Mierzejewski (1976a, b) and below. The preservation of molecular structures as DNA in amber fossils has been doubted, see ROSS (1998: 32-33).

Structures of fossil spiders in Baltic amber

Finds of PETRUNKEVITCH: (a) PETRUNKEVITCH (1950: Fig. 1) figured remains of organs of a member of the family Oecobiidae, *Mizialia blauvelti* (PETRUNKEVITCH 1942) (sub *Paruroctea*): the heart and parts of the ovary - but are these remains really from the heart and from the ovary? - (b) PETRUNKEVITCH (1950: 325, figs. 136, 176) described and figured remains of cells of the hypodermis and even remains of nuclei of *Eoathanatus diritatis* PETRUNKEVITCH 1950 (?= *Ablator*). I am in doubt about these findings, especially of the nuclei, and the "cells" may be nothing else than the scale-shaped structure of the epicuticula.

Sclerotized remains of the cuticula are present probably in all spiders and most other arthropods in amber; I cracked amber pieces which contained males of *Orchestina* SIMON (Oonopidae), *Balticoroma serafinorum* n. gen. n. sp. (Anapidae) and *Acrometa* sp. (Synotaxidae), and I found hard remains of prosoma, legs, pedipalpi and eye lenses.

Various male genital structures are excellently preserved, e.g. in *Paraspermophora* ?*perplexa* n. gen. n. sp. (Pholcidae) (photo 53), *Archaea* ?*paradoxa* KOCH & BERENDT (Archaeidae) (photo 63), *Hersiliopsis madagascariensis* n. gen. n. sp. (Hersiliidae) (photo 87), *Hyptiotes stellatus* n. sp. (Uloboridae) (photo 101), *Baltsuccinus flagellaceus* n. gen. n. sp. (Baltsuccinidae) (photo 182), *Spinilipus glinki* n. sp. (Cyatholipidae) (photos 198-199), *Eopopino rudloffi* n. sp. (Nesticidae) (photo 239), *Eodictyna communis* n. gen. n. sp. (Dictynidae) (photo 287), *Copaldictyna madagasca-riensis* n. gen. n. sp. (Dictynidae) (photos 303-307), and *Eomafachia wegneri* n. sp. (Zoropsidae s. l.) (photo 316), *Gorgopsina frenata* (KOCH & BERENDT 1854) (Salticidae) (photo 424). In *Balticoroma reschi* n. gen. n. sp. (Anapidae) the structures of the expanded pedipalpus are preserved in a splendid way (photo 147). Rarely female

genital organs are well preserved, e.g. the epigyne of *Mizalia* sp. indet. (Oecobiidae) (photo 97), Cyatholipidae sp. indet. (photo 209), ?*Custodela parva* n. sp. (Linyphiidae) (photo 252), *Eohahnia succini* PETRUNKEVITCH (Dictynidae s. l.: Hahniinae) (photo 297) and *Protoorthobula bifida* n. gen. n. sp. and ?*Protoorthobula* sp. indet. (Corinnidae) (photos 381 and 485); in the last case structures of the vulva are recognizable as well. A plug (in German "Begattungszeichen") - a bulbal secretion of the male pedipalpus which may seal the egigynal opening after a copulation - is preserved in *Sosybius kochi* n. sp. (Trochanteriidae) (fig. 1) and in *Acrometa cristata* PETRUNKEVITCH 1942 (Synotaxidae) (coll. GRABENHORST AR-54).

Spinnerets and their spinules are occasionally well preserved, see e.g. the photos 19 (Segestriidae), 922-293 (Hersiliidae indet.), 285 and 305 (Dictynidae, spinnerets and cribellum) and 349 (Zodariidae).

Spiders' threads and webs including remains of sticky droplets and cribellate capture threads are occasionally excellently preserved, see the photos 526-573, fig. 3.

The tracheal fold is very well preserved in an indet. female of the family Cyatholipidae (photo 209).

The extravasation of haemolymph - the special blood of spiders and other arthropods - can frequently be observed in fossil spiders after the autotomy of leg articles, see e.g. the photos 89, 91, 254-255. Remains of blood are preserved at a broken metatarsus of a member of the family Theridiidae (fig. 4) and at the break after a patella in the holotype of *Custodelela hamata* n. gen. n. sp. (Linyphiidae) (fig. 5). Remains of blood are preserved on both anterior patellae of the holotype of *Gerdiopsis infragens* n. gen. n. sp. (Hersiliidae) (photo 91).

Sense organs: Eye lenses are well observable in numerous fossil spiders, see the photos. In the left posterior median eye of *Eotrochanteria kruegeri* n. gen. n. sp. (Trochanteriidae) probably the canoe-shaped tapetum is preserved (fig. 6). Trichobothria and other sensory hairs are frequently well preserved (e.g. fig. 7). Slit sense organs are reported and figured e.g. from *Succiniopsis kutscheri* n. gen. n. sp. (Zoropsidae s. l.).

Remains of a questionable sperm web and questionable spermatozoa are preserved with the holotype male of *Custodela acutula* n. sp. (Linyhiidae) (photos 249-250).

Glands: Remains of droplets of poison at the tip of a fang are rarely preserved in fossil spiders, e.g. in *Spinilipus glinki* n. sp. (Cyatholipidae) and in *Sosybius perniciosus* n. sp. (Trochanteriidae) (fig. 2, photo 389). Sternal glands of the Theridiosomatidae: See WUNDERLICH (1988). Questionable pores of pheromone glands of an Anapid spider: See fig. 8. Tibial gland plates of a Telemid spider: See fig. 9. Cheliceral glands and their secretions of members of the family Archaeidae are occasionally preserved, see e.g. photo 74. Coxal glands are occasionally recognizable in fossil spiders.

The preservation of soft parts of fossil arthropods including spiders - e.g. muscles - has been reported several times, see KOHRING (1998: 96, fig. 7), MIERZEJEWSKI (1976a, b) and the papers of VOIGT. Questionable remains of muscles are preserved in certain spiders in Baltic amber, e.g. in *Balticoroma serafinorum* (photo 151) and *Baltsuccinus flagellacea* n. gen. n. sp. (Baltsuccinidae) (photo 184). See furthermore PETRUNKEVITCH (1950: 262, fig. 209).

Original colours are only rarely preserved in spider inclusions in amber. Pigments of chromatophores are rarely preserved in fossils, see Voigt (1998: 6).

Kinds of camouflage/ornamentation (in German: Schutztracht) are preserved in certain members of the Oxyopidae in Dominican amber (photos 98-99) and the Salticidae in Dominican amber as well as in Baltic amber (photos 417, 419-420 and 430), see the chapter on this item in this volume. The yellow colour is not a pigment but a

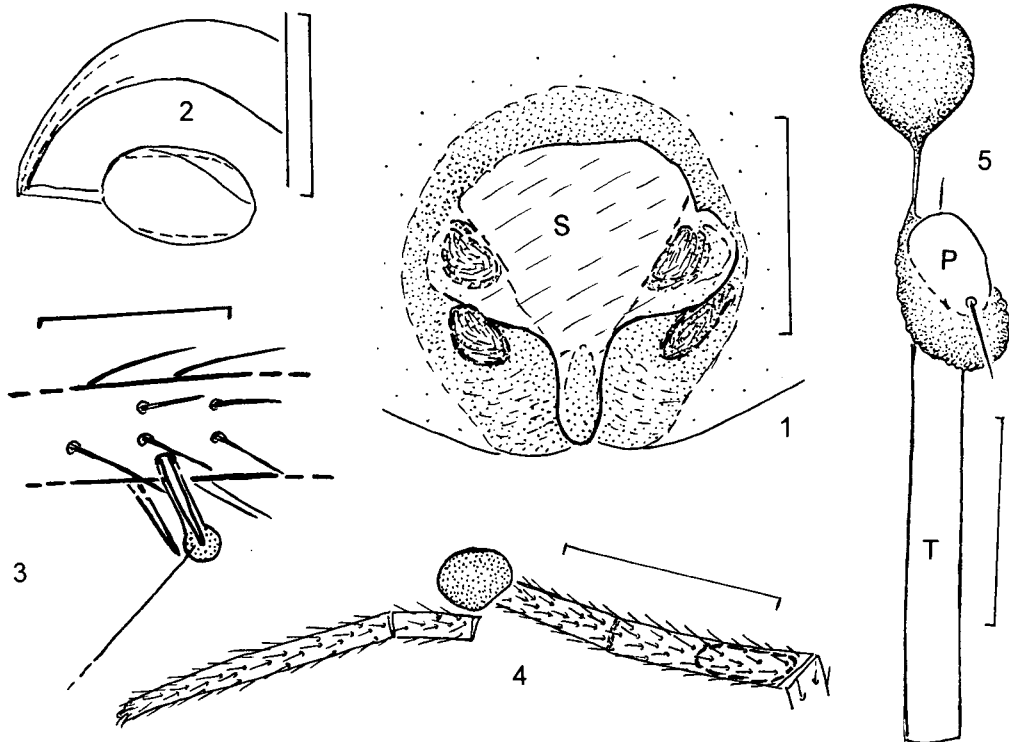


Fig. 1) Epigyne of *Sosybius kochi* n. sp. (Trochanteriidae, holotype) with a secretion S (plug), which seals the large groove in the centre. M = 0.5mm. - "Begattungszeichen" (S), das die große Grube der Epigyne des weiblichen Holotypus der Schenkelringspinne *Sosybius kochi* n. sp. ausfüllt.

Fig. 2) A droplet with remains of poison at the tip of the left fang of *Sosybius perniciosus* n. sp. (Trochanteriidae). M = 0.5mm. - Ein Tröpfchen mit Resten von Gift an der Spitze der linken Giftklaue der Schenkelringspinne *Sosybius perniciosus* n. sp.

Fig. 3) A thin emulsion, a droplet and a thin thread on a median spigot of the left posterior spinneret of *Gardiopsis infringens* n. gen. n. sp. (Hersiliidae, male holotype). M = 0.2mm. - Eine dünne Emulsion, ein Tröpfchen und ein dünner Spinnfaden auf einer mittleren Spinnspule der linken hinteren Spinnwarze der Kreiselspinne *Gardiopsis infringens* n. gen. n. sp. (Holotypus, Männchen).

Fig. 4) A droplet of blood (remains of haemolymph) at the broken right second metatarsus of a member of the family Theridiidae indet. (F154/BB/CJW). M = 0.5mm. - Reste eines Blutströpfchens an dem gebrochenen Metatarsus des zweiten rechten Beins einer unbestimmten Kugelspinne (F154/BB/CJW).

Fig. 5) Two remains of droplets of blood (haemolymph, dotted, one is hanging at a stalk) at the break (autotomy) between tibia (T) and patella (P) of the right second leg of *Custodelela hamata* n. gen. n. sp. (male holotype, Linyphiidae). M = 0.5mm. - Zwei Reste von Blutströpfchen (punktiert; eins hängt an einem Stielchen) an der Bruchstelle (Autotomie) zwischen Tibia (T) und Patella (P) des rechten zweiten Beins der Baldachinspinne *Custodelela hamata* n. gen. n. sp.

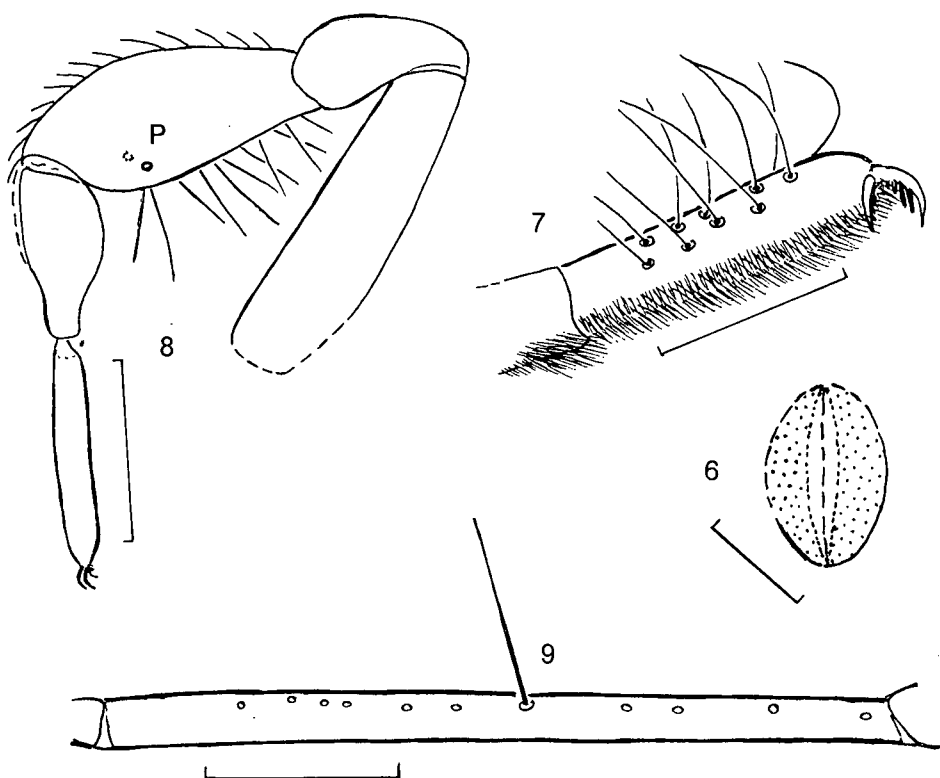


Fig. 6) Left posterior median eye of *Eotrochanteria kruegeri* n. gen. n. sp. (holotype male, Trochanteriidae) in which remains of the canoe-shaped tapetum probably are preserved. M = 0.1mm. - Linkes hinteres Mittelauge von *Eotrochanteria kruegeri* n. gen. n. sp. (männlicher Holotypus, Trochanteriidae), in dem möglicherweise Reste eines kahnförmigen Tapetums erhalten sind.

Fig. 7) *Sosybius mizgirisi* n. sp. (holotype, Trochanteriidae), male, retroventral aspect of the right second tarsus, with a ventral scopula and long dorsal trichobothria. M = 0.5mm. - Lange obere Becherhaare und untere "Haarbürste" des zweiten rechten Fußgliedes der Schenkelringspinne *Sosybius mizgirisi* n. sp.

Fig. 8) Right anterior leg of the male holotype of *Balticoroma reschi* n. gen. n. sp. (Anapidae), prolateral aspect. Note the supposed pores (P) of probable pheromone glands of the thickened femur. M = 0.2mm. - Rechtes Vorderbein des männlichen Holotypus der Zwerg-Kugelspinne *Balticoroma reschi* n. gen. n. sp., vordere Seite. Man beachte die Poren (P) möglicher Pheromondrüsen des verdickten Schenkels.

Fig. 9) A row of ten dorsal gland plates of the right posterior tibia of ?*Telema moritzi* n. sp. (female, paratype, Telemidæ). M = 0.2.- Eine Reihe von zehn oberen "Drüsen-Plättchen" auf der rechten hinteren Tibia der weiblichen Höhlen-Sechsaugenspinne *Telema moritzi* n. sp.

structural colour of hair. See also PETRUNKEVITCH (1950: 261-262).

The light medium part of the sternum of an ?Araneidae indet. (F1172/BB/CJW, photo 136) is a case of depigmentation; remains of lateral pigments are preserved. Annulated legs are preserved in certain fossil spiders in Baltic amber, e.g. in ?*Bararaneus annulatus* n. gen. n. sp. (Araneidae) and *Eotrechalea annulata* n. gen. n. sp. (?Trechaleidae) (indistinctly recognizable in photo 336)

The original redbrown colour of the cuticula has outlived mainly at the heavily sclerotized prosoma and opisthosomal scuta in members of the Anapinae (photos 152ff) and Comarominae (photos 143ff) of the family Anapidae.

Red eyes of extant spiders (mainly from the anterior median eyes) are known (a) from certain Theridiidae, e.g. *Episinus* and related genera (see WUNDERLICH (1988: 131)) and (b) from certain Thomisidae, e.g. *Misumena vatia* and *Diaea dorsata*, see BELLMANN (1997: Figs. pp 189, 193). HOMANN (1934) reports a special pigment distribution for Thomisid eyes: "There is a narrow black pigment spot in the centre, surrounded by yellow and red pigment and finally bordered by a black pigment ring ("iris")". HOMANN also described that the retina appears black when viewed straight on, but yellow when the retina is pulled sideways. - Red anterior median eyes are present in numerous subfossil arthropods in copal (a) from the Dominican Republic (*Episinus antecognatus* WUNDERLICH 1986, see WUNDERLICH (1986: 77) (SMF) and (b) from Madagsacar (e.g. F828/CM/CJW), Diptera and other insects and spiders, e.g. *Eriauchenius* sp. (Archaeidae) and Theridiidae (photo 435). - In Baltic amber spiders I found indistinct red anterior median eyes in members of the families Anapidae: Mysmeninae (photo 177), Linyphiidae (CJW) and Synotaxidae, in *Eosynotaxus wegneri* n. gen. n. sp. (fig. 228) and *Gibbersynotaxus* n. gen.

See furthermore the chapters on the reproductive behaviour, digestive liquid and excrements in this volume.

Diplopode in Copula

Herr Tausendfuß wollt sich gern paaren
Vor Abermillionen von Jahren
Sturm und Drang schienen unausweichlich
Frau Tausendfuß gab Liebe reichlich
Doch um ein fremdes Weiblein zu ergattern
Ließ Bruder Leichtfuß tausend Füßlein flattern.

Entzückt vom fremden Fahrgestell
Verließ er sein Zuhause quickschnell
Errötend folgt er ihrer Spur
Im Safte voll, mit Liebes Schwur
Ob er sie herzlich lieben will
Mit Trippeltrapp und Hochgefühl?

Grad als er kam zu seinem Ziel
Traf sie des Schicksals Würfelspiel...
Aus Baumes Rinde quoll mit Kraft
Des Harzes wundersamer Saft
Umgeben sind sie bald vom goldnen Guß
Welch Überraschung für Herrn Tausendfuß

Heut sieht man sie vereint im Schrein
Als prächtigen Inklusenstein
Des Sammlers Herz ist tiefgerührt
Was zu dem Fingerzeig wohl führt
Die Moral des zwiefachen Ergüßchen':
Fremdgehen verklemmt die heißen Füßchen
Hans Jörg Müllenmeister

CHANGES BY MISTAKE, FAKES and IMITATIONS of organic inclusions in amber (VERWECHSLUNGEN, FÄLSCHUNGEN und NACHAHMUNGEN von organischen Einschlüssen in Bernstein)

Photos 83, 179, 441-447

Introductory remarks

GRIMALDI et al. (1994: 253) defined amber forgeries as "...living species purposefully embedded in amber or in matrix that simulates natural amber, with the intention of deceiving a buyer or scientist,...". In my opinion this definition has to be enlarged and has to include not only members of extant species but also members of extinct species and mixtures of both, as is known from, e.g., the ape-man, the "Pittdown forgery". - In contrast to fakes (forgeries) the intention of imitations is not to deceive, but to produce a nice piece which is clearly said to be false (not amber) (it may contain inclusions). See WINKLER (2002).

I. CHANGES BY MISTAKE

In collections of amber dealers one can occasionally find pieces which are seemingly changed by mistake. At a "Mineralien- und Fossilienbörse" in Munich in the year 1996 I discovered in a dealer's "Baltic amber" collection a member of the spider genus *Lyssomanes* HENTZ 1844 (Salticidae). This male would have been the first record of the genus *Lyssomanes* and the whole subfamily Lyssomaninae in Baltic amber, too. *Lyssomanes* is known from Dominican ambers. There was no white emulsion on the body of the spider and soon it became clear to me that the spider was preserved in Dominican but not Baltic amber.

Lepthyphantes lamellatus WUNDERLICH 1988 was described from Dominican amber. In fact this is a member of the genus *Custodella* PETRUNKEVITCH, and the holotype is preserved in Baltic amber, see the paper on the family Linyphiidae in this volume.

I am not quite sure about the origin of the amber which contains the holotype of ?*Stenoonops rugosus* WUNDERLICH (n. sp.) - Baltic amber? See the paper on the family Oonopidae (the superfamily Dysderoidea) in this volume.

According to HOFFEINS & HOFFEINS (pers. commun.) at the end of the eighties of the 20th century a large amount of amber was transported from Bitterfeld to Russia. Thus one cannot exclude that some Bitterfeld amber is handled as "Samlandic" amber (!).

II. FAKES

More common than changes by mistake are fakes and imitations of amber and inclusions. Numerous materials as glas, plastics, horn, bone, stone, jet, casein, celluloid, phenolic resin and copal have been used, see e.g. ANDREE (1939), POINAR & POINAR (1999: 191-193), ROSS (1998: 6-9), SHEDRINSKY (1999: 207-214). Fakes have been produced at least for 2000 years. The "Baltic amber" fly *Fannia scalaris* has been shown to be a fake and the holotype is nothing else than an extant specimen which has been put in a piece of Baltic amber. This "Piltown fly" is one of the most famous fakes of organic inclusions in Baltic amber, see ROSS (1998: 5, fig. 12). This clever method to produce falsified "Baltic amber" inclusions has already been used in the 18th century, see e.g. BACHOFEN-ECHT (1949: 181), WEITSCHAT & VOIGT (1992): The amber piece is split up usually along an amber layer, excavated, and filled with the extant animal or plant and artificial amber-like resin or, e.g., canada balsam, and finally glued together. So parts of such an "amber" piece may include also stellate hairs and true fossils.

A striking old fake is the spider species *Entomocephalus formicoides* HOLL 1829, which was considered a crossing of a spider and an insect and preserved in Baltic amber by HOLL, a geologist (fig. 1).

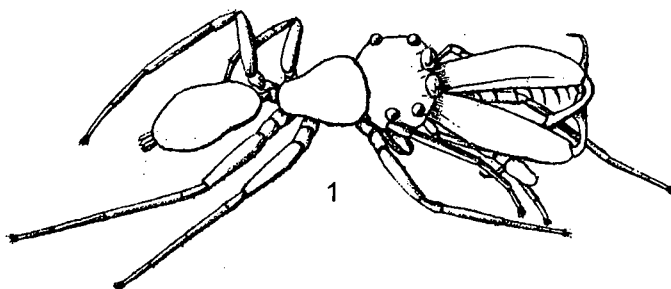


Fig. 1) An ant-shaped spider of the genus *Myrmarachne* MACLEAY (♂), a fake in copal from Madagascar, see above. Note the long protruding chelicerae and the seemingly tripartite body of the spider which is few mm long. Taken from SCHWEIGER (1819: Fig. 68a). - See photo 440.

PETRUNKOVITCH (1958: 372) listed this taxon among members of the family Archaeidae, but according to the description it is in fact a member of the family Salticidae, genus *Myrmarachne*. In my opinion the holotype - the single specimen of this species - is a fake, most probably preserved in copal from Madagascar. *Myrmarachne* is unknown from Baltic amber, but I have seen members of it in copal from Madagascar. Already GOEPPERT & BERENDT (1845: 30) recognized a member of the genus *Myrmarachne* (sub *Poryphorus*) in copal from Madagascar which previously was supposed to be preserved in Baltic amber. See the papers on the Salticidae and on the Archaeidae (superfamily Eresoidea) in these volumes.

Another interesting fake was reported by SCHLÜTER & GNIELINSKY (1987: 19): A piece containing a specimen of a probably extant beetle - the Cicindelinae genus *Odontocheila* - was originally assigned to the Baltic amber about one hundred years

ago, but was later suggested to be embedded in copal from Madagascar. (According to WEITSCHAT & WICHARD (2002: 154) - based on a paper of RÖSCHMANN (1999) - the fossil beetle is not identic with the extant *Tetracha carolina* LINNAEUS).

Stellate hairs - see WEITSCHAT & WICHARD (2002: Fig. 22) and various coloured photos in this volume - are very frequent and typical for the Eocene European ambers (Baltic, Bitterfeld, Ukrainian deposits) as well as is the **white emulsion** - see the photos - at least on one side of an animal inclusion. Such white emulsions may disappear during the heating of a piece of amber in an autoclave. - Imitations have usually been more simply produced, see below: On the polished surface of a piece of Baltic amber the artificial resin with the spider is glued; so the product is a chimera. The volume of the artificial resin may be about 1/6 to 1/4 of the whole piece.

Up to now I have never found or known of an amber fossil transferred from one kind of amber to another kind of amber.

Investigators of the biogeography may be careful in their conclusions; the present author was misled by faked inclusions in copal from Madagascar which were sold as Dominican amber, see below and WUNDERLICH (1998, 1999). Some dealers ignore the serious confusions they cause by their fakes. - G. POINAR - Lapidary Journal, 54: 9 (2000) - warned of forged "Chinese amber": Material was bought in Europe, reworked in China and sold in Tucson/USA. "Unfortunately, even biologists might be fooled into describing new species which could be published with erroneous biogeographical inferences. So amber collectors beware."

Selected examples of fakes and the discrimination of real fossil inclusions:

A) General remarks:

(1) A specialist may recognize an extant species in a falsified piece. As MENGE - in KOCH & BERENDT (1854) - already knew and in contrast, e. g., to the erroneous opinion of WEITSCHAT & VOIGT (1992: 218) no fossil arthropod species in Baltic amber has survived up to now. Only in young resins (copals) an extant species may occur. Therefore the determination of species is a proper method to recognize fakes. In four of five cases I was successful in the determination of spiders in imitated ambers to species level, see below.

(2) In falsified and in true fossil spiders - as well as in several other arthropods - the leg position is usually different: In most fossil spiders - and in most dead extant spiders in alcohol - the legs are bent beneath the prosoma but in several fakes the legs are stretched, see the photo of *Larinioides cornutus*. In this case the living or recently killed spider has been placed in nearly its natural leg position on the surface of the plastic or amber piece before it was imbedded in the artificial resin.

(3) Inclusions in heated ambers and copals are usually +/- deformed and darkened; exceptions may, e.g., exist in strongly sclerotized beetles. Heated amber-like true resin is often copal from Madagascar, but there are also ambers which were heated naturally: (a) some Dominican amber pieces were probably heated by volcanos and (b) - rarely; heated by a fire in the former forest? - there also exists naturally heated Baltic amber. Numerous Baltic amber inclusions - which were originally covered by a

white emulsion - were heated in an autoclave for clearing and after this procedure the arthropod inclusions are darkened and more or less deformed.

(4) Usually the falsified inclusions are large and well visible but tiny arthropods and stellate hairs - which are lacking in artificial resins and plastics - may occur in a piece which has a portion of amber, see below: "Imitated Baltic amber inclusions".

B) The discrimination of amber, copal, plastics etc.:

1) Amber - artificial resins (similar: Plastics):

(a) A simple method to distinguish amber from artificial resins and plastics: Because of its low specific gravity only amber pieces swim on the surface of salt water which has a high percentage of salt (120g salt in 1l water); other materials sink to the ground. Also all imitations studied by me - see below - sank down to the ground although the portion of artificial resin was only 1/4 to 1/6 (the rest was Baltic amber).

(b) In most pieces of Baltic amber - but not in plastics or artificial resins - several syn-inclusions are present, e.g., stellate hairs (see above), pollen grains, tiny balls of excrement, mites and detritus particles.

(c) The margins of imitations and fakes - where amber and artificial resin has been glued together - frequently show gaps which are up to 0.3mm wide, e.g. in some of the pieces which were studied by me.

(d) The "sweet" smell of Baltic amber is quite different compared to the "bad" smell of artificial resins or plastics after heating/melting with a hot needle or after dry grinding.

(e) According to some authors - e.g. SCHLEE & GLOECKNER (1978) - the areas where amber and artificial resin is glued together are better visible with the help of UV-light. I failed in such observations.

2) Baltic amber - Dominican amber, both not heated: Animal inclusions in Baltic amber are frequently covered by a white emulsion at least on one side, and stellate hairs are frequent. Such an emulsion is absent in Dominican ambers and stellate hairs are very rare. The typical "sweet" smell of Baltic amber which results from dry grinding is absent with Dominican ambers (also in all kinds of copal and artificial resins). See also the tab. in the book of WUNDERLICH (1986: 16). After only ten years the surface of some pieces of Dominican amber - e.g. in my personal collection - show more or less distinct fissures which may occur after several decennia in Baltic amber pieces, too.

3) Heated Baltic amber - heated Dominican amber: Arthropod inclusions are usually deformed in heated ambers and copals. The discrimination of the two amber kinds may be difficult because the typical "sweet" smell and often the typical white emulsion are gone in heated/autoclaved Baltic amber. But the stellate hairs - which are typical for Baltic ambers - are usually absent in Dominican ambers.

4) Samlandic amber from the Bitterfeld locality - Eocene European ("Baltic") amber from other localities: The discrimination is very difficult and not sure. After G. Heck (pers. commun.) there is the possibility to distinguish not heated Bitterfeld and non-Bitterfeld amber by the Pyrolysis gas chromatography method with the certainty of 85%. - Usually the pieces from Bitterfeld are smaller and large pieces are completely

absent (W. WEITSCHAT, pers. commun.). Possible qualitative and quantitative differences in the fossil faunas are discussed below; see also the paper on the spider family Archaeidae (sub Eresoidea) in these volumes.

5) Amber - copal (not heated forms; see also the following paragraph): Copals are usually geologically young resins (few years up to several thousand years old), most often more or less clear white to light yellow coloured - occasionally yellowish-orange to brownish - and the surface is attacked/may be destroyed much faster by alcohol and ether than the usually yellow amber which is never clear white. In contrast to ambers the very young copals are more or less soft, and coloured animal inclusions may occur, see WUNDERLICH (1986: Fig. 354). In copal usually extant species are present, in amber only extinct species occur. Copal forgeries have a long history, about 2000 years (!), see GRIMALDI et al. (1994: 261).

6) Heated copals - heated or not heated ambers: Natural or manipulated copals are sold by several dealers as amber because amber is much more expensive. For about 100 years the "Spiller's method" has been used to produce amber-like materials from copals by using an autoclave: Heating and simultaneously applied high pressure; see MARCUSSON & WINTERFELD (1912: 193-194). The discrimination of ambers and manipulated copals may be difficult because the usually white and soft copal changes in the autoclave to yellowish or brownish and becomes hard, and it will be more resistant against attacks/solutions by alcohol and ether. The frequent deformations of the inclusions have already been mentioned above. Furthermore heated Baltic amber has lost its typical "sweet" smell and frequently the white emulsion of the inclusions. Physical methods may give hints for discrimination; according to SHEDRINSKI et al. (1999) the pyrolysis gas chromatography mass spectrometry is preferable to the pyrolysis gas chromatography; see above, HECK (1996, 1997) and WUNDERLICH (1998, 1999) (unsatisfactory results by pyrolysis gas chromatography). According to MÜLLENMEISTER (2001: 34) the dielectric constant factor, the torsion modul and the attenuation spectrum of copal from Madagascar may be similar to Baltic amber after handling in an autoclave. According to MARCUSSON & WINTERFELD (1912: 195) the percentage of H₂S in Baltic amber is usually about ten times higher (0.34-0.42%) than in the hardened copal from Zanzibar (0-0.06%). I failed in the proof of H₂S in Baltic amber by plumbic acetate (Bleiacetat). - Origin of resins: Most of the Baltic amber has been produced by Pinaceae; needles or its remains are not quite rare in this fossil resin. Dominican ambers and copals from the Dominican Republic and Madagascar are produced not by Pinaceae but by Leguminosae. So they cannot include needles, except from needle trees nearby. - The faunas: Species - as well as certain higher taxa - are differing in different fossil resins; an exception may be copal from Madagascar and East Africa which contains related taxa. Besides cosmopolitan genera - e.g. the spider genera *Orchestina* (Oonopidae) and *Dipoena/Lasaeola* (Theridiidae) - there are numerous typical arthropod genera in ambers and copals. Several genera are typical for Baltic ambers, e.g. *Archaea* (Archaeidae), *Acrometa* (Synotaxidae), *Balticoroma* (Anapidae) and *Clypea* (= *Nanomysmena*). *Palaeodictyna* (Dictynidae), *Veterator* (Trochanteridae), *Corythalia* and *Lyssomanes* (both Salticidae) are typical for Dominican - some also in Mexican - ambers. With the exception of *Corythalia* and *Lyssomanes* (both family Salticidae) these genera are extinct; only the extant genera *Corythalia* (american) and *Lyssomanes* (cosmopolitan) occur in copals, too. - Besides families which are cosmopolitan in their distribution there are distinct differences in the Araneae also on family level: E.g., members of the spider family Archaeidae are not rare in East African and Madagascan copals as well as

in Eocene European ("Baltic") ambers - its genera are different in copal and amber! - but members of this family are unknown from other fossil resins except Burmese amber. Thus findings from the biogeography may be more successful in this matter than results of various other methods. See WUNDERLICH (1986, 1988, 1998, 1999) and the paragraph below: "Dominican amber" as falsified copal from Madagascar, ^{14}C -method, and the paper on the family Anapidae s. l. in these volumes.

In the following I focus on spider inclusions which were proven by me.

C) Falsified copal from Madagascar - Dominican amber.

Remark: See also above the short report on the Dominican amber inclusion of a spider of the genus *Lyssomanes* which was offered - not as a falsification - by a dealer as a fossil in Baltic amber, and the paper on spiders in copal from Madagascar in these volumes.

About six years ago I bought a larger collection of inclusions - including spiders - as "Dominican amber" from the firm MÖCK near Stuttgart. According to the brothers MÖCK (pers. commun.) the previous owner of this collection was their father. Most of the inclusions were more or less deformed, some were darkened, similar to naturally heated Dominican amber, see the figure below and the photo of *Eriauchenius* sp.

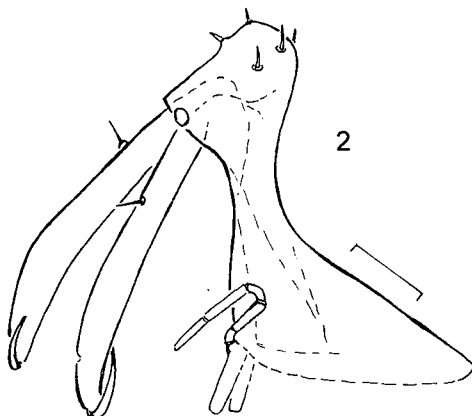


Fig. 2) Lateral aspect of the deformed prosoma of a juvenile spider of *Eriauchenius* sp. (Archaeidae) (CJW) preserved in heated copal from Madagascar which was sold to the author as Dominican amber. - M = 0.2mm. See photo 83).

In two papers I reported/described spiders of the families Archaeidae, Anapidae: Mysmeninae and Linyphiidae: Erigoninae which are preserved in this "Dominican amber", see WUNDERLICH (1998, 1999). Most surprising was the discovery of members of the Archaeidae: Subfamily Archaeinae, which are known from Baltic amber fossils, copal from Madagascar and extant from Madagascar, South Africa and Australia but not from the Americas.

According to results of G. HECK with the help of a physical method - the pyrolysis gas chromatography - this resin seemed to be Dominican amber, see WUNDERLICH (1999). New findings show that this resin is not Dominican amber but copal from Madagascar which has been falsified, manipulated/heated in an autoclave, and some of my previous conclusions on the biogeography of the family Archaeidae have to be revised, see the papers on the family Archaeidae - the superfamily Eresoidea - in these volumes and on spider inclusions in copal from Madagascar.

In the following I state different reasons/arguments for the above mentioned resin collection (from the firm MÖCK) being a falsification:

- According to investigations of M. A. GEYH of the Niedersächsisches Landesamt für Bodenforschung in Hannover with the help of the C¹⁴-method (two pieces, CJW) (pers. commun.) the fossil resin is very young and has been produced in 1963. One piece has been separated from the amber piece which (CJW) contains *Eriauchenius* sp. indet., an extant Ethiopian genus, see below.

- ?*Archaea* sp. (juv.), sensu WUNDERLICH (1999), F71/MC/AR/ARC/CJW, is in fact a member of the extant genus *Eriauchenius* O. PICKARD-CAMBRIDGE, see the papers on the family Archaeidae in the Eresoidea and on fossils in copal from Madagascar in these volumes. Recently I discovered an adult male of *Eriauchenius gracilicollis* in copal from Madagascar (CJW); see the photos.

- According to H. ONO (pers. commun.) the frequent members of the family Thomisidae in the resin collection - FF809, FF811 and FF812/KM/AR/THO/CJW - are members of an Ethiopian genus - *Apyretina* - which do not occur in the Neotropics. See the paper on spiders in copal from Madagascar in this volume and the photos 446-7.

- RUDOLF SCHUH from A-2801 Katzelsdorf (pers. commun.) determined a beetle of the family Colydiidae (= Zopheridae: Colydiinae) - FF77/CM/COL/CJW - as *Recho-des coquereli* FAIRMAIRE 1869, the most frequent species of this genus on Madagascar. According to SCHUH there are no related Neotropical species or genera.

III. IMITATED - seemingly fossil - Baltic amber inclusions

In June 1997 I had the opportunity to buy some imitations of Baltic amber inclusions - including five spiders - for the price of about 10 DM (= 5 Euro) each in Nida/Lithuania. The dealer declared the pieces as imitations and as produced in Poland. I was able to determine four specimens to species level and one to genus level. Distribution: These taxa are extant and frequently present in Central Europe but none of the gene-

ra is known from fossils. - Ecology: One of the species - *Steatoda* sp. - should have been taken from a tree or from a house, *Larinioides cornutus* occurs in open areas and the margins of forests, *Lepthyphantes minutus* lives mainly in coniferous forests. - I describe only *Lepthyphantes minutus* more closely because there are three imitated specimens. - Method of producing and recognizing such kind of imitations and fakes: See above, "a clever method" and "a chimera". - A white emulsion is absent in the studied specimens; remains of the colour of body and/or legs are present.

a) *Lepthyphantes minutus* (BLACKWALL 1833) (Linyphiidae) photo 444.

See fig. 3 below, the coloured photo and the figure p. 224 in the book of SAUER & WUNDERLICH (1997).

Material (in artificial resin combined with Baltic amber): FF/72/AR/LIN/CJW (♂), FF/73/ AR/LIN/CJW (♂) and FF74/AR/LIN/ CJW (♀).

The body length of the males is 2.7 and 3mm, the female is 3.6mm long. The opisthosoma of the males is distinctly deformed; these spiders were most probably embedded after drying out. The glued areas are well visible. The legs of all spiders are annulated and bent beneath the prosoma; at least one leg of each specimen is bro-

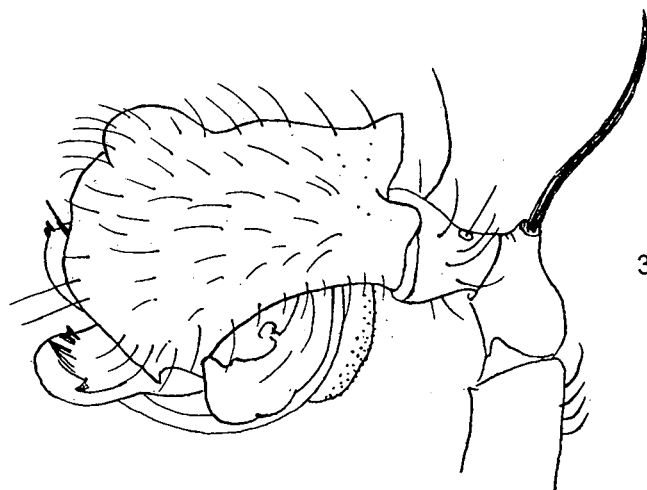


Fig. 3) Right pedipalpus prolaterally (inside position) of the extant male spider of *Lepthyphantes minutus* (BLACKWALL 1833), family Linyphiidae; taken from WIEHLE (1956: Fig. 290). - This species has been found in a collection of imitated Baltic amber

ken off and wanting behind the patella. This kind of autotomy is frequent in the family Linyphiidae. The legs of one of the males - FF74/AR/ LIN/CJW - are stretched out similar to its living position which is quite unusual in fossil amber spiders. In the same piece an area of the original oxidated surface of the amber - which bears fine fissures - is preserved and is now covered by the artificial resin together with the spider. Thus a part of the original outside of the amber piece is now at the inside of the forgery! - The male FF72 is orientated with the dorsal surface to the amber piece.

b) Larinioides cornutus (CLERCK 1757) (Araneidae), photos 441-443.

Material (in artificial resin combined with Baltic amber): 1 ♂, FF75/AR/ARA/CJW.

The body length of the spider is 8mm, the ventral side is orientated to the amber piece, the spiny legs are annulated and stretched out, one leg is broken off behind the patella, another ?through the patella, the colour of the opisthosoma is partly preserved, the genital organs are well observable.

c) Steatoda sp. indet.

Material (in artificial resin combined with Baltic amber): 1 ♀, FF76/AR/THE/CJW.

The body length of the spider is 8mm. Because of numerous crevices and bubbles the spider is hard to observe.

Zum Krankheitsbild und zur Behandlung der SUCCINITOSE

Es handelt sich um eine Suchterkrankung, die insbesondere im Norden Deutschlands verbreitet ist. Es wurde von einer hohen Infektiösität berichtet. Eine erfolgreiche und dauerhafte Therapie ist bisher nicht bekannt.

Die Symptome sind: Langer Hals, gerötete Augen, verinnerlichter Blick, gelegentlich Vereinsamung oder Abmagerung nach einer unfreiwilligen Hungerdiät (weil alles Geld für den Kauf von Bernstein-Einschlüssen draufgegangen ist), Entzugserscheinungen (bis der Dealer mit frischer Ware eingetroffen ist), sporadisch unmotiviertes zufriedenes Lächeln, Telefonitis.

Eine Linderung der Symptome bringt möglicherweise der Erwerb weiterer schöner Inkluden aus der Sammlung des Verfassers dieser Bände. Eine Heilung des Erkrankten ist theoretisch denkbar durch die Schenkung seiner gesamten Sammlung an ein geeignetes Museum; ernst gemeinte Anfragen nimmt Dr. W. W. sicher sehr gern entgegen!

J. W.

CONCLUSIONS FROM INCLUSIONS AND SYNINCLUSIONS IN AMBER (RÜCKSCHLÜSSE AUS EINSCHLÜSSEN UND BEGLEITENDEN EINSCHLÜSSEN IM BERNSTEIN)

Every organic inclusion in amber tells a story of a vanished world. Even more interesting are investigations of events and behaviour documented by syninclusions, e.g. the mating behaviour, the spinning behaviour or the fight of a spider with an enemy; see the chapters on the mating behaviour, spiders webs, preservation, prey, enemies, etc. Moreover from the preservation, the position and the morphology of certain spiders conclusions can be drawn on patterns of the biology of spiders. In the spider-eating members of the family Mimetidae - see below (2) - conclusions from syninclusions and from the morphology overlap. From the existence of certain organisms we can conclude on climate conditions, see the chapter on climate and ecology. I want to focus here on the "frozen behaviour" of selected inclusions in Baltic amber.

(1) Conclusions from the preservation and from the position of spider inclusions in the fossil resin (Rückschlüsse aus Konservierung und Position der fossilen Spinnen-Einschlüsse)

In which way has a spider been entombed in the fossil resin, and was the spider still alive? The "natural" position of the legs (which are not bent under the body, e.g. photos 47, 100) in certain spiders and its position upon a layer of resin within the amber - e.g. males of the families Leptonetidae (photo 47), Dictynidae (photo 288) and Thomisidae (photo 568) - indicate that these spiders were entombed alive. The Thomisidae has furthermore drawn a dragline from an attachment disc on a layer in the resin, and another line runs away from the disc. The presence of these structures indicates that this spider has landed - probably as an aeronaut - on the partly hardened but still sticky surface of a resin layer.

Furthermore the presence of poison (photo 389), autotomized legs and of remains of blood on the stumps of legs (see e.g. the photos 91, 95, 254-255, 396, 638) allow the conclusion that these spiders were captured alive in the resin; see the description of the holotype of *Pimoida multispula* n. sp. (Pimoidae). The position of the legs, which are more or less bent under their body (e.g. photos 32, 36, 71-72, 82) indicate, that these - and all the partly decomposed spiders (photos 473-494) - were entombed when just dying or after their death.

A special "resting position" (in German: "Ruhehaltung") (photo 391 of an extant spider) is rarely preserved in fossil spiders besides members of the Segestriidae, e.g. in a member of the family Trochanteriidae (*Sosybius* sp. indet., photo 390). Apparently the dying spider did not change its special leg position.

(2) Conclusions from syninclusions (Rückschlüsse aus den Beifängen)

Conclusions on the ecology (Rückschlüsse auf die Ökologie)

Various pollen grains, stellate hairs, flowers, needles and twigs of Gymnospermae in numerous amber pieces are preserved together with fossil spiders and indicate a diverse and mixed Baltic amber forest. Syninclusions may give hints at the ecology of certain fossil spiders, at their habitats and biotopes. I will give two examples: A member of the order Trichoptera is preserved with the holotype of *Pimoida multicusculi* n. sp. (Pimoidae) and indicates a habitat of the spider near an open/running water; see the chapter on the climate and the biotopes of fossil spiders. A large spiders' egg sac of is connected with a twig of the genus *Thuites* (Cupressaceae) (F122/BB/CJW); thus this female - of the family Araneidae? - was a dweller of *Thuites*; see the chapter on egg sacs. - See furthermore the photos 427-428 and 547.

Most of the next conclusions concern the behaviour besides conclusions on the ecology (In German: Neben der Ökologie betreffen die meisten der folgenden Rückschlüsse das Verhalten):

Spiders of the family Mimetidae (in German: Familie Spinnenfresser) are specialised spider-eaters (see the paper on this family in these volumes and WUNDERLICH (1986: 44, figs. 332-333)). They possess peculiar long bristles on articles of the two pairs of anterior legs which help to fix their dangerous prey, see the photos 242 and 246). In a striking piece of Baltic amber (F1206/BB/CJW) a juvenile male Mimetidae indet. is situated on a thread within the capture web of a female *Custodella* (Linyphiidae). Both spiders (and a second female *Custodella*) are preserved in the same layer of the amber (photo 615). Extant Mimetidae are known to attack Linyphiidae in their capture web, and these syninclusions indicate the same behaviour already in the Early Tertiary. Also extant spiders of the family Archaeidae mainly feed on spiders, and this behaviour is documented in Baltic amber for the first time, photo 626.

Conspicuous is the co-occurrence of several spiders of the Hahniinae (Dictynidae s. l.) and Comarominae (Anapidae) (photo 143); see the papers on these families.

If a spider co-occurs with an ant in the same piece of amber there may be connections between both groups of arthropods; see the paper on the relationships of spiders and ants. Certain extant and fossil spiders as members of the families Zodariidae (mainly), some Salticidae, Theridiidae, Trochanteriidae (*Sosybius*) and others (a) feed on ants or (b) mimic ants (are ant-shaped). Certain members of the Zodariidae combine both.

(a) Ants are the main prey of spiders which is preserved in Baltic amber, see the photos 629-647. In one case a fossil Zodariid spider collected three ants and tried to keep them together before it was entombed in the fossil resin (photo 633).

(b) Ant mimicking spiders in Baltic amber are mainly known from members of the families Corinnidae and Zodariidae; the myrmecomorphy is most distinct in the families Archaeidae (photos 75-76) and Corinnidae (photos 376-378). Fig. 1 (based on F1/BB/CJW) is the reconstruction of a fossil member of *Eomazax* (Corinnidae), whose ant model is still unknown. (An ant - *Lasius* sp. indet. - near the male of a Zodariid spider (indet.) may be the model of this spider species, photo 606).

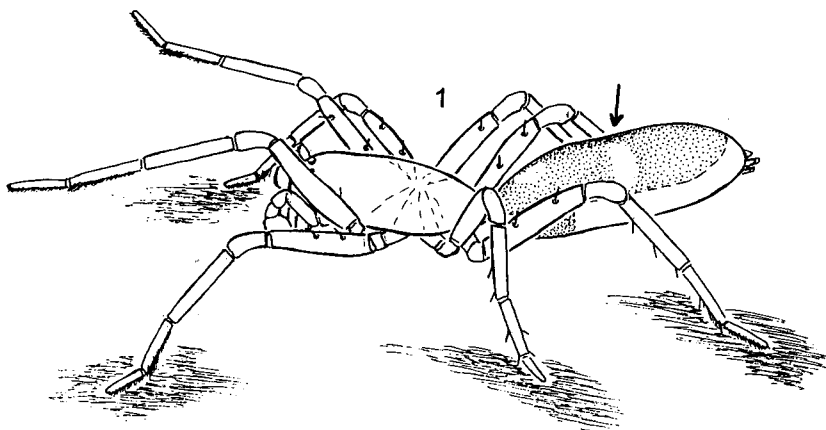


Fig. 1) Reconstruction of a male ant-shaped spider of the family Corinnidae (*Eomazax* sp. indet.) in Baltic amber, lateral aspect, body length 5.8mm. Note the weak saddle-shaped opisthosomal constriction at the white band (arrow) and the raised slender anterior legs. (Rekonstruktion einer ameisen-ähnlichen männlichen Ameisen-Sackspinne (Gattung *Eomazax*) im Baltischen Bernstein, Seitenansicht, Körperlänge 5.8mm. Man beachte die undeutliche sattelförmige Einschnürung am weißen Querverband des Hinterkörpers (Pfeil) und die schlanken, erhobenen Vorderbeine).

Some mites are enemies of spiders; photo 614 shows a mite attacking a spider of the family Theridiidae in Baltic amber. Both arthropods are heavily armoured.

A probably parasitoidic wasp (Diapriidae indet.) is preserved with the holotype of the Jumping Spider (Salticidae) *Distanilinus paranutus* n. gen. n. sp. in Baltic amber (photo 604). The actual relationships between both arthropods (a parasitoidic behaviour of the wasp?) are unknown. - See also the parasitoidic Braconid wasp with a Linyphiid spider, photo 181.

Spiders threads and webs are important syninclusions of the fossil spiders. The special cribellate silk can best be identified if its producer - a cribellate spider - is preserved in the same piece of amber (e.g. photos 530-533). - In one case (F133/BB/CJW, photos 563-564) a female spider, a part of its capture web as well as remains of its egg sac and prey are preserved in the same piece of amber. If all these objects had been preserved in different pieces of amber we would never know their relationships. - A questionable sperm web is preserved together with a male Linyphiidae of the genus *Custodela*, photos 249-250. A female spider of the family Synotaxidae in Baltic amber guards its egg sac, photo 522. Remains of sperm: e.g. photos 166-167.

Fossil spiders which keep their prey in their fangs or between their legs give evidence concerning the kind of their peculiar prey, e.g. spiders (photo 626), ants (photos 438, 630-631, 633, 635, 639-642), cicades (photo 653) and Diptera (photo 667-670, 678). A spider is rarely preserved together with its prey in its capture web; e.g. a member of the family Linyphiidae with a midge, photo 674.

(3) Behaviour and determination (Verhalten und Bestimmung)

Usually both sexes of spider species are preserved in different pieces of amber, and their conspecificity is unsure - we cannot assign males to females of the same species. In rare cases we fortunately find a pair of spiders in the same piece of amber (photo 33, *Orchestina* sp.) or even a mating couple; these spiders must be conspecific. A fossil mating couple furthermore gives evidence of the copulatory position in this species as well as of a special mating behaviour, e.g. in a couple of the genus *Orchestina* SIMON (Oonopidae), see WUNDERLICH (1981), (1986: Fig. 294) and the paper on the family Oonopidae (superfamily Dysderoidea) in these volumes. - A couple of *Custodela* sp. indet. (Linyphiidae) (CJW) is preserved close together in the same piece of amber, probably the case of a so-called "post copula".

(4) Conclusions from the morphology of fossil spiders (Rückschlüsse aus dem Körperbau fossiler Spinnen)

Strong posterior legs in combination with a well developed visual sense (large anterior or median eyes, photo 589) in fossil Jumping Spiders (Salticidae) indicate a jumping behaviour already in spiders of the Baltic amber forest. Jumping is used in extant spiders in connection with the prey capture and the flight.

The posterior leg pair is usually used as "jumping legs" in spiders; it may be combined with the third leg pair. Most often the posterior femora are thickened, rarely the third femora (see below: *Palaeospinisoma*). Never is the anterior or the second leg pair the jumping leg pair; in these cases the spider would move backwards while jumping! (Strong anterior femora in the male sex only (photos 149-151) are used in a different function, the mating behaviour, see below).- Strongly thickened posterior femora in fossil members of the genus *Orchestina* SIMON (Oonopidae) (e.g. photo 29) allow the conclusion that the jumping behaviour was already present in this genus in the Early Tertiary. In most members of the genus *Fossilianapis* n. gen (Anapidae: Anapidae) in Baltic amber the posterior femora are also more or less thickened (photo 159) and these legs may have been jumping legs. - According to the strong posterior femora and the distinctly thickened third femora (photo 364) in *Palaeospinisoma femoralis* n. gen. n. sp. (Liocranidae) the members of this species have been excellent jumpers; see the paper on this family. Solely thickened third femora are quite unusual in spiders.

Peculiar structures of fossil male spiders are preserved in connection with the courtship behaviour, see the chapter on this item in this volume; e.g. (a) strongly thickened anterior femora (photos 149-152), metatarsal or tibial "clasping spines" (e.g. photos 14, 154). With the help of such structures the males fix(ed) the females during the copula. (b) Ventral spines of the male opisthosoma (photos 362-363, 365) are used to produce vibrations during the mating behaviour of certain extant and fossil Liocranidae. Stridulating files - they are present in both sexes and are also used to produce vibrations during the mating behaviour - are preserved in fossil taxa of several families, e.g. in most fossil and extant members of the family Linyphiidae (photo 261). Such files are also present in the Archaeidae, certain fossil Araneidae (photo 130), in all Spatiatoridae and probably in the fossil Pimoidae; compare certain Dictynidae, too. Hence Early Tertiary spiders behaved as extant relatives in this respect.

THE CLIMATE OF THE AMBER FORESTS AND THE BIOTOPES OF THE FOSSIL SPIDERS (DAS KLIMA DER BERNSTEIN-WÄLDER UND DIE LEBENSÄRÄUME DER FOSSILEN SPINNEN)

See the chapters on palaeobiogeography and palaeofauna.

Introductory remarks: Mainly the syninclusions of the fossil spiders, the comparison with extant relatives and the fossil flora allow conclusions on the biotopes of the fossil spiders. In contrast to numerous insects most spiders prefer a special structure of the environment but no special plants; some also need a peculiar microclimate or microstructure as they exist in ants nests - see e.g. the genus *Mastigusa* MENGE (Dictynidae s. l.) -, or on bark, in holes of trees, in caves. ect.

Basically it seems a problem to regard higher - supraspecific - (fossil) animal or plant taxa as indicators of (palaeo)climates because of their intrafamilial and intrageneric variability concerning the climate (as well as the ecology). An example is the extant spider genus *Diplocephalus* BERTKAU 1883 (Linyphiidae): Species of this genus live at lower altitudes up to higher mountains in quite different climates. Another example from the Solifugae: By far most of the species are "associated with dry, desert climates. However, very few Wind scorpions do live in tropical forests today, scampering up and down tree trunks in search of a meal...", see POINAR & POINAR (1999: 78). Conclusions from extant relatives on extinct taxa - e.g. members of tropical taxa or "mountain animals" as Pimoidae (Araneae) - are basically not quite certain because of probable changes of their climatic requirements: Today's Elephantidae occur mainly in the tropics but the extinct Mammoth lived in cold regions. Nevertheless such taxa whose members occur today without exception e.g. in the tropics or in mountains are of special interest concerning conclusions. - To return to *Mastigusa*: Most extant specimens occur in ant nests - in which a peculiar microclimate exist -, and possess reduced eyes, but all specimens in Baltic amber have large eyes; so one may conclude that the fossil spiders of this genus were free-living in the Early Tertiary and the preference of their biotopes changed during the last fifty million years.

(1) The Dominican amber forest

The Dominican amber originated in a tropical forest of the Island of Hispaniola which was mainly hot and dry (as today); the spider fauna comprises much more tropical elements than the fossil fauna of the Baltic amber forest - e.g. Barychelidae, Microstigmatidae, Theraphosidae, Caponiidae, Ochyroceratidae, Selenopidae and Salticidae: Lyssomaninae, which are absent in Baltic amber -, see the papers of PENNEY, e.g. (2002) and the books of WUNDERLICH (1986: 36) (1988).

(2) The Early Tertiary European amber forests

I want to focus on the better-known fauna of the Baltic amber forest *sensu stricto*; the fauna of the Ukrainian amber forest has been studied only superficially; on the Bitterfeld amber fauna: See the chapter on palaeobiogeography.

(a) The climate and the landscape

During the existence of the Early Tertiary Baltic amber forest the Baltic region was about 10-15 degrees further south than today; see LOURENCO & WEITSCHAT (1996: 188) and WEITSCHAT & WICHARD (2002: 28). So the climate of the Baltic amber forest was mainly subtropical, up to about 4 degrees warmer than today, similar to the South Mediterranean or Florida today. We find remains of plants and animals in Baltic amber which have mainly or exclusively a tropical distribution, e.g. palmae and termites as well as members of the spider families Ctenizidae, Dipluridae, Tetrablammidae, Hersiliidae, Archaeidae, Deinopidae, Theridiosomatidae, Anapidae s. l., Araneidae: Nephilinae, Cyatholipidae, Synotaxidae, Trochanteriidae, Thomisidae: Stephanopinae and Salticidae: Cocalodinae. At the border of Eocene and Oligocene a global cooling - see WEITSCHAT & WICHARD (2002: 27-28, figs. 17-18 - caused the disappearance of the subtropical forests as well as most probably the extinction of numerous (most?) plants and animals including the listed higher spider taxa of the Baltic amber forest.

The insect fauna of the Baltic amber forest includes many groups that bred in fresh-water - Ephemeroptera, Plecoptera, Trichoptera, several families of Diptera -, so there were larger humid parts within the Baltic amber forest. According to ANDERSEN (2000: 283) "The presence of lotic-adapted groups of aquatic insects (Plecoptera, Trichoptera) suggests that the amber-forest was penetrated by flowing water, from quiet streams to fast flowing water, implying a mountain-landscape with the possibility of changing altitude-dependent climate zones, from temperate to subtropical-tropical", see also WICHARD & WEITSCHAT (1996), WEITSCHAT & WICHARD (1998); according to CZECHOTT (1961) also moderate zones existed. Certain spiders prefer humid biotopes, e.g. most Tetragnathidae and Theridiosomatidae, several Anapidae s. l. and Cyatholipidae.

Mixtures of syninclusions of tropical, temperate and even moderate climates may occur in crossings of climate zones in mountain regions. Specimens of certain spiders may have been transported - e.g. by the wind when ballooning - even for larger distances, and from a moderate mountain climate to a tropical climate. The - rare - presence of spiders of the family Pimoidae in Baltic amber may be an example of such cases: All species live in moderate to temperate mountain regions today as do members of the Nymphomyiidae (Diptera). According to GRISWOLD (2001: 6) "Cyatholipids are typically found in cool, moist tropical montane and temperate lowland forest... In the tropics they occur above 800m on mountains, while in the south temperate regions they occur down to sea level." Cyatholipid spiders are not too rare in Baltic amber.

(b) The biotopes and the habitats

See the papers on numerous spider families in these volumes and WUNDERLICH

(1986: 43-44). Three corrections to spider taxa which are mentioned in this book: *Amaurobius* in Baltic amber = *Eomatachia* (Zoropsidae s. l., *Deinopis* in Baltic amber ?= *Menneus* (Deinopidae), Sparassidae (= Heteropidae, Eusparassidae) of the genus *Sosybius* = questionable Trochanteriidae.

Concerning the reconstruction of the palaeoenvironment of the Baltic amber forest: Without doubt this forest was a diverse mixed forest; needles of *Pinus* have been found in amber pieces together with flowers and stellate hairs of oaks, other Fagaceae and various other deciduous trees; pollen grains of pines and oaks are occasionally fixed at the same threads of spider silk or together with spiders, e.g. with the holotype of *Gardiopsis infrigens* n. gen. n. sp. (Hersiliidae). Most of the Baltic amber was most probably produced by pines and their relatives. - On wet biotopes: See above. On dry biotopes: The - extremely rare - inclusions of animals which prefer dry and probably open (sunny) biotopes - e.g. Plectreuridae (Araneae) (photo 14), Solifugae (photos 688-689) and Opilioacarida (Acari) (photos 691-692) - point at some steppe-like parts within or near the Baltic amber forests as do - according to BACH-OFEN-ECHE (1949: 28, 189-190) - plant taxa as *Sciadopitys* (Taxodiaceae) and Santalaceae. These findings stand in contrast to the statement of LOURENCO & WEITSCHAT (1996: 189). Most probably certain plants built peculiar and more or less isolated associations, see ANDREE (1929: XIV), which contained a special fauna. The existence of such "mosaic biotopes" would explain the rareness of certain arthropods in the Baltic amber.

The great abundance and diversity of insects indicate that there was plenty of prey for the fossil spiders in numerous biotopes and habitats of the Baltic amber forest, e.g. on the ground, under stones and in the vegetation: On and under the bark of trees, on twigs and on leaves. The most frequent prey of spiders in Baltic amber are ants, and ant-hunting spiders as members of the families Segestriidae, Theridiidae, Zodariidae and Trochanteriidae (e.g. *Sosybius* PETRUNKEVITCH) are not rare in Baltic amber, see below. - Only few "ground spiders" as Gnaphosidae are to be expected in amber, and it is no surprise that members of the Gnaphosidae are actually quite rare in Baltic amber, although few extant Gnaphosidae are bark dwellers. Most extant Hahniinae are also "ground spiders", but members of related species are dwellers of higher strata including the bark of trees.

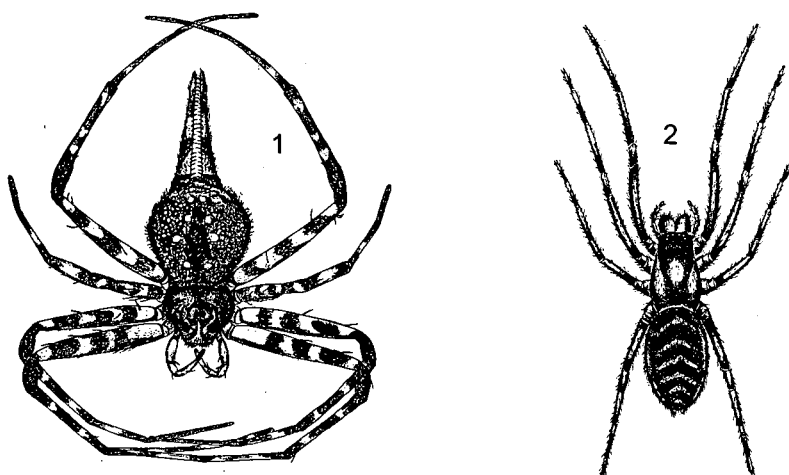
Obviously most of the preserved spiders lived on the resin-producing Conifera as pines, on their bark, twigs and leaves. Here they built their capture webs - as most members of the superfamily Araneoidea (Orb Weavers and their relatives) -, waited for prey as the Crab Spiders (Thomisidae) or were free hunters as members of the Jumping Spiders (Salticidae), *Orchestina* (Oonopidae) and *Sosybius* (Trochanteriidae). Occasionally drops of the fossil resin fell down and entombed a ground living spider. Other spiders were transported by the wind as ballooners to the resin from quite different biotopes (see above), and some were probably members of a non-forest fauna.

How can the peculiar biotope/habitat of a special fossil spider be recognized?

(a) Plant and animal syninclusions **may** give a hint at special biotopes and habitats of spiders, but such syninclusions may have been blown to the resin by the wind together with the - usually juvenile - spider, see the paper on ballooning spiders (threads and webs). - A larger egg sac - F122/BB/CJW (photo 501) - is fixed by threads to a small twig of *Thuites*. The unknown spider which built this egg sac - probably a member of the families Araneidae or Zygeliidae - surely lived on this Cupressaceae. - Ac-

according to the occurrence of members of the Trichoptera which are preserved in the same pieces of amber as the holotypes of *Opellianus kazimirasi* n. gen. n. sp. (Theridiosomatidae) and *Pimoida multicusculi* n. sp. (Pimoidae), water should have been near the habitats of these spiders.

(b) The ecology and the behaviour of extant relatives of spiders may indicate a special habitat: The members of the numerous species of the genus *Dipoena* THORELL (Theridiidae) - see WUNDERLICH (1986: 180-183) - build their capture webs in higher strata of the vegetation (as do most members of other Araneoidea), and so we can suppose that the frequent specimens of this genus in Baltic amber were dwellers of higher strata, too. - Extant members of the family Hersiliidae fix their prey on the surface of the bark of trees by encircling them with the help of numerous threads from their long posterior spinnerets (fig. 1, photos 86-93). A similar behaviour is present in specimens of the related Oecobiidae, see the genus *Mizalia* KOCH & BERENDT of the Baltic amber forest (photos 94-97). - Extant specimens of the genus *Orchestina* SIMON (Oonopidae) (photos 28-35) live on the ground, on and beneath the bark of trees as well as on twigs and leaves in higher strata of the vegetation (personal observations). The high frequency of the tiny members of this genus in Baltic amber indicate that they were hunting - e.g. for Collembola - on bark, twigs and leaves already in the Early Tertiary. - Extant species of the family Segestriidae build their tubes under the bark of trees (fig. 2); fossil *Segestria* are not rare in Baltic amber and even their tubes are preserved (photos 14-22, 527). Tubes were probably also built by specimens of the genus *Eomatachia* PETRUNKEVITCH (Zoropsidae s. l., photos 67-74) (similar to extant Amaurobiidae) which were not rare in the Baltic amber forest. - Numerous extant large-eyed members of Jumping Spiders (Salticidae) hunt on the bark of trees; their large eyes, their strong posterior legs as well as



Figs. 1-2: Two extant bark-dwellers, 1) a member of the family Hersiliidae hanging in its typical head-down position on the surface of bark; 2) a member of the family Segestriidae; these spiders are waiting for prey in a tube under the bark near the entrance. Related spiders of both families are preserved in Baltic amber. The body length is few mm. - Taken from DIPPENAR-SCHOEMAN & JOCQUE (1998).

their frequency and diversity in Baltic amber indicate such a habitat (and behaviour) already in the Early Tertiary.

(c) The shape of the body may give a hint at their habitat, too: A strongly flattened body, a laterigrade leg position (as well as frequently a short anterior and a long third pair of legs) point to the presence of a bark-dweller, e.g. hunting spiders of the families Pisauridae (photos 325-334), Philodromidae and Trechaleidae (questionable determinations) (photos 335-337), Trochanteriidae (photos 389-394) (e.g. *Sosybius*) and probably members of the family Scytodidae (photo 40); these spiders possess long anterior and short third legs.

VOM WINDE VERWEHT (siehe Foto 568)

Vom späten Sommerwind getragen,
schwebt ein Luftgeist am Altweiberfaden.
Mit diesem Feingespinst als Luftgefährt
treibt er ins Harzbett, wie Figura lehrt.
Der Spinne Lebensfaden ward' zerrissen
alsbald im harzerfüllten Ruhekissen.
Ihr Wegfaden indes, der blieb erhalten,
mit dem Jungspinnen Reiselust entfalten.

H. J. Müllenmeister

FOSSIL SPIDERS' CAPTURE WEBS, DRAGLINES AND BALLOONING LINES (FOSSILE FANGNETZE, WEGFÄDEN UND FLUGFÄDEN)

See also the chapters on exuviae, egg sacs, retreats, the prey of spiders and on the families of web-building spiders as Pholcidae and Araneoidea in this volume.

Photos 526-573, 577-578.

Introduction

Fossil spiders' threads in amber can be confused with hyphae of Fungi; both may be mixed on the same object (e.g. F1320/CJW), hyphae may grow on a spider's body and probably even on a spiders' thread (!) (e.g. F1317/CJW), see below. Hyphae are usually finer than spider's threads, they most often possess more branches and much more blind ends as well as - occasionally - "capitulae", but no sticky droplets. Also several larvae of Lepidoptera and Diptera build threads, which may be preserved in amber, e.g. certain extant tropical larvae of the Diptera: Mycetophilidae build

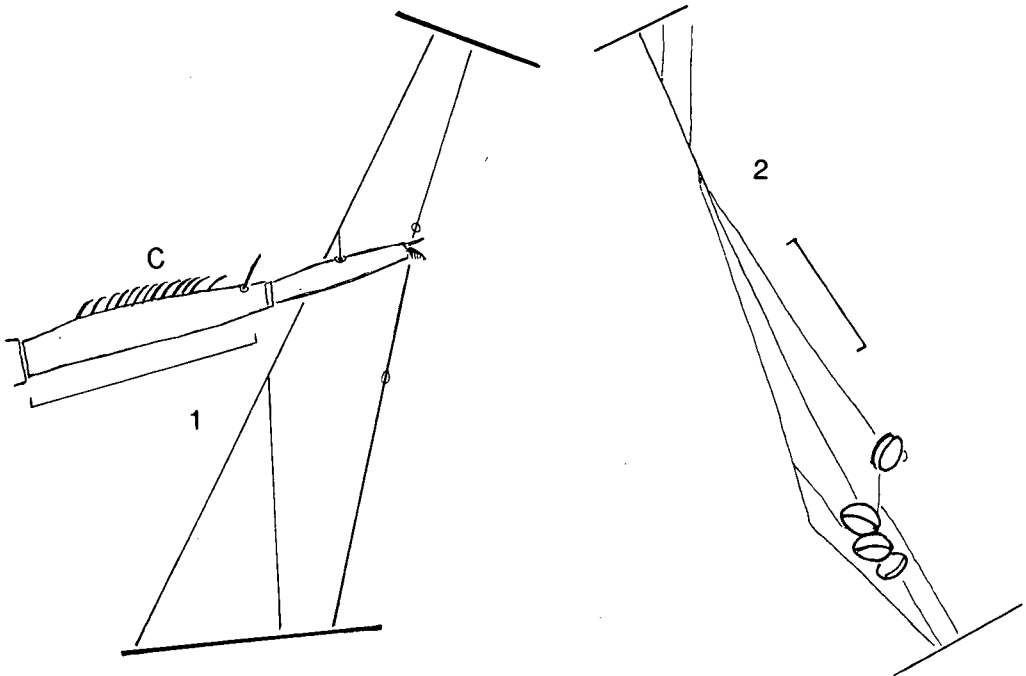


Fig. 1) Few ecribellate threads at the left tarsus IV of a cribellate fossil spider, Dictynidae indet., ♀ (F810/BB/CJW). Note the metatarsal calamistrum (C). M = 0.5mm;

fig. 2) Four pollen grains at threads near the anterior spinnerets of a fossil spider, Zodariidae indet., ♂ (F184/BB/CJW). M = 0.1. - Vier Pollenkörner an Spinnfäden.

sticky capture threads. Furthermore Embia, Pseudoscorpions and certain mites are able to produce fine threads. - Fossil spiders' threads may be more or less modified in the old amber: They may, e.g., be oxidated, droplets may be swollen or shrunken; nothing is known about the modifications of cribellate threads in amber, which may be very well preserved, see below. Also the position of the threads of a fossil web is usually quite different from their original position, and orb webs are too large to be completely kept in a piece of amber.

Spiders' threads capture all kinds of "aerial plankton" as stellate hairs, pollen grains (e.g. of pines, F886, and of oaks, fig. 2, F184, F1195), dust, tiny particles of detritus, insects' excrements, hairs, tiny wingless arthropods (e.g. mites) as well as ballooning spiders with their threads, see below. So the webs of fossil spiders are a kind of "environmental indicator".

Spiders' threads have numerous functions; see FOELIX (1996), the book edited by SHEAR (1986) and SAUER & WUNDERLICH (1996: 186-193): According to various authors the oldest function is probably the ability of females to build covers of egg sacs, but in my opinion the stabilization of the tubes and retreats may be the oldest function of the threads. Many spiders hide in tubes or masked retreats, spiders of numerous taxa build capture webs; e.g. the Cribellates and Pholcidae, almost all the members of the Orb weavers and their kin (superfamily Araneoidea) and Agelenidae and their kin. All spiders except the Mesothelae use moulting threads (which may be preserved on the exuviae), draw draglines (e.g. F1173/CJW) including attachment points along their path, the wingless spiders produce ballooning (aeronautic) threads, and males of almost all spiders use a special sperm web before mating, because a penis is absent in spiders, see below. Almost all kinds of such threads are found with the fossil spiders in amber, only fossil ballooning threads - which may be confused with draglines - have not been recognized with full certainty by me.

To my knowledge the first notes on fossil spiders' capture webs were given by MENGE (1856: 9-10), incl. a part of an orb web and remains of sticky droplets. BACHOFEN-ECHT (1934) also reports on capture webs of fossil spiders, see below. The geologically oldest remains of a capture web incl. remains of sticky droplets was recently reported by ZSCHOKKE from the Lebanese Cretaceous amber which is 130 million years old; it was probably produced by a member of the Araneoidea family Theridiidae; see Nature, 424: 636-637 (2003).

I have seen thousands of pieces of amber which contain spiders' threads or webs, hundreds are kept in my private collection, about 40 have been studied by me more closely, numerous selected pieces are waiting for closer studies, e.g. more than 60 pieces in Baltic amber, 4 from the Bitterfeld deposit and 12 in Dominican amber.

Slightly shortened translation of the introduction into German:

Einleitung

Fossile Spinnfäden im Bernstein können mit Pilz'fäden (Hyphen) verwechselt werden; beide können vermischt auf demselben Objekt - z. B. auf dem Körper einer Spinne - wachsen oder möglicherweise sogar auf Spinnfäden, siehe unten. Pilzfäden

sind gewöhnlich dünner als Spinnfäden, meist besitzen sie eine größere Anzahl von Verzweigungen und wesentlich mehr blinde Enden wie auch - gelegentlich - "Köpfchen, aber keine Klebfäden. Verschiedene Larven von Schmetterlingen und Zweiflüglern erzeugen ebenfalls Fäden, die im Bernstein erhalten sein können, z. B. spinnen man-che heutige Pilmücken Fangfäden. Weiterhin sind Embien, Pseudoskorpione und manche Milben in der Lage Fäden zu spinnen. - Fossile Spinnfäden im alten Bernstein können mehr oder weniger verändert sein: Sie können z. B. oxidiert sein, die ursprünglich klebrigen Fäden können geschwollen oder geschrumpft sein. Über eventuelle Veränderungen cribellater Fäden im Bernstein ist nichts bekannt, siehe unten. Auch ist die Position fossiler Spinngewebe verglichen mit ihrer ursprünglichen Position sehr verschieden, und Radnetze sind zu groß, um vollständig im Bernstein erhalten zu sein.

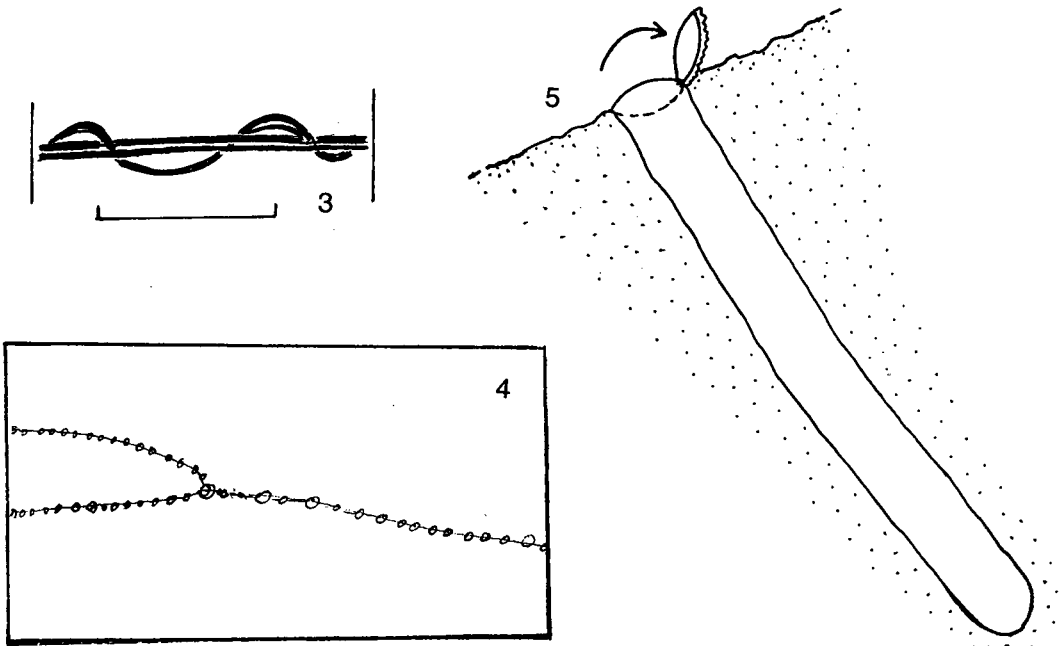


Fig. 3) A small sector of a thread of an unknown spider species: A double screw-shaped thread is twisted around and between a straight double ground thread (F1322/BB/ CJW). One thread of each pair appears stronger, the double nature of the twisted thread is only partly visible. $M = 0.1$;

fig.4)Part of a branched ecribellate thread of an unknown spider species which is bearing numerous tiny droplets (F807/BB/CJW), probably originating from a member of the family Cyatholipidae. In the same piece of amber a male of the cribellate *Eodictyna communis* n. gen. n. sp. is preserved. The diameter of a droplet is ca. 0.003mm;

fig. 5) Trapdoor (its lid is opened here, arrow) and underground tube of an extant Trapdoor spider (Ctenizidae). The tube may have a diameter of more than 1cm, is usually built on an oblique surface and lined with silk. The lid may be held shut by the spider, the top of the lid may be camouflaged with debris. Related Trapdoor spiders are known from Baltic amber, but a fossil tube is unknown. - Falltür und Wohnröhre einer heutigen Falltürspinne. Der Deckel wurde geöffnet (Pfeil).

In Spinnfäden verfangen sich alle Arten von "Luftplankton", z. B. verschiedenste Haare wie Sternhaare, Pollenkörner (z. B. von Kiefern und Eichen), Staub, winzige Partikel zerfallender organischer Reste (Detritus), Exkreme von Insekten, winzige flügellose Gliederfüßer (z. B. Milben) wie auch am Fadenfloß segelnde Spinnen, siehe unten.

Spinnfäden haben vielfältige Aufgaben. Die älteste ist möglicherweise die Fähigkeit der Weibchen, die Eikokons mit einer schützenden Hülle zu versehen; viele Spinnen verstecken sich in Röhren oder getarnten "Verstecken", Spinnen zahlreicher Gruppen bauen Fangnetze, z. B. die "Cribellaten" (Besitzer eines Spinnsiebs und Kräuselkamms), Zitterspinnen, fast alle Radnetzspinnen und Verwandte sowie die Trichterspinnen und ihre Verwandten. Alle Spinnen - mit Ausnahme der Gegliederten Spinnen (Mesothelae) benutzen "Häutungsfäden" - sie können bei Häutungsresten (Exuvien) erhalten sein -, ziehen Wegfäden, die "Anheftungspunkte" entlang ihrer Wegstrecke besitzen, sie erzeugen "Flugfäden", und die Spinnen-Männchen fast aller Arten bauen ein besonderes "Spermanetz" bevor sie sich paaren, weil Spinnen keinen Penis besitzen, siehe unten. Fast alle derartigen Arten von Fäden sind bei den fossilen Spinnen im Bernstein erhalten, lediglich fossile Flugfäden - sie können mit Wegfäden verwechselt werden - habe ich nicht mit letzter Sicherheit erkannt.

Die ersten Angaben über Fangnetze fossiler Spinnen stammen meines Wissens von MENGE (1856: 9-10), einschließlich des Teils eines Radnetzes und der Überreste klebriger Tröpfchen. Auch BACHOFEN-ECHT berichtet von Fangnetzen fossiler Spinnen, siehe unten.

Über die geologisch ältesten Reste eines Fangnetzes - in 130 Millionen Jahre altem Libanesischem Bernstein aus der Kreidezeit - ist kürzlich von ZSCHOKKE berichtet worden; es ist mit klebrigen Tröpfchen besetzt und ist möglicherweise von einer Kugelspinne gebaut worden.

Ich habe Tausende von Bernstein-Stücken in Bernstein gesehen, die Spinnfäden oder Netze enthalten, Hunderte sind in meiner Sammlung aufbewahrt; etwa 40 habe ich näher untersucht, zahlreiche harren eingehender Studien, z.B. mehr als 60 ausgesuchte Stücke im Baltischen Bernstein, 4 vom Fundort Bitterfeld und 12 vom Dominikanischen Bernstein: F1351/CJW.

(1) Webs, capture webs, tubes and single web threads (Netze, Fangnetze, Röhren und einzelne Netzfäden)

Members of numerous groups of spiders are not hunters or waiting for prey, but build capture webs. Numerous fossil webs, capture webs and single threads are preserved in amber. Fossil threads may be more or less modified/deformed, see the introduction.

Web spiders have evolved quite different types of capture webs and threads: *Segestria* (Segestriidae) constructs one of the most simply types: The spider hides in a tube, and from the opening of the tube simple "signal threads" are radiating; such signal threads have not been known from fossils up to now. The web of *Amaurobius* (Amaurobiidae) and probably *Eomatachia* (Zoropsidae) is similar, and also the Fun-

nelweb Mygalomorphs (Dipluridae) and some Funnel weavers (Agelenidae) hide in a tube. Agelenidae, Sheet-web weavers (Linyphiidae) and other spiders construct partly horizontal sheets, the Daddy long-legged spiders (Pholcidae) and the Cobfooted spiders (Theridiidae) build irregular webs, the Araneidae, Tetragnathidae, Zygeliidae and Uloboridae (e.g.) build orb webs.

Within each capture web there is a special catching area. In this area different types of capture threads exist which are basically different: (a) In the catching area of numerous ecribellate groups of spiders - as the Pholcidae and most members of the superfamily Araneoidea (e.g. Araneae, Linyphiidae and Theridiidae) - threads are present, which bear sticky droplets (fig. 4, photos), (b) in the catching area of the cribellate spiders (figs. 7-8, photos) - as the Uloboridae, most Dictynidae and Zoropsidae - extremely fine and dry cribellate threads are present, which are sticky through the adhesiveness of their "catching wool". In (c) the remaining spiders - as the Agelenidae and certain ecribellate Dictynidae - a catching area with sticky threads (sticky droplets or cribellate lines) is absent.

Occasionally a spider and its web can be found in the same piece of amber, e.g. with *Acrometa* sp. indet. (Synotaxidae) (F1040/CJW) and *Epeirotypus* sp. indet. (Theridiosomatidae) (F405/BB/AR/THR/CJW), see also the papers on the families Anapidae, Linyphiidae and Theridiidae, and in some pieces a *Segestria* (Segestriidae) or its exuvia is preserved with its tube, e.g. F927/CJW.

Remains of its web may clump together and be eaten by a spider. Such a lump of threads is probably preserved in a large piece of amber, F569/CJW, near the remains of a large egg sac and threads with droplets, see the photo. These relatively thick and wiry threads may have been a part of the surface of the egg sac.

Remains e.g. of prey - which are used as a kind of camouflage - are deposited in the capture webs of certain extant Araneidae. I have not recognized such "decorations" in a fossil capture web up to now.

(1a) Tubes-shaped webs (Röhrenförmige Gewebe)

Photos 526-527, 551.

In my opinion most fossil tubes in Baltic amber come from members of the family Segestriidae - see the photos -, few from members of the Agelenidae, Amaurobiidae and Dipluridae (fossil Amaurobiidae are only known from a single specimen). Several exuviae of the Segestriidae are preserved within their tube-shaped web; so the origin of the tube is sure. The tube of an extant Trapdoor spider (Ctenizidae) is shown in fig. 5. Trapdoor spiders are known from Baltic amber, but the fossil tube of these spiders is unknown.

F755/BB/AR/CJW: A large part of a deformed web, 1 1/2cm long, may have been the part of the tube of a larger spider. At the margin of the amber piece remains of tiny spiders' leg articles and wiry threads are present which may come from the surface of a spiders' egg sac.

F822/BB/AR/DIP/CJW: A large questionable exuvia of a member of the family Dipluridae is preserved with a large and incompletely preserved tube-shaped web. One of the spiders' tibiae is 4.3mm long.

F927/BB/AR/SEG/CJW: The exuvia of a *Segestria* sp. indet. (Segestriidae), length of the right leg I 8.5mm, is preserved in its tube-shaped web which has a diameter of 1cm. The tube consists of two layers of partly dense threads and is partly cut off on both sides. Numerous particles of detritus and insects' excrements as well as pollen grains, stellate hairs and probably a Nematoda are preserved in the web.

F929/BB/AR/SEG/CJW: The exuvia of a *Segestria* sp. indet. (Segestriidae), length of an anterior tibia 2.1mm, is preserved in its tube-shaped web which has a diameter of 1cm; the length of the preserved part of the tube is 1.5cm, a part of its surface is cut off. Several particles of detritus and stellate hairs are present within or on the inner surface of the tube. The presence of stellate hairs indicates that this is a part which was not far away from the former entrance of the tube.

F1013/BB/AR/CJW: A large and incomplete tube with partly two layers of silk on its sides its preserved in a piece of amber, which is 3.8cm long. Numerous particles of detritus, insects' excrement and stellate hairs are hanging in the web, see the photos.

F1164/BB/AR/CJW: A tube-shaped web with questionable excrement.

F1220/BB/AR/?ZOR/CJW (Bitterfeld deposit): With the exuvia of a ?*Eomatachia* sp. indet. the part of a probable tube is preserved.

F1303/BB/AR/CJW: The larger part of a tube-shaped and deformed web has a diameter of 1.15cm. Few droplets are present in the web. Outside near the web three ants are preserved, which are apparently not the prey of a spider.

Coll. H. FLEISSNER: A well preserved tube-shaped web in which an exuvia (Segestriidae?) is present.

Coll. S. ZSCHOKKE, no. Ba/8: A fragment of a tube-shaped web is preserved with two exuvia, probably of *Eomatachia* sp. (Zoropsidae).

(1b) Capture webs with sticky droplets (Fangnetze mit Klebtröpfchen)

Photos 537ff.

Spiders' threads which bear droplets, are not rare in Baltic and Dominican amber; I have seen numerous pieces. Occasionally we are lucky to find both - a thread or web and its producer - in the same piece of amber. I regard the parts of the following capture webs which have droplets as originating from a spider in the same piece of amber (see below): F455, F1040 and F1080. The tiny droplets of F1080, which all have almost the same size (as in fig. 4) are preserved with a member of the family Cyatholipidae. Probably all such threads with tiny droplets have been produced by members of this family, see F738 and F807. - But a web may not originate from the spider nearby: PETRUNKEVITCH (1950: 304-305, figs. 99, 104) regarded droplets in threads as originating from a member of the genus *Ephalmator* PETRUNKEVITCH (Ephalmatoridae), but in my opinion the tiny "droplets" which are shown in fig. 99 are artefacts and the threads which are shown in fig. 104 originate most probably from a member of the superfamily Araneoidea. See F807/ BB/AR/CJW below.

Capture threads with droplets in Baltic amber originate mainly from the following Araneoid families: Anapidae s. l., Araneidae, Cyatholipidae, Linyphiidae, Nesticidae (see fig. 264 in the book of WUNDERLICH (1986), Synotaxidae, Tetragnathidae, Theridiidae, Theridiosomatidae and Zygellidae. The largest droplets - they may be swollen after the embedding - may originate from members of the Araneidae, Tetragnathidae and Zygellidae which build orb webs. BACHOFEN-ECHT (1934, fig. 7) regarded some threads in Baltic amber as a part of an orb web, but it may well be the part of a web of a non-orbweb-building spider, e.g. of the Theridiidae. A well preserved part of an orb web in Dominican amber was published by POINAR & POINAR (1999: 73, figs. 70). The large droplets on a spiders' thread in Dominican amber - see WUNDERLICH (1986: Fig. 4) - may have been a part of an orb web, too; F1190/DB/AR/CJW, see below.

Only the first two pieces in the following list are Dominican amber (DB), the remaining pieces are Baltic amber (BB):

F918/DB/AR/CJW: A large thread with large droplets which include tiny bubbles is preserved in Dominican amber.

F1190/DB/AR/CJW: Large droplets on a spider's thread in Dominican amber may have been part of an orb web, probably of a *Nephila* sp. (Araneidae).

F136/BB/AR/CJW: A large part of a capture web - an orb web? - which has large droplets, is hanging on large parts of plants which are partly oxidated. Droplets of some liquid, probably water are also hanging in the web.

F137/BB/AR/CJW: A 17mm long spider's thread with large droplets which are up to 1.5mm long.

F140/BB/AR/CJW: The part of an irregular web, probably of a member of the family Theridiidae is bearing well preserved droplets of different size.

F141/BB/AR/CJW: A part of a probable orb web with small to large droplets and prey: A Diptera and 1/2 Formicidae.

F145/BB/AR/CJW: A 2cm long three-lined spider's thread which has no droplets is full of stellate hairs and has a connection to threads which are covered by larger droplets and are connected with a plant's scale leaf. Close to the three-lined thread a winged member of the Aphidina is preserved.

F183/BB/AR/CJW: A large part of an irregular web, partly with droplets which most often have a diameter of 0.05-0.07mm, the most tiny droplets have a diameter of 0.01mm. Furthermore preserved are two questionable irregular droplets of excrement, length ca. 1.4mm, and some droplets of questionable water which have a diameter of up to 0.75mm. The web is in connection with remains of impressions of a plant's branch on the surface of the amber piece.

F405/BB/AR/THR/CJW: A male *Eoepeirotypus* sp. indet. (Theridiosomatidae), body length 1.2mm, is hanging in a part of his capture web which has tiny droplets. A potential prey, a mite which is 0.43mm long, is hanging in the web closely in front of the spider.

F406/BB/AR/THR/CJW: A male *Eoepeirotypus* sp. indet. (Theridiosomatidae) and a part of a capture web similar to F405.

F569/BB/AR/CJW: In a piece of amber which has a size of 6.5 x 4.5 x 3cm remains of a large egg sac, wiry spiral threads, e.g. a lump of thick, wiry and spiral threads are preserved (photos), as well as spider's threads which bear small to large droplets. The lump has a size of 2mm, some swollen droplets are up to 1.5mm long, the globular egg sac has a diameter of 2cm. These structures were probably produced by a large spider of the familie Araneidae, Tetragnathidae or Zyiellidae.

F577/BB/AR/CJW: A 1.65cm long spiders' thread with tiny to large droplets (0.8mm long) is preserved at the margin of a piece of amber. Several droplets are partly cut off; they are filled with amber and a thread, which bears tiny droplets, is running through the droplets. Few Diptera are preserved in different layers of the amber piece.

F738/BB/AR/CJW: The larger part of a questionable capture web consists mainly of fine irregular and branched threads which are bearing tiny droplets as in fig. 4. There is also a strong and straight thread which is 4cm long and in contact with the fine threads. In the same layer an attachment disc is preserved, which has a diameter of 0.5mm and from which some probable draglines (or ballooning threads?) are spreading. In another layer of the amber two beetles are preserved and a spider, probably of the family Zyiellidae.

F753/BB/AR/CJW: A part of a larger capture web with small droplets may have been produced by a member of the family Theridiidae or Linyphiidae. Most threads are preserved in the same level; several droplet-bearing threads are preserved in a parallel position.

F807/BB/AR/CJW: Threads with tiny droplets (fig. 4) which are preserved in the same piece of amber as a male of the cribellate *Eodictyna communis* n. sp. (Dictynidae) in the same layer of the amber. The diameter of the tiny droplets, which may originate from a member of the family Cyatholipidae, is about 0.003mm.

F1040/BB/AR/CJW: A partly oxidated male *Acrometa* sp. indet. (Synotaxidae), body length ca. 3.2mm, is preserved with a tiny insect hanging in a part of his irregular capture web which is bearing tiny and few larger droplets being up to 0.25mm long.

F1080/BB/AR/CJW: A thread which is partly covered with tiny droplets as in fig. 4 is situated just above the left side of the opisthosoma of the holotype of *Cyathosuccinus elongatus* n. sp. (Cyatholipidae). These tiny droplets are probably typical of the fossil members of the family Cyatholipidae in Baltic amber; see also F738 and F807.

F1194/BB/AR/CJW: A 3 1/2cm long thread is covered with tiny to large - 3mm long - swollen droplets, in which the ground thread is observable. The thread may have been a part of an orb web.

F1321/BB/AR/CJW: Few spiders' threads which are covered with droplets are preserved with a fly in a 2 1/2cm long piece of amber.

CJW: With the male (paratype c) of *Balticoroma serafinorum* n.gen.n.sp. (Anapidae: Comarominae) threads are preserved which bear droplets. The origin of this capture threads is doubtful, see the paper on the family Anapidae in these volumes.

(1c) Cribellate threads and capture webs (Cribellate Fäden und Fangnetze)

Photos 528ff.

The fine and dry "wool" of cribellate spiders' silk is let out by a "spinning sieve", the cribellum, see the papers on the families Dictynidae, Deinopidae, Eresidae, Filistatidae, Oecobiidae, Uloboridae and Zoropsidae in these volumes, which produce such threads. These spiders possess an additional comb-shaped structure on the metatarsus IV (retrodorsally), the calamistrum (fig. 1), which helps to distribute these threads. (Cribellum and calamistrum may be absent in both sexes or reduced in the male sex especially of certain Dictynidae and Oecobiidae).

The first fossil cribellate threads were published by PETRUNKEVITCH (1942: Fig. 404) from a member of the family Zoropsidae, *Eomatachia succini* PETRUNKEVITCH 1942, see fig. 7. In this figure no fine structures are drawn. Cribellate threads are very complicated structures - see fig. 6, EBERHARD & PEREIRA (1993), FOELIX (1996), KULLMANN (1975), OPELL (1989), OPELL et al. (1999) and PETERS (1983, 1984, 1987, 1987, 1991, 1992) -, and we do not know their modifications which are caused by the resin and by aging within a period of millions of years.

How can a cribellate thread be recognized? I have never observed a thread coming out directly from a cribellum of a fossil spider. I found several threads and part of webs in the same piece of amber as a cribellate spider, e.g. F807/CJW, F810/CJW (Dictynidae), F1221/CJW (Zoropsidae: *Eomatachia* sp. indet.) and F1260/CJW (Dictynidae). We cannot be sure that a spider spun a thread or a web in the particular piece of amber in which the spider is kept, but the probability is high that both belong together. Furthermore: Only within the catching area of a capture web (of a cribellate spider) cribellate threads are present. Within the piece F1260/BB/CJW ecribellate as well as cribellate threads are present together with a member of the family Dictynidae. Within the piece F886/BB/CJW a "mixed" web of a thread with droplets and probably a web part of *Eomatachia* sp. indet. (Zoropsidae) with an exuvia are present. Comp. F1317 (prey).

F574/BB/AR/CJW: A 2 1/2cm long, partly two-dimensional cribellate part of a capture web (or two webs?) with two thick questionable radii. Numerous particles of detritus indicate that this was the part of an old web.

F807/BB/AR/DIC/CJW: In the same piece of amber and in contact with the tip of the left tarsus III of a male of *Eodictyna communis* n.gen.n.sp. (Dictynidae) branched thin spider's thread are preserved, which is bearing numerous tiny droplets (fig. 4) which probably are ecribellate threads not originating not from the cribellate Dictynidae.

F810/BB/AR/DIC/CJW: A larger part of a spider's ecribellate web is partly in contact with the female of a Dictynidae indet. (fig. 1, photo). One of these threads is in contact with the tip of the right tarsus IV, the left tarsus III and with the base of the left tarsus IV. Only very few single tiny droplets are present; numerous tiny droplets on the threads are absent.

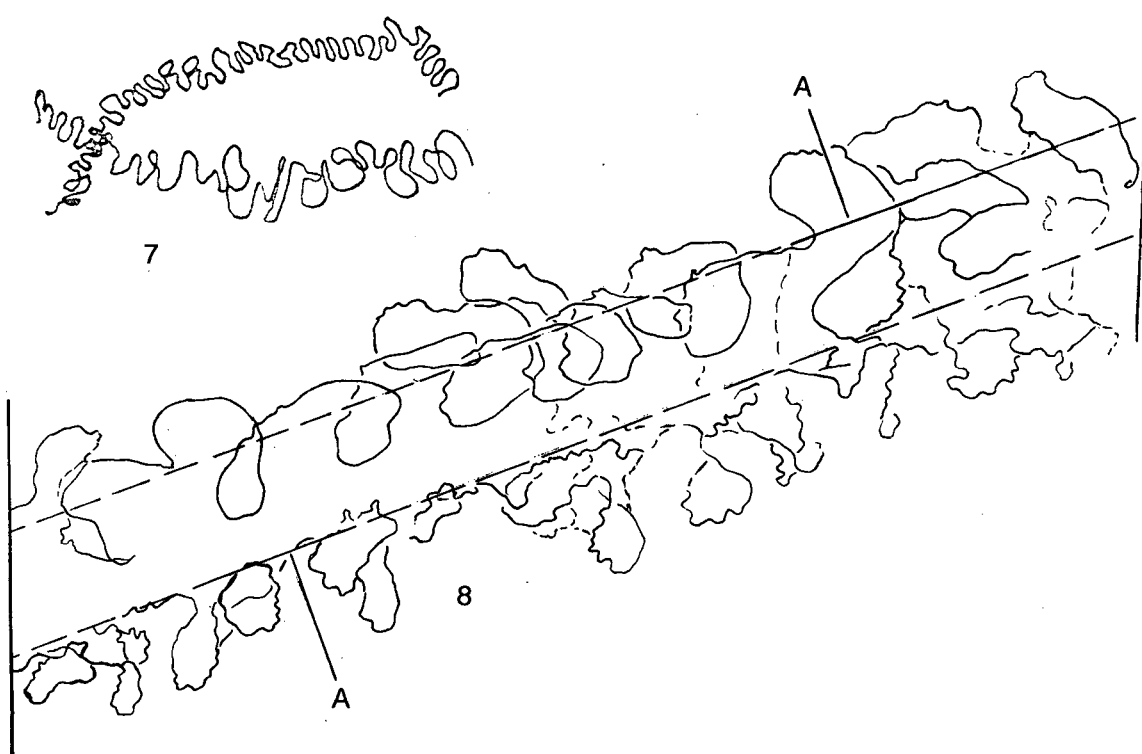
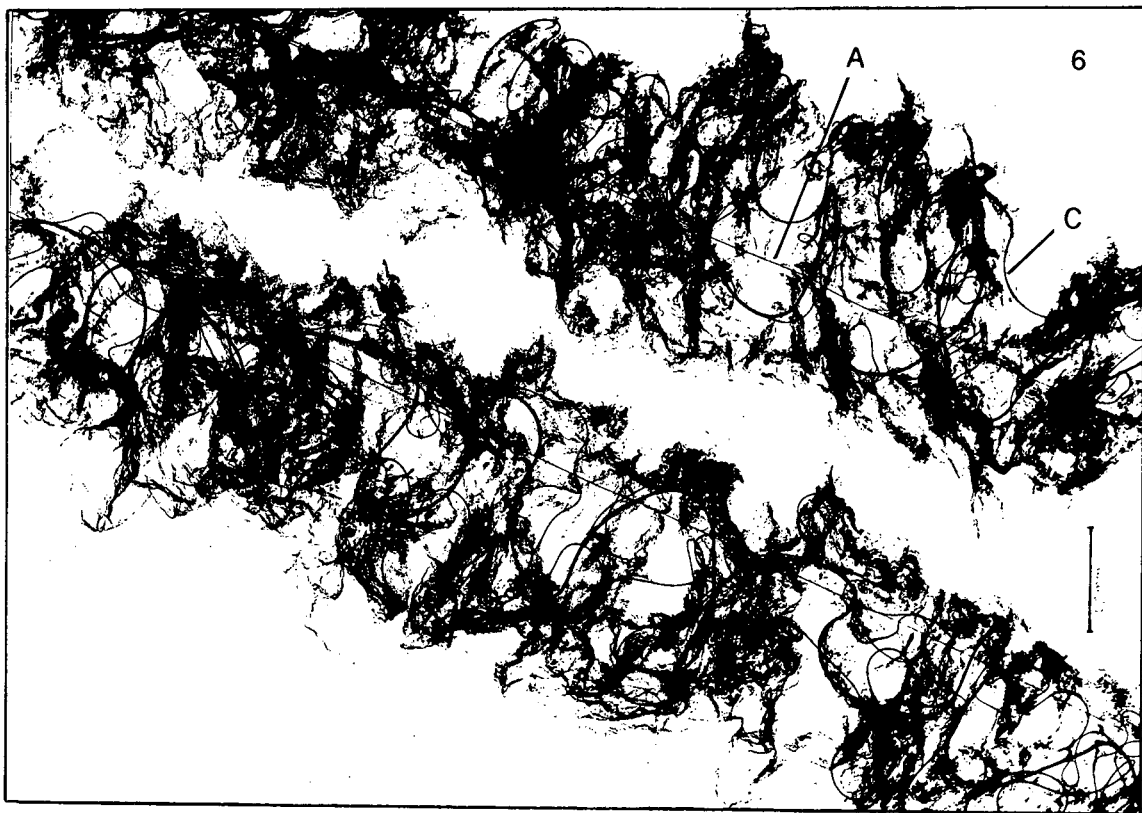


Fig. 6) Hackled band (calamistrated strands) of the extant cribellate Eresidae *Stegodyphus sarasinorum*. According to the divided cribellum the capture woof is applied in two separate bunches onto two very thin and straight axial fibers (warps) (A). These thread elements are accompanied by three pairs of curled threads (C) different in diameter and length. They function as reserve-warps one after the other when the whole thread is expanded. $M = 0.1$. Taken from KULLMANN (1975:Fig.25), transmission electron photograph. - "Gekräuselter"(cribellater) Fangfaden einer heutigen Röhrenspinne. Auf zwei sehr dünnen, gestreckten Achsenfäden ist dem zweigeteilten Spinnweb(Cribellum) zufolge die Fangwolle in zwei getrennten Strängen aufgelagert. Begleitet werden diese Fangelemente von drei Paar gekräuselten Randfäden, die unterschiedlich dick und lang sind. Sie treten nacheinander als Ersatzachsenfäden in Funktion, wenn der Gesamtfaden gedehnt wird. Nach KULLMANN (1975: Abb. 25);

fig. 7) Cribellate capture threads of the fossil spider *Eomatachia succini* (PETRUNKEVITCH 1942) (Zoropsidae) in Baltic amber. - Taken from PETRUNKEVITCH (1942: Fig. 404). - Cribellate Fangfäden der fossilen Spinne *Eomatachia fossilis* (Zoropsidae) im Baltischen Bernstein;

Fig. 8) A cribellate capture thread (hackled band, curled threads with calamistrated strands) of a fossil spider indet. in Baltic amber, probably *Eomatachia* sp. indet. Compare figs. 6 and 7. Collection of V. ARNOLD, no. VA1128. Drawn from a photo. Note the two thin and straight axial fibers (A) which are accompanied by one pair of curled threads. At the right side (below) probably the indistinct remains of the actual capture woof ("wool") are observable. The length of the threads is almost 0.4mm. - Cribellate Fangfäden (gekräuselte Fäden mit "calamistrierten Strängen"), die möglicherweise von einer Spinne der Gattung *Eomatachia* stammen, vgl. Abb. 6 und 7. Sig. V. ARNOLD Nr. AR1128. Beachte die beiden dünnen und geraden Achsenfäden (A), die von einem Paar gekräuselter Fäden begleitet werden. Rechts unten sind möglicherweise undeutliche Reste der eigentlichen Fangwolle undeutlich erkennbar.

F1221/BB/AR/CJW: In the same piece of amber with an exuvia of *Eomatachia* sp. indet. (Zoropsidae) similar threads are preserved as in F1260. Probably tiny reserve warps are observable, see EBERHARDT & PEREIRA (1993: Figs. 5-7).

F1260/BB/AR/CJW: Larger parts of a spiders' web are preserved with a female Dictynidae indet. Branched threads in contact with the base of the left calamistrum are bearing tiny droplets and therefore are not cribellate threads. Left of the spiders' body a branched cribellate thread is preserved, which is about 1cm long. Around a distinctly spaced pair of axial fibers some curled threads are observable with the help of a light-microscope (!).

F1323/BB/AR/CJW: A large part of a spiders' capture web including well preserved cribellate threads is preserved in a 6cm long piece of amber. At least in one part the calamistrated strand may be enfolded.

Coll. V. ARNOLD no. AR-1128 (Bitterfeld deposit): A part of a spider's (Araneae indet.) capture web including well preserved cribellate threads is preserved. See the

photo and fig. 8. Pollen grains are also present, some are hanging in the threads. Some calamistrated strands are indistinctly observable with the help of a light-microscope (!), but they are probably not recognizable in the photo.

(1d)The remaining types of capture webs: Irregular webs and sheet webs (ecribellate webs without droplets); certain single web threads (Übrige Fangnetz-Typen)

Photos 538ff.

Usually only fragments of fossil capture webs are preserved. So, e.g., the sheet of a Linyphiid or Theridiid spider - which is separated from its droplets-bearing catching-area - is hard to determine. The same is true for a tube-less part of a tubes' remains of a member of the Segestriidae, Agelenidae and probably of the Zoropsidae (*Eomatachia*), see above, e.g. F1220/BB/CJW.

The determination of single web threads is difficult. Numerous families use droplets in their catching area or they use cribellate threads, see above. Occasionally a single thread or a part of the wiry marginal threads of the special kind of an egg sac is preserved, see the paper on the egg sacs. Enigmatic threads of an unknown spider - a double screw-shaped thread - is twisted around and between a straight double ground thread, F1322/BB/ AR/CJW (fig. 3, photo). One thread of each pair appears stronger; the double nature of both threads is only partly visible. The longer thread is more than 2cm long, the shorter one is 6mm long. Droplets are absent in the unbranched threads. Quite similar is a thread which is 1.45mm long, F1197/BB/AR/CJW.

A part of an irregular web in Baltic amber is preserved with *Eocryphoea gracilipes* (KOCH & BERENDT 1854) sensu PETRUNKEVITCH (1950: 276-277, Fig. 179) of the Dictynidae: Cryphoecinae.

In the list below few further irregular webs are shortly described:

F134/BB/AR/CJW: The larger part of an irregular web; parts of the threads are oxidated.

F143/BB/AR/CJW: A 3 1/2cm long part of an irregular web without droplets is preserved with some screw-shaped threads. One of two ants is strongly spun in in threads at the margin of the web.

F754/BB/AR/CJW: A large irregular three-dimensional spider's web without droplets is preserved in contact with a female spider, body length ca. 3.3mm and its exuvia, probably a member of the family Theridiidae. The surface of the amber piece has numerous fissures.

F1013/BB/AR/CJW: A large irregular web and a juvenile spider are present in a 4 1/2cm long piece of amber. Very few droplets originate most probably not from a spider. Parts of the threads are strongly modified/enlarged by oxidation, see the photo.

(2) A questionable fossil spiders' sperm web (ein fragliches Spermanetz)

Photos 249-250

Introduction

Spiders lack a penis; therefore the males have to transfer their sperm from their genital opening on the venter of the opisthosoma (fig. 9) to their - secondary - copulatory

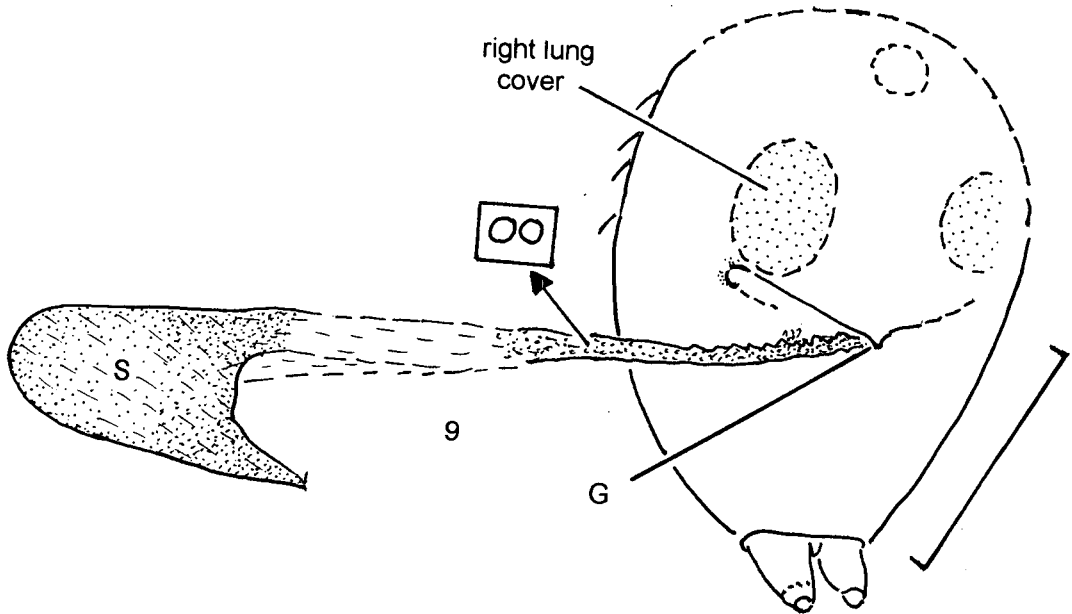


Fig. 9) *Custodela acutula* n. sp. (Linyphiidae), Bitterfeld deposit, coll. KUTSCHER AR-17, ♂, opisthosoma ventrally and slightly from the right side, with a droplet of secretion (S) originating from the genital opening (G), which may be sperm which apparently has been washed away by a resin flow, and which is probably held together by a sperm web. The diameter of one of the two enlarged particles in the rectangle (spermatozoa cells?) is about 0.008mm. M = 0.5mm. - Fraglicher Sperma-Tropfen (S), der aus der Geschlechts-Öffnung (G) einer Baldachinspinne ausgetreten ist - Fundort Bitterfeld, coll. M. KUTSCHER AR-17 -, der möglicherweise von einem Spermanetz zusammen gehalten wird, Ansicht von unten. Durchmesser eines der beiden im Rechteck vergrößert dargestellten Partikel (Spermien?): 0.008mm. M = 0.5.

organs, their two pedipalpi, which are situated in front of the legs and have a special terminal part, the bulbus, which is more or less spherical. (The female pedipalpus is

leg-shaped, but smaller). The bulbus has a special structure, the embolus, which is more or less spirally or needle-shaped and which transfers the sperm to the female genital opening. If the female genital opening is more or less sclerotized it is called epigyne. - Spiders are unable to transfer their sperm directly from their genital opening to the pedipalpi or to the female genital opening; therefore they use a "platform": They spin a small special "sperm web" - see FOELIX (1996: Fig. 158) -, rarely a single line, where they deposit a drop of sperm from their genital opening. Next they suck the sperm from the underside of the sperm web into their embolus and bulbus, and are then ready to mate.

Such a sperm web of a fossil spider has never been described before, and the existence of a true sperm web in this case (fig. 9) is uncertain because threads are not observable in the piece AR-17 from the collection of M. KUTSCHER from the Bitterfeld deposit. The preservation of remains of sperm cells is also unsure.

Translation of the introduction into German:

Spinnen besitzen keinen Penis. Daher müssen die Spinnen-Männchen ihr Sperma von der Geschlechts-Öffnung (Abb. 1) auf der Unterseite des Hinterkörpers zu ihren abgeleiteten Paarungs-Organen übertragen, ihren beiden Pedipalpen, die sich vor den Beinen befinden, und die am Ende einen besonderen Teil besitzen, den mehr oder weniger kugelförmigen Bulbus. (Der weibliche Pedipalpus ist beinförmig, aber kleiner und besitzt kein besonderes Endglied). Der Bulbus besitzt eine besondere Struktur, den mehr oder weniger spiraligen oder nadelförmigen Embolus, der das Sperma zur weiblichen Geschlechts-Öffnung überträgt. (Sofern die weibliche Geschlechts-Öffnung mehr oder weniger verhärtet (sklerotisiert) ist, wird sie Epigyne genannt). - Spinnen-Männchen sind unfähig, Sperma direkt von ihrer Geschlechts-Öffnung zum Pedipalpus oder zur weiblichen Geschlechts-Öffnung zu übertragen. Daher benutzen sie eine "Plattform": Sie spinnen ein kleines besonderes "Spermanetz" - siehe FOELIX (1996: Abb. 158) -, selten einen einzigen Faden, auf dem sie einen Sperma-Tropfen aus ihrer Geschlechts-Öffnung absetzen. Anschließend saugen sie nach dem Füllfederhalter-Prinzip das Sperma von der Unterseite des Spermanetzes her in den Embolus und den Bulbus auf. Nun sind die Spinnen-Männchen zur Paarung bereit.

Ein derartiges Spermanetz ist bisher von keiner fossilen Spinne beschrieben worden. Die tatsächliche Existenz eines fossilen Spermanetzes in Bernstein (Abb. 9) ist unsicher, weil Spinnfäden an dem Sekret-(Sperma?-)Tröpfchen des Bernsteinstückes aus Bitterfeld - Sammlung KUTSCHER, AR-17 -, nicht zu beobachten sind. Die Konservierung von Resten von Spermazellen ist ebenfalls unsicher.

(3) Moulting threads (Häutungsfäden)

Photo 452.

Moulting threads on spider's exuviae in amber are not rare, see the paper on the exuviae. Moulting threads are preserved e.g. with exuviae of *Ummidia* (Ctenizidae, F117/CJW) and of the Clubionoidea, F1173/CJW.

(4) Draglines, ballooning threads and attachment discs (Wegfäden, Flugfäden und Haftpunkte)

Photos 565-573.

Most spiders - except the Mesothelae - and the Scytodidae - draw a "dragline" (in German: Wegfaden, Sicherheitsfaden) along their path (fig. 10). In certain distances the dragline is fixed on the ground as an "**attachment disc**" (in German: Haftpunkt). The presence of an attachment disc - see fig. 12 and the photos, FOELIX (1996: Fig. 98) - indicate that a thread in amber is in fact a dragline or a ballooning line, but not a thread from a web. An attachment disc is an area which consists of many delicate threads which are not or only indistinctly observable in the photos of the fossils, and most probably of a secretion. Attachment discs are not so rare with fossil spiders in amber, they may easily be overlooked; see below, F263, F264 and F738/CJW.

Draglines are spun from the pair of the anterior spinnerets and are therefore double at least for the first distance; each line may consist of several threads (figs. 10-13, photos). Bridge threads and ballooning threads are similar or even identical, see below. A dragline can carry the spiders' weight; a fleeing or falling spider is able to climb up along its dragline and can get back to its starting point. Besides this function of security a dragline may bear pheromones which may play (e.g.) a role during the mating behaviour. In the amber forests numerous spiders have been stuck on the resin after they had fallen or were drifted by the wind or had jumped into the resin. I saw hundreds of such fossils in Baltic amber; below I will give few short descriptions.

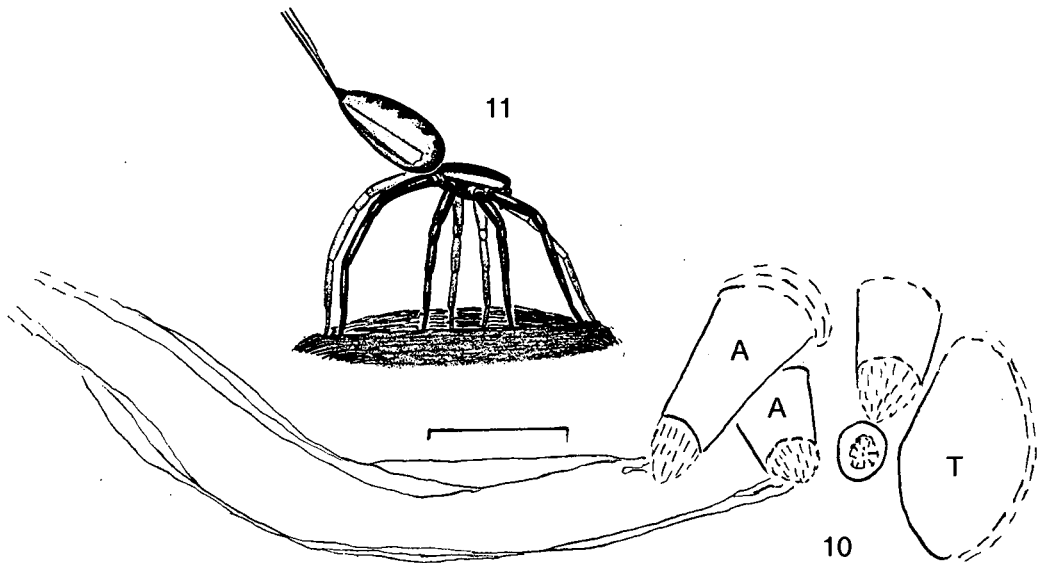


Fig. 10) Draglines which originate at the anterior spinnerets (A) near the anal tubercle (T) of a fossil spider in Baltic amber, *Spinizodariion ananulum* n. gen. n. sp. (Zodariidae), ventral aspect. M = 0.2;

fig. 11) An extant ballooning spider, lateral aspect. Note the raised opisthosoma. Taken from BROSTOWE, modified. The threads are prolonged by the wind, see the text. - Eine heutige Spinne, die einen Flugfaden "herausschießt", Seitenansicht.

F738/BB/AR/CJW: Questionable draglines - and/or threads from a capture web - are partly connected with a well preserved attachment point in which remains of a secretion and many fine irregular threads are observable. The lines are partly doubled and are covered with numerous tiny droplets similar to the fig. 4. In another layer of the amber a male member of the family Zygeliidae is preserved.

F746/BB/AR/SYN/CJW: A basally double dragline is originating from the anterior spinnerets of a male *Anandrus* sp. indet. (Synotaxidae). The tarsal claws of the right leg IV are in contact with a part of ?this thread.

F919/BB/AR/CJW: A dragline is preserved at a small *Dipoena* sp. indet. (Theridiidae), body length 1.8mm; the spider is dorsally partly cut off. At the surface of a 2.8mm long and slender drop of resin inside the piece of amber also a thin spider's thread is preserved which may be a part of the dragline.

Further draglines are preserved (e.g.) with a subadult male Theridiidae indet., F427/CJW, the holotype female of ?*Menneus pietrzeniukae* n. sp. (Deinopidae), a juvenile questionable member of the Liocranidae indet., F264/CJW, two questionable Trechaleidae: a subad. ♀ indet. and the holotype male of *Eotrechalea annulata* n. gen. n. sp., as well as several Salticidae: A male of *Eolinus* sp. indet., F266/CJW, the holotype male of *Distanilinus filum* n. sp., F267/CJW and a male of *Gorgopsina frenata* (KOCH & BERENDT 1854), F268/CJW, a juvenile male Mimetidae, F1258/CJW.

Ballooning (figs. 10-12). In contrast to most insects the spiders are wingless. For their dispersal numerous spiders - rarely the Mygalomorpha - use a unique method: From an elevation - e.g. a plant's branch - they produce a doubled line (each line may consist of several threads) which may be caught and elongated by the wind (fig. 11) until the spider lets the branch go. Thus spiders are able to balloon as aeronauts; occasionally spiders have been found on ships several hundred kilometers from the nearest land. This is only a passive flight, spiders cannot navigate. Usually juvenile spiders balloon, but smaller adults may balloon, too.

In extant spiders and in temperate climates most aeronautic spiders are members of the family Linyphiidae, e.g. members of the genus *Erigone* AUDOUIN. In late summer the air may be "full" of such ballooning spiders and their threads - gossamer in the Indian summer (German name: "Altweibersommer"). In SW-Germany I caught two ballooners from the air, adult males of *Xysticus* sp. indet. (Thomisidae) in a late summer and *Pachygnatha listeri* SUNDEVALL (Tetragnathidae) in the mid of February (!). The body length of these spiders are about 4mm. Numerous juveniles of a mygalomorph spider, *Atypus piceus* (SULZER) were observed in a summer as ballooners near Pforzheim.

From my observations and from reflections I conclude that in the Early Tertiary ballooning was a common behaviour as in extant spiders, but up to now it has not been reported from fossil spiders. Is there any evidence of aeronautic behaviour in the fossil spiders? Certainly fossil spiders draw draglines (see above), but is there a sure indication that they were also ballooners at that time? Unfortunately there is no direct possibility to distinguish fossil draglines and ballooning lines; the origin of the ballooning lines may be the anterior spinnerets as the draglines and the bridge lines (a proof is unknown to me). Dwellers of the bark or other higher strata of the vegetation

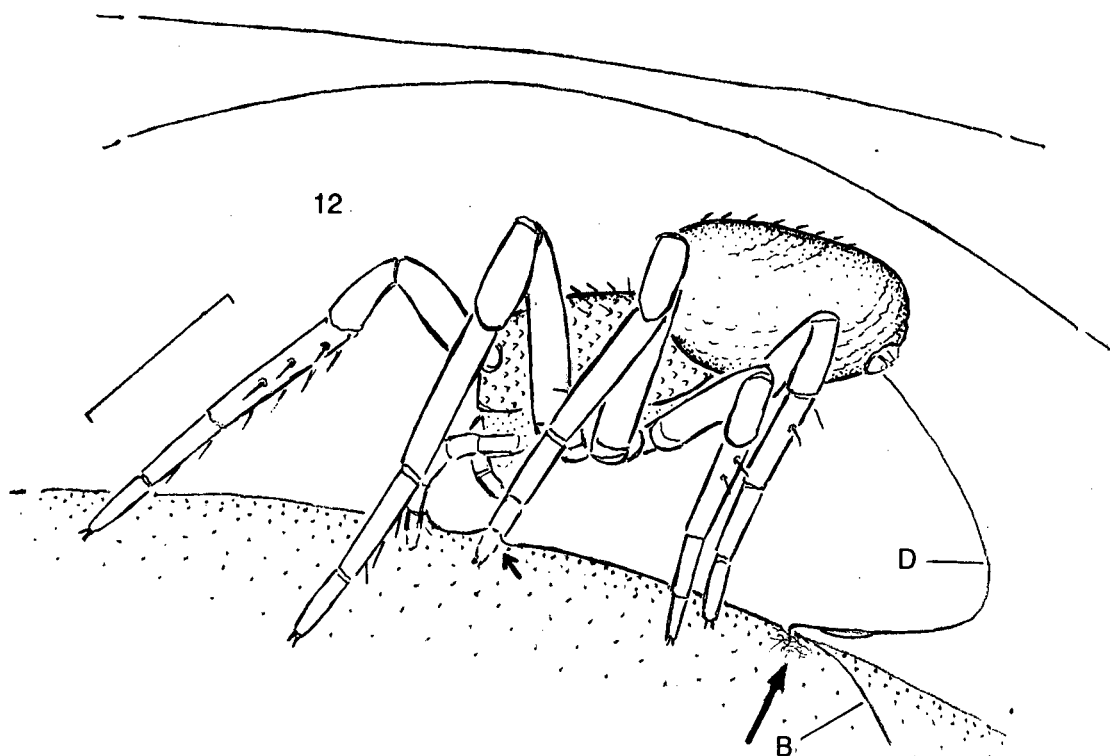


Fig. 12: Attachment disc (long arrow), dragline (D) and questionable ballooning line (B) with a fossil juvenile Thomisidae in Baltic amber, *Syphax* sp. indet., F263/CJW.

Lateral aspect of the spider which is situated on a basal layer of the amber (dotted). A thicker layer of resin is covering the spider and the threads, the final layer above is thinner. Obviously The spider landed on the basal layer and failed to draw out from the sticky resin the left pedipalpus and the left leg II (short arrow). The attachment disc was built shortly after the landing on the surface of the basal (dotted) dotted layer. A short part of the questionable ballooning line is drawn (compare the photo 568); it has a blind ending. The resin flow which covered the spider arrived from the left side in the drawing (from the area in front of the spider in their natural position) and drifted the spider with its dragline to the right side in the drawing (downwards on the tree's bark); so the dragline was lengthened. - M = 0.5mm.

Abb. 12: Haftpunkt (langer Pfeil), Wegfaden (D) und fraglicher Flugfaden (B) einer fossilen jungen Krabbenspinne der Gattung *Syphax* im Baltischen Bernstein, F263/CJW. Seitenansicht der Spinne, die auf einer Schicht im Bernstein (punktiert) "sitzt". Eine dickere Harz-Schicht bedeckte die Spinne und ihre Fäden, die endgültige (oberste) Deckschicht ist dünner. Offensichtlich landete die Spinne auf der punktiert dargestellten Bernstein-Schicht und versuchte vergeblich den linken Pedipalpus und das linke Bein II (kurzer Pfeil) aus dem klebrigen Harz herauszuziehen. Der Haftpunkt wurde kurz nach der Landung auf der Oberfläche der unteren Schicht gebildet (langer Pfeil). Ein kurzer Abschnitt des fraglichen Flugfadens (B) ist dargestellt (vgl. das Foto 568). Der Harzfluß, der die Spinne bedeckte, kam von links in der Zeichnung (von vorn) und verdriftete Spinne und Fäden zur rechten Seite (abwärts an der Baumrinde); auf diese Weise wurde der Wegfaden verlängert. - M = 0.5mm.

vegetation - e.g. the frequent members of the genera *Acrometa*, *Dipoena*, *Eomatachia*, *Orchestina* and *Segestria* - are no good candidates to be found as aeronauts among the fossil spiders. In contrast to these spiders we have to look for spiders who mainly lived on the ground - as Lycosidae and Thomisidae - away from the resin-producing trees. Lycosidae - like Linyphiidae: Erigoninae - are unknown from the Baltic amber forest although both are good ballonners at least the juveniles. Adult Thomisidae are extremely rare in Baltic amber, adults of the genus *Syphax* are even unknown, so they certainly did not live in higher strata of the resin-producing trees. But juvenile Thomisidae of the genus *Syphax* KOCH & BERENDT 1854 have occasionally been found in Baltic amber. Were these juveniles blown by the wind to the fossil resin as aeronauts? In fact I have found single threads with a juvenile member of *Syphax*, F263/CJW, which originate on its anterior spinnerets (F263). The spider is 2.5mm long, completely and well preserved. A dragline, an attachment disc and a questionable ballooning line are well observable; the dragline is curved and 3.7mm long. The reconstruction of the "frozen behaviour" of this exciting spider has been tried above (fig. 12).

Similar to the Thomisidae only very few adult specimens of the family Pisauridae have been found in Baltic amber, but various juveniles. Pisauridae are usually larger spiders, and they lived probably on plants away from the resin-producing trees; the juvenile ballooners were occasionally drifted into the sticky resin.

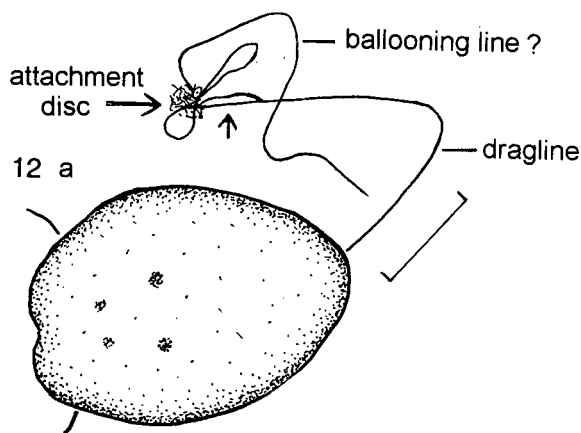


Fig. 12a) The same spider, dorsal aspect of opisthosoma and threads. Note the fine threads of the attachment disc and the blind end of the questionable ballooning line. M = 0.5mm.

Addendum

(1) Spiders' threads as food. Some spiders eat the old and useless threads of their webs after they have clumped them together - kind of recycling. Such a lump of wiry and spiral threads, which is 2mm long, is preserved in a large piece of Baltic amber, F569/BB/AR/CJW.

Another lump of thin hairs, diameter 0.5mm, is preserved on the left patella IV of the holotype male of *Palaeonephila brevis* n. gen. n. sp. (Araneidae; coll. F. KERNEGGER). The lump has probably been transported by a flow in the resin from the anterior legs to the posterior leg. According to COMSTOCK (1953: 21) some authors believed to have observed a bunch (or tuft) of threads at the end of a ballooning line; so I do not want to exclude that the spider may have been a balloonier.

(2) Wrapping lines. Threads of members of the family Hersiliidae, which originate from the posterior spinnerets - e.g. T. 20, fig. a) in the book of WEITSCHAT & WICHARD (1998) - are "wrapping lines" which have the function to wrap the prey and to make it defenceless. A similar "wrapping behaviour" is known from numerous other spider families, too, e.g. the Araneidae, the Oecobiidae and the Theridiidae, see the chapter on the spiders' prey in this volume.

(3) *Arachnomycelium filiforme* GRUESS 1931. Photo 536, compare photo 533.

Material: F807/CJW, F1140/CJW, F1207/CJW, F1317/CJW. The deposition of the pieces of amber which were studied by GRUESS is unknown to me.

On 1931 GRUESS described and figured as a fungus a structure in Baltic amber which he gave the new name *Arachnomycelium filiforme*; see the chapter on decomposition and fig. 4 in this volume. According to GRUESS (1931: 66) *Arachnomycelium* is a fungus which looks like spiders' threads, was branched, up to 2cm long, bears sporangia, and fed on the sweet excretions of aphids.

With some hesitation I consider *Arachnomycelium* sensu GRUESS (fig. 4) a chimæra, a mixed structure of at least two components: (1) long threads of **spiders' silk**, (2) short structures (which stand out from the long threads and may bear sporangia) as parts of a **fungus**. The fungus *Arachnomycelium* may have been the decomposer of the spiders' threads; see the chapter on decomposition in this volume.

GRUESS apparently considered *Arachnomycelium filiforme* to be a single species. As the first revising author I refer *Arachnomycelium filiforme* to the fungal component; the tracks of spiders - the threads of silk - remain unnamed (is not an ichnotaxon) and were probably produced by spiders of the superfamily Araneoidea. A closer study on the fungal component will probably be published by RIKKINEN and the present author.

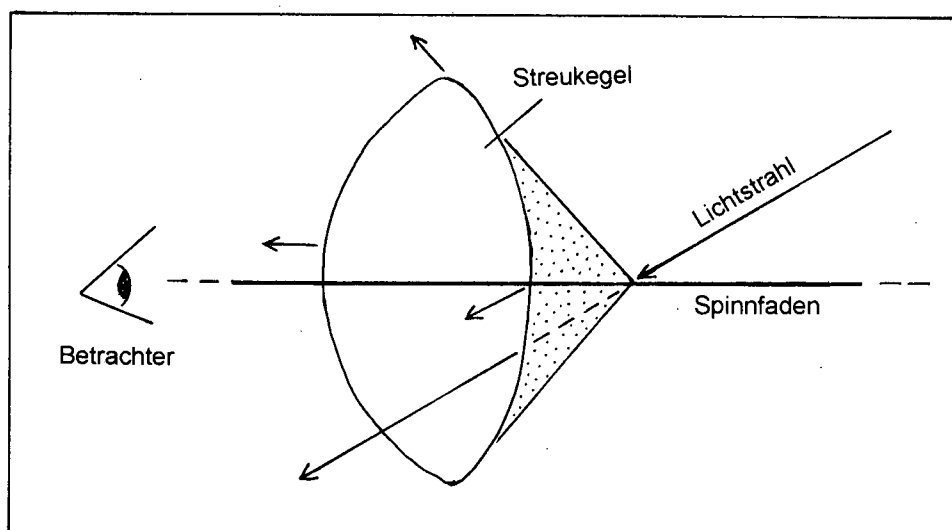
Daß wir den nur wenige Tausendstel Millimeter dicken Spinnfaden überhaupt wahrnehmen, verdanken wir einem optischen Phänomen: der Lichtstreuung. Der Faden erscheint - wie durch eine Lupe betrachtet - in seiner Stärke "sichtbar vergrößert".

Wie ist das zu erklären? Trifft ein Lichtstrahl schräg auf einen Spinnfaden, dann wird dieser Strahl entlang der Mantellinie des entstehenden Streukegels rund um den Spinnfaden gestreut. Der Spinnfaden stellt physikalisch gesehen einen extrem dünnen Zylinder dar, dessen Dicke in der Größenordnung der Wellenlänge des Lichtes liegt. Das Licht wird also nicht - wie an einer spiegelnden Fläche - ausschließlich in der Einfallsebene reflektiert. Die Spitze dieses Kegelmantels "entspringt" dem Spinnfaden (Rotationsachse), an der Stelle, an der das Licht auftrifft. Aus einem einzigen Strahl entstehen unendlich viele neue Strahlen, die das auftreffende Licht in der Fortpflanzungsrichtung kegelförmig "erweitern".

Was wir beim schräg auftreffenden Sonnenlicht an einem Spinnfaden wahrnehmen, ist das Streulicht rund um den Spinnfaden. Je nach der Position des Betrachters (Abb.) trifft immer einer der unendlich vielen Streukegel das betrachtende Auge. Die aufleuchtende Stelle des Spinnfadens wandert mit der Betrachterposition mit.

Andererseits können wir auch ohne direktes Sonnenlicht den Spinnfaden dadurch wahrnehmen, daß anhaftende Teilchen wie Staub und Tau den Spinnfaden sichtbar erscheinen lassen.

Übrigens, wieso in doppelt polarisiertem Licht ein dünner Spinnfaden - etwa ein Wegfaden - im Mikroskop erkennbar wird, hängt damit zusammen, daß dieses Licht "parallel-gerichtet" ist. Es rotiert nicht wie normales Licht (zirkular-polarisiert) um seine Ausbreitungsrichtung.



A RETREAT, A TUBE AND A POSSIBLE MOULTING CHAMBRE OF FOSSIL SPIDERS (EIN SCHLUPFWINKEL, EINE WOHNRÖHRE UND EINE FRAGLICHE HÄUTUNGSKAMMER FOSSILER SPINNEN)

Spiders of numerous taxa hide and protect themselves in a retreat or a tube (in German: Schlupfwinkel, Wohnkammer, Wohnröhre) at day or at night (e.g., numerous members of the Clubionidae and Salticidae), during moulting or even during the copulation (e.g., members of the genus *Cheiracanthium* C. L. KOCH 1839 (Clubionidae)). The retreat may be masked similar to many egg sacs, see the photos and the figs. p 269 and 283 in the book of SAUER & WUNDERLICH (1997) and the paper on egg sacs in this volume.

(1) A fossil retreat Photo 524.

Material in Baltic amber: A juvenile spider of an indet. family in a retreat, F1160/BB/AR/CJW.

The almost globular retreat is apparently not hanging in a web; its diameter is about 6mm. Few thin threads hold together two large and outstanding scales of a deciduous tree, particles of detritus and excrement, a flattened light bubble (or a member of the Myxomycetes?) stellate hairs and at least one splinter of amber which mask the object, see the photo. Inside some leg articles and parts of an opisthosoma - or of two spiders? - can be observed, a bubble is lying in the opisthosoma. The body length of one of the spider(s) may be 2 1/2mm; because of its poorly observable structures a closer determination seems impossible. This object may be a retreat; I will not exclude that it originates from a member of the family Zodariidae.

(2) A fossil tube Photo 527.

Material in Baltic amber: An exuvia of *Segestria* sp. indet. (Segestriidae) in a tube of spiders' threads, F927/BB/AR/SEG/CJW.

The largest diameter of the incomplete oval tube may have been about 10mm, the length of the preserved part is 14mm, see the photo. On the surface and within the tube some particles of detritus are preserved. Its outer surface is connected to a small part of possible detritus, and has originally probably been connected with parts of a plant. - The presence of an exuvia within the tube allow to determine family and genus of the producer of the tube; see the paper on the Dysderoidea: Segestriidae in these volumes. The length of the tibia I of the exuvia is 2mm, thus the body length of the spider may have been 3.5-4mm.

(3) A possible moulting chambre

Photo 526.

Material in Baltic amber: A possible moulting chambre of a spider, with an exuvia (?Theridiidae) outside, F130/BB/AR/?THE/CJW.

The possible moulting chambre has a size of 4.3 x 3mm and hangs in a larger part of a spider's web; it has an opening and is masked by particles of detritus (remains of bark), excrement and splinters of amber. The position of the exuvia is outside the chambre near the opening and almost in contact with the outer surface; its prosoma is 0.9mm long. According to the chaetotaxy the spider is most probably a member of the family Theridiidae. According to the leg spination it is older than a first or second instar, thus the "chambre" may not be an egg sac, but a "moulting chambre", although the position of the exuvia is outside the chambre and not inside.

DIGESTIVE FLUID AND EXCREMENTS OF FOSSIL SPIDERS (VERDAUUNGS- FLÜSSIGKEIT UND EXKREMENTE FOSSILER SPINNEN)

Photos 574-582.

Spiders digest their prey first of all outside their body; they filter their liquified food with a hairy wirelike basket of their mouth parts and they suck in the liquid pap through the narrow mouth opening with the help of muscles of the pharynx and the stomach within the prosoma. So (1) their digestive system remains free of hard particles and of most intestinal parasites; (2) their excretion ("excrement") is liquid, it consists of drops in contrast to the dry excrement balls of insects, which are frequent and can occasionally be identified in webs or on the anus of fossil spiders in amber. The spiders' excrement is first stored in a "pocket" and periodically passes to the outlet of the anus, which is located just above the spinnerets and is dorsally covered by the anal tubercle (A in fig. 1).

(a) Fossil digestive liquid

Digestion and reception of food in spiders are very unusual processes (see above). Spiders do not possess a set of strong teeth as mammals to grind their food. Certain spiders - as most of the larger Mygalomorpha and Araneidae - knead their prey strongly with the help of their chelicerae and cheliceral teeth and suck them out, so that their prey becomes a ball of leg remains and other hard cuticula, the exoskeleton (e.g. photos 629, 675-678). In spiders the digestion happens outside from the body. A certain time after the prey has been bitten (see the bite marks, photos 657, 659, 663), poison (e.g. photo 389) and eventually digestive liquid are injected - the prey may have been fixed by threads (e.g. photos 636-637) - the spider may suck out its food. Some spiders - e.g. Mimetidae and Theridiidae, in which cheliceral teeth are reduced or even absent -, suck out their prey through the bite mark. Numerous spiders vomit digestive liquid on their prey; the prey of a fossil theridiid spider - an ant - is apparently covered by remains of such vomited digestive fluid (photo 639), and the spider was entombed in the resin before it had time to suck out its prey. See also photo 676), a captured Diptera.

In some cases the spiders apparently excreted digestive fluid from their mouth parts into the fossil resin when dying, e.g. *Custodelela hamata* n. gen. n. sp. and *Custodelela stridulans* n. sp. (photo 253), both members of the family Linyphiidae. In the photo 253) the droplet of digestive liquid is situated below the spider below the centre of the photo and is distinctly covered with a white emulsion.

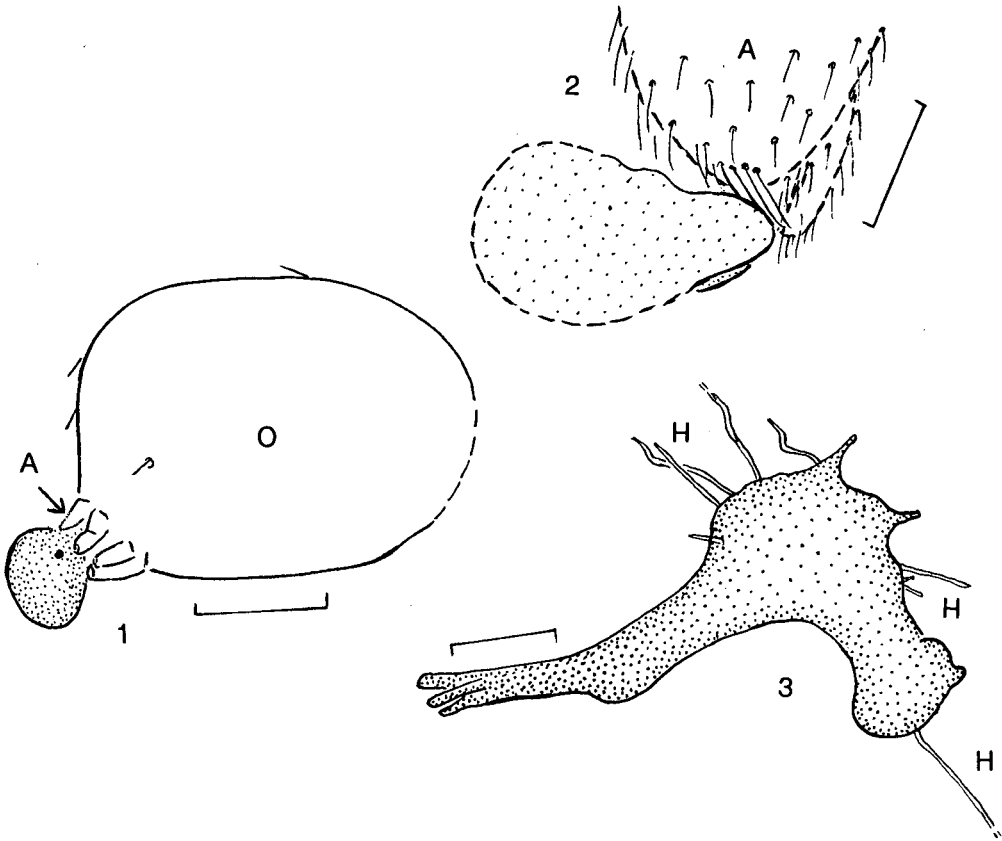


Fig. 1) A droplet of excrement (dotted) which is preserved directly behind the spinnerets and the anal tubercle (A) of a questionable member (a juvenile female) of the family Theridiidae in Baltic amber, F639/BB/CJW, seen from the right side. Only few hairs of the spider's opisthosoma (O) are drawn. The delivery of the excrement's droplet seems to result from the shock of being entombed in the resin. M = 0.2mm. - (Exkrement-Tröpfchen (punktiert), erhalten direkt hinter den Spinnwarzen und dem After-Deckel (A) einer fossilen fraglichen Kugelspinne im Baltischen Bernstein, gesehen von rechts. Die Ausscheidung scheint vom Schock der Einbettung in das Harz herzurühren).

Fig. 2) A droplet of excrement (dotted) which is preserved directly behind the anal tubercle (A) of the male holotype of *Gorgopsidis bechlyi* n. gen. n. sp. (Salticidae), dorsal aspect, Baltic amber. M = 0.2mm. - (Exkrement-Tröpfchen (punktiert), erhalten direkt hinter dem After-Deckel (A) des männlichen Holotypus der Springspinne *Gorgopsidis bechlyi* n. gen. n. sp. von oben, Baltischer Bernstein).

Fig. 3) An irregular opaque droplet - most probably remains of a spider's excrement - in the tube-shaped part of a spider's web which is not drawn, F1164/BB/CJW. Probably decomposing hyphae (H) are growing on the droplet. M = 0.2mm. - (Unregelmäßig geformtes und undurchsichtiges Tröpfchen - fraglicher Rest der Ausscheidung einer Spinne - in einem röhrenförmigen Spinngewebe. Vermutlich wachsen zersetzende Pilzfäden (H) auf dem Tröpfchen).

(b) Fossil excrements

Fossil excrements of insects are not rare and are occasionally preserved e.g. with Diptera in Baltic amber. To my knowledge fossil spiders' excrements have never been reported - why not? In contrast to most insects' excrements (which are hard and formed) the excrements of spiders are liquid and nothing is known about modifications of such substance e.g. crystals of guanine - in resin. So the peculiar liquid kind of such excretion makes it difficult to identify it in amber. The best way to recognize the excrement of a fossil spider is to search for a droplet on its anus near the anal tubercle (which covers the anus) behind the spinnerets. Occasionally such a droplet can be found in this area of a fossil spider (figs. 1-2, photos 296, 574-576, 580) which was produced while the spider was dying.

The identification of a droplet of excretion within a spiders' web is more difficult. Certain spiders deposit their excrement near the margin of their web - "sanitary behaviour", see TIETJEN (1986: 201-202). In other extant spiders the excretion is distributed in an accidental way within the web. In some cases of fossil spider webs these droplets cannot be determined with certainty; they might be something else, e.g. remains of droplets of water, e.g. F183/BB/CJW and F1164/BB/CJW. See the photos 577-579, 581-582).

In the following I list and describe shortly selected remains of fossil spiders' excrements in Baltic amber (some are only questionable remains of excrement):

F179/BB/CJW: About 10 bubbles which may contain excrement are preserved behind the spinnerets of a member of the family Theridiidae. Within the opisthosoma a large bubble is preserved which may be decomposing gas, and so the bubbles outside the opisthosoma may be remains from the decomposition, too.

F183/BB/CJW: Several droplets of probable remains of excrement are preserved in a capture web of a spider of the superfamily Araneoidea in which remains of sticky droplets are present; their length is ca. 1.4mm and they are situated in the capture area.

F427/BB/CJW: A subadult male Theridiidae indet., body length 1.3mm, with a droplet of excrement directly behind the spinnerets.

F569/BB/CJW: In the large part of a spider's (Araneoidea) web several droplets are preserved which may be remains of a spider's excrement.

F639/BB/CJW: A droplet of excrement which has a size of 0.2mm (fig. 1, photo) is preserved directly behind the spinnerets and the anal tubercle of a questionable member (a juvenile female) of the family Theridiidae indet. in Baltic amber. The delivery of the excrement seems to result from the shock of being entombed in the resin.

F1164/BB/CJW: In a tube-shaped spider's web in Baltic amber several irregular droplets are preserved which are opaque and which have a length of 0.5-6mm (fig. 2).

Hyphae growing on the droplets may be a hint that these droplets are in fact remains of spiders' excrements.

F1244/BB/CJW: A tiny droplet of a questionable spider's excrement is preserved directly below the anal tubercle of an Araneae indet., in Baltic amber, a probably adult female.

F1254/BB/CJW: A droplet of a spider's excrement, 0.2mm long, is preserved directly behind the anal tubercle of a questionable member (a juvenile female) of the family Insecutoridae in Baltic amber.

Museum Ziemi no. 13619: A droplet of excrement is preserved above the anal tubercle of the male paratype of *Cymbiohahnia parens* n. gen. n. sp. (Dictynidae s. l.: Hahniinae) (photo 296).

EGG SACS, BROOD CARE AND SPIDERLINGS (EI-KOKONS, BRUTPFLEGE UND JUNGSPINNEN)

Photos 494-523.

Introduction: I focus on fossils in Baltic amber in which spider's egg sacs are not too rare, I saw about 40 pieces, 20 are kept in the private collection of the author (CJW), 10 from the Bitterfeld deposit are kept in the private collection of M. KUTSCHER in Sassnitz. Most of the egg sacs in question are not determined to family level, only one exists with its identified producer in the same piece of amber, a female of the genus *Acrometa* PETRUNKEVITCH (Synotaxidae), see below (F133). All the material is waiting for closer studies in the future.

Most published extant egg sacs - e.g. fig. p. 121 (right corner) in the book of BELL-MANN (1997), in which numerous egg sacs of extant spiders are published - and fossil egg sacs - e.g. fig. 105 in the books of JANZEN (2002) and WEITSCHAT & WICHARD (2002: T. 20, fig. a) - are well observable, but fossil egg sacs are frequently overlooked or not recognized because they are masked by detritus and other particles, and the eggs or spiderlings are hidden, see the photos. In certain fossil pieces the eggs or the instars or their exuviae are well observable because the pieces are partly cut off, see the photos and fig. 1 below.

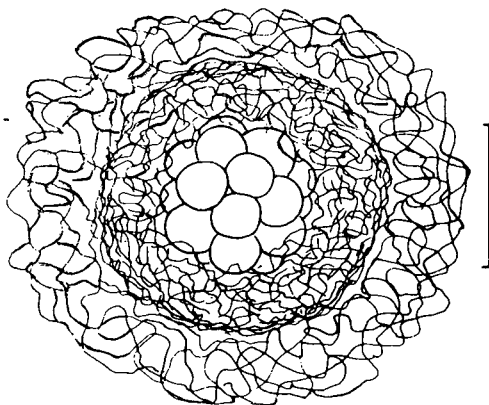


Fig. 1) Egg sac of a fossil spider (Araneae: Probably Mimetidae or Theridiidae) in Baltic amber which contains more than 20 eggs (three are partly cut off). The inner layer is covered by fine threads, the outer part is built by loose and thicker threads, coarse and wiry silk -. Zool. Mus. Copenhagen. M = 0.2mm. - Abb. 1) Eier-Kokon einer fossilen Spinne, möglicherweise einer Spinnenfresser-Spinne oder Kugelspinne, mit mehr als 20 Eiern, drei sind angeschliffen. Die innere Schicht wird von feinen, die äußere Hülle wird von größeren Fäden gebildet.

Appearance of the egg sacs: Its shape may be globular (most often), pear-shaped or flat and lense-shaped (e.g. in *Zelotes*); it may be white or coloured, may possess humps, may have a smooth (leathery or papery) surface (F248/CJW) or loose, coarse and wiry threads (fig. 1) or it is held together by only few threads, e.g. in members of the Pholcidae, it may be masked with soil or different particles, detritus, excrement, moss, stellate hairs etc. (photos) as a protection, probably against certain parasitoidic wasps, it may be hidden in a folded leaf together with the mother - e.g. in numerous Clubionidae, see ROBERTS (1995: Left fig. p. 57) -, or hanging on a long(er) stalk (*Ero*, *Theridiosoma*), probably a certain protection against ants.

How can the spiderlings leave their egg sac? In some cases we find a "praedetermined" exit which can be opened by the spiderlings. Such an outlet may exist, e.g. in *Argyrodes* (Theridiidae) at the bottom of the egg sac (photo) but is unknown in spiders of the Early Tertiary. In numerous other spiders the mother bites small holes in the surface of its egg sac as outlets (see below).

Size: Certain tiny spiders - as some Anapidae and some Theridiidae - build large egg sacs which may be even more voluminous than their body, see the fig. p. 175 in the book of SAUER & WUNDERLICH (1997). The largest egg sac in Baltic amber - F248/CJW, only about 1/6 of it is still present, the remaining parts are cut off - originally had a diameter of probably more than 2cm; the body length of the spider which produced it - probably a member of the genus *Sosybius* PETRUNKEVITCH - may have been 3cm or more, see below. This fossil egg sac is also of special interest because it has several openings on its surface which most probably were bitten by the mother as outlets for the spiderlings (photo). - F122 has a length of about 2cm.

The eggs may hibernate in their sac (e.g. in *Argiope*) and the young hatch out the following spring.

Inside an egg sac we can find two to about one thousand eggs, remains of egg covers, spiderlings (first or second instars) (photos), and occasionally - larva of parasitoids, see below.

Broodcare: The females of numerous taxa guard their egg sac - occasionally several sacs -, they may stay on or nearby their egg sacs, e.g. on the surface of a stone or a leaf (usually the bottom side), a stone or under bark, for example in most Ground Spiders and Crab Spiders, see PÖTZSCH (1963: Fig. 13). In some taxa the female opens the sac periodically gives some fluid from her mouth. Numerous members of the superfamily Araneoidea attach them in their capture web, some hide them in their retreat (e.g. *Larinia*, Araneidae) and some *Achaearanea* (Theridiidae), see PÖTZSCH (1963: Fig. 42) or within the stabiliment and remains of prey (e.g. *Cyclosa*). Numerous females of the superfamily Dysderoidea as well as some others as the Pisauridae - see BELLMANN (1997: Figs. p. 141, 143) -, few Synotaxidae (photo), Ctenidae and Sparassidae bear their egg sac with the help of their fangs and pedipalpi under the sternum or mouth. Females of the families Nesticidae - see PÖTZSCH (1963: Fig. 34), Lycosidae and Trechaleidae as well as some Theridiidae as members of *Rugathodes* bear their egg sac attached to the spinnerets, see BELLMANN (1997: Figs. p. 145-151), PÖTZSCH (1963: Fig. 33). Females of few taxa guard additionally their spiderlings in special ways: Lycosidae bear the spiderlings on their opisthosoma, Pisauridae watch them in a special "nursery web", see BELLMANN (1997: Figs. p. 141, 145) similar to some Araneidae, e.g. ♀ of *Argiope*. Females of the Eresidae as well as of certain Amaurobiidae, and Theridiidae see PÖTZSCH (1963: Fig. 46) even feed their spiderlings; in some of these spiders the spiderlings eat the body of their mother which is being dissected by a special enzyme.

Shortened translation into German (without most citations - ohne die meisten Zitate):

Das Aussehen der (Ei-)Kokons: Die meisten Kokons sind mehr oder weniger kugelförmig, birnenförmig oder linsenförmig abgeflacht, sie sind weiß oder farbig, ihre Oberfläche ist höckerig oder glatt, papier- bis lederartig oder besteht aus feinen bis groben, unregelmäßigen (wollartigen) Fäden (Abb. 1). Manche Eier werden lediglich durch wenige Fäden zusammengehalten, z. B. bei den Zitterspinnen. Zahlreiche Kokons - auch fossile Kokons im Bernstein - sind in vielfältiger Weise getarnt und teilweise gegen Feinde wie Wespen geschützt; sie können bedeckt sein mit Schmutzteilchen, zerfallenden Pflanzenteilen, Beuteresten, Kot-Bällchen von Insekten, Moosteilchen, Sternhaaren u. a. (siehe die Fotos). Manche Sackspinnen-Weibchen verbergen ihren Kokon (wie auch sich selbst) in gefalteten Blättern, andere hängen ihn an einen Stiel - z.B. manche Feldspinnen (Liocranidae) und Spinnenfresserspinnen (Mimetidae) -, möglicherweise ein gewisser Schutz gegen Ameisen.

Wie können die Jungspinnen ihren Kokon verlassen? In einigen Fällen finden wir einen "vorherbestimmten" Ausgang, den die Jungspinnen öffnen können; ein derartiger Ausgang ist von Spinnen des Frühen Tertiärs unbekannt. Die Weibchen anderer Arten beißen als Ausgänge kleine Löcher in die Wand des Kokons, siehe unten.

Größe. Manche winzige Spinnen - z. B. einige Kugelspinnen - bauen Kokons, die größer sind als sie selbst, vgl. die Abb. S. 175 im Buch von SAUER & WUNDERLICH (1997). Von dem größten erhaltenen Kokon im Baltischen Bernstein - F248/CJW - ist nur etwa ein Sechstel erhalten, er mag einen Durchmesser von mehr als 2cm gehabt haben und ist möglicherweise von einem Weibchen der Gattung *Sosybius* gebaut worden, das ca. 3cm lang gewesen sein könnte. Dieser Kokon ist von besonderem Interesse, weil er mehrere Löcher in seiner Wand besitzt (Foto), die vermutlich die Mutter als Ausgänge für ihre Jungspinnen gebissen hat. Die Eier überdauern bei manchen Spinnen den Winter, und die Jungspinnen schlüpfen im nächsten Frühjahr.

Im Inneren eines Kokons finden wir zwei bis etwa eintausend Eier, Reste von Eihüllen, Jungspinnen (Fotos) sowie gelegentlich die Larven von parasitenartiger Wespen oder Fliegen, vgl. unten.

Brutfürsorge: Die Weibchen zahlreicher Spinnen bewachen ihren Kokon - es können auch mehrere sein -, sie sitzen auf oder neben dem Kokon, z. B. an der Oberfläche eines Steins oder Blattes (gewöhnlich der Unterseite) oder unter Baumrinde, so z. B. die meisten Plattbauchspinnen und Krabbenspinnen, siehe PÖTZSCH (1963: Fig. 13). Die Weibchen mancher Arten öffnen gelegentlich den Kokon, um ihre Jungen mit Flüssigkeit aus ihrem Mund zu füttern. Von zahlreichen Vertretern der Überfamilie der Radnetzspinnen-Verwandten (Araneoidea) wird der Kokon im Fangnetz befestigt oder in ihrem Versteck bewacht. Zahlreiche Weibchen der Überfamilie der Sechsaugenspinnen-Verwandten (Dysderoidea) und einige andere wie Jagdspinnen (Pisauridae) tragen ihren Kokon mit Hilfe der Giftklauen und Pedipalpen unter dem Sternum und dem Mund. Weibchen der Familien Höhlenspinnen (Nesticidae), Wolfspinnen (Lycosidae) und einige weitere wie manche Kugelspinnen transportieren ihren Kokon, der an den Spinnwarzen angeheftet ist. Wolfspinnen-Weibchen transportieren sogar ihre Jungspinnen, und zwar auf dem Hinterkörper. Jagdspinnen-Weibchen bewachen ihre Jungspinnen im speziellen Netz, einer "Kinderstube". Am weitesten entwickelt - vergleichbar mit demjenigen der Säugetiere - ist das Brutpflegeverhalten bei den Röhrenspinnen (Eresidae) sowie einigen Finsterspinnen (Amaurobiidae) und Kugelspinnen (Theridiidae), bei denen die Mütter ihre Jungspinnen von Mund-zu-Mund füttern. Bei einigen dieser Spinnen wird schließlich der Körper der Mutterspinne durch ein besonderes Enzym aufgelöst und von den Jungen verspeist.

Parasitoids of spiders' eggs are known from wasps, the family Ichneumonidae - see PÖTZSCH (1963: Figs. 73-74, 76) -, e.g. the genus *Pimpla* which already existed in the Baltic amber forest, from members of the Diptera which were already present in the Baltic amber, too - among Asilidae, Chloropidae and Sarcophagidae - and finally from beetle larvae of the Melyridae: Malachiinae - see SACHER & KLAUSNITZER (1992) - the genus *Malachius* existed in the Baltic amber forest. Up to now I have not discovered such a fossil parasitoid with a fossil egg sac, but see the paper of POINAR on this matter in these volumes. A parasitoid larva would be hard to observe in a masked egg sac.

The fossil eggs and the egg sacs (most of the objects are only briefly described)

An egg sac in copal from Madagascar (photo):

Material: F 1157/CM/AR/CJW.

Description: The piece of copal was heated. The egg sac is empty, 2.6mm high and 1.6mm wide. It hangs in a part of a capture web (above) and has a larger outlet at the bottom. Similar egg sacs are known from extant members of the Theridiidae, e.g. from the genus *Argyrodes* SIMON 1864, see the fig. 335 in the book of WUNDERLICH (1986).

Eggs in Dominican amber:

"Many female spiders, such as members of the family Pholcidae ... carry their eggs to protect them", see POINAR & POINAR (1999: 74, Figs. 72). In this spider the lump of eggs is lying in a short distance below its prosoma.

Eggs and egg sacs in Baltic amber and the Bitterfeld deposit

The first fossil egg sacs in Baltic amber were mentioned by MENGE (1856: 10) but they were not described; the material is most probably lost. An egg sac of the superfamily Clubionoidea in Baltic amber which is parasited by a Hymenoptera: See the paper of POINAR in this volume.

It is striking that most of the unmasked objects (nine) - among the treated inclusions - do not come from the Bitterfeld deposit but from "Kaliningrad amber" and only five from the Bitterfeld deposit. The reverse relation exist in the masked egg sacs: Only two come from the "Kaliningrad amber" but nine from Bitterfeld. The reason for this mis-proportion is simply the fact that M. KUTSCHER in Sassnitz studied the inclusi-

ons in Bitterfeld amber most closely and discovered most of the masked egg sacs but he studied only few inclusions of other deposits.

a) Lumps of eggs

A lump of eggs is preserved with the fossil female of a member of the spider family Synotaxidae, see the paper on this family in these volumes and the photo. The female carries its egg sac in a similar way as members of the Pholcidae (photo 522).

An incomplete egg sac: Coll. THOMAS no. 24, PIHUB: A lump of about a dozen eggs which have a diameter of 0.65-0.8mm build a globe of about 2mm in diameter in a position directly to the left below the left legs I and II of a spider which may be the mother. The eggs are not held together by threads but are partly covered with hyphae of a fungus. There is no base (bottom) of the lump of eggs and probably the production of the egg sac was interrupted. The female of the spider - her anterior spinnerets are cylindrical, not widely spaced, gnathocoxae and posterior median eyes are hidden - is probably a member of the family Gnaphosidae and has a body length of 6mm. The opisthosoma of the spider is strongly deformed, numerous hyphae grow on the prosoma. There is the part of an irregular web which is partly in contact to the spider and which has no sticky droplets. All the right legs of the spider are lost behind the coxa, they have probably been amputated by a parasitoidic wasp, but according to the deformed opisthosoma I do not want to exclude that the spider was the prey of another spider. The prosoma, the pedipalpi and the left leg I are covered by hyphae. Further syninclusions: The exuvia of a tiny spider's instar is preserved on the opisthosoma of the spider, 1/2 male of the genus *Orchestina* (Oonopidae), particles of excrement and stellate hairs are preserved in the same piece of amber.

b) Unmasked egg sacs Photos 495-506.

Most of these egg sacs - not F248 - may originate mainly from members of the superfamily Araneoidea, probably most often from Theridiidae, Mimetidae, Zygellidae and Araneidae. - F375/BB/CJW: See the photo 563.

F119/BB/AR/CJW: The oval egg sac is hanging at few thick threads, its size is 2.8 x 3.2mm, 2 of the about 1 dozen eggs are partly cut off. There are two layers of silk, the inner layer consists of numerous thin threads, the outer layer consists of loose wiry threads similar to fig. 1.

Coll. H. FLEISSNER: The globular egg sac has a diameter of 3.6mm and is hanging on a 12mm long thread, a part is cut off. The outer surface is leathery or papery, eggs are not observable. Similar egg sacs are built from certain members of the superfamily Clubionoidea.

F121/BB/AR/CJW from the Bitterfeld deposit: The almost globular egg sac has a size of 5.5 x 5.2mm and is hanging on some threads. The structure of the surface is similar to F119. Inside some instars are observable.

F122/BBAR/CJW: A large egg sac which consists of a wiry outer layer of a size of almost 20 x 10 x 13mm and an "inner" layer - which contains probably 100 eggs - of a size of 10.5 x 7.5 x 5mm. The diameter of the eggs is about 1mm. The producer of the egg sac may have been about 2cm long. Egg sacs of certain extant members of the family Araneidae - as *Araneus* - are similar. A 17mm long branch of a member of the genus *Thuites* (Cupressaceae), a part of a wood and a part of bark (photo) - which all are part of the spider's web - are also preserved in the piece of amber. Thus the female which produced the egg sac was a dweller of *Thuites*. Did the *Thuites* produce the fossil resin or were all the parts blown to another kind of resinproducer by the wind?

F188/BB/AR/CJW are the remains of a large egg sac which is badly preserved, deformed and partly cut off. Inside some instars are observable.

F248/BB/AR/CJW: The diameter of the large papery or leathery egg sac is about two cm, it is partly cut off, only about a quarter may be left (it may originate from a female which was 2 - 3cm long) and its original shape was most probably flattened. Inside remains of egg covers and hyphae of fungae are present, hyphae are growing on the outer margin, too. At least 20 exuvia are preserved in the webs of the spiderlings; their body length was about 2mm. Five slit-like openings - about 1 - 1.5mm long - in the surface of the egg sac were probably bitten by the mother as outlets to the spiderlings. The producer may have been a larger member of genus *Sosybius* PETRUNKEVITCH 1942 (Trochanteriidae).

F1139/BB/AR/CJW: The almost globular egg sac is hanging on a long and thin thread, its diameter is 3.7mm, the surface may have only one thin layer of fine irregular threads. Inside about 40 eggs are observable, their diameter is about 0.5mm.

F1148/BB/AR/CJW from Bitterfeld: The size of the pear-shaped egg sac is 6 x 7mm, a small part is cut off. Remains of at least 30 exuviae are preserved in the inner part.

F1158/BB/AR/CJW: The almost globular egg sac has a diameter of 2.8mm, is hanging on a long stalk and is only fairly well preserved. Eggs or spiderlings are not observable.

F1159/BB/AR/CJW: The egg sac is hanging in a larger irregular web, its size is 7.5 x 4mm. It is of the "Mimetid type" (wiry threads of the outer surface), eggs or instars are not observable.

c) Masked egg sacs

Photos 507-521.

Because of particles of detritus etc. most of the masked egg sacs are hard to recog-

nize. F133 is most remarkable because of its unique syninclusions: The adult female of an identified spider genus - the mother -, her young (spiderlings), an egg sac with egg covers and exuviae inside, a capture web as well as several remains of prey.

F133/BB/AR/SYN/CJW: In a large piece of amber - 6 x 5.5 x 2.3cm - are preserved: (a) The female of *Acrometa* sp. indet. (Synotaxidae), (b) a large part of its capture web, (c) an egg sac with egg covers and exuviae of spiderlings, (d) 8 spiderlings, (e) prey and possible prey. Furthermore are preserved: Hyphae, large and oxidated remains of plants, numerous stellate hairs, pollen grains (including air bag pollen grains) and tiny balls of excrement; some objects are hanging on the threads of the capture web.

(a) The female of *Acrometa* PETRUNKEVITCH 1942 indet. has a deformed opisthosoma and is 2mm long. The tips of the left tarsus I and the right tarsus III are cut off, all sides of body and legs are covered by a thin white emulsion, the sclerotized epigyne is observable with its wide opening. The tip of the left tarsus IV is in contact with at least five threads of the capture web. A thread is running from the right anterior spinneret in the direction of a possible prey (indet.) and to a part of the capture web.

(b) The capture web is filling most parts of the large piece of amber. It is irregular, sticky droplets are most probably absent, stellate hairs, pollen grains, an egg sac, prey etc. are hanging in its threads, see below.

(c) The diameter of the globular egg sac is 4.5mm; it is hanging in the web at one end of the piece of amber, 4.8mm behind the tip of the left tarsus IV of the spider; it is partly cut off on two sides. The outer surface consists of loose threads which are covered with particles of detritus, tiny balls of excrement, stellate hairs, splinters of amber as well as remains of Arthropods including remains of a dissected insect (bug?) larva (photo). Remains of numerous - probably more than 30 - egg covers and exuviae of spiderlings are preserved in the egg sac.

(d) The eight spiderlings - probably second instars, body length about 0.8mm - are well preserved, their opisthosomae are deformed, their legs are bent under the body as are their mother's, a thin white emulsion is present, they are 11-20mm away from the egg sac.

(e) Prey and possible prey: Besides some unidentified remains of questionable prey there is a partly dissected member of the Collembola, body length 1.6mm, which is hanging in the web 1.3cm away from the egg sac, the hind part of a second Collembola is present, too. Remains of a partly dissected insect larva - probably a bug - is preserved at the margin of the egg sac. Remains of a questionable prey indet., diameter 1.5mm, are preserved in contact with the right tarsus IV of the female. A beetle of the family Curculionidae, body length 3.7mm, is present in contact to threads of the capture web; apparently the beetle is complete and not spun in; it was probably not a prey of this spider.

The presence of splinters of amber within the outer surface of the egg sac gives a hint that the spiders were dwellers of the bark of the resin-producing tree, most probably a Conifera.

F569/BB/AR/CJW: Large remains of a masked and almost globular egg sac, diameter 1.8cm, are hanging in a spider's web with droplets. The egg sac is hollow and empty (not filled with amber), partly cut off on both sides, and masked by particles of detritus and bark. Instars and exuviae are absent. The producer of this egg sac must have been a large spider, probably of the family Araneidae.

F1038/BB/AR/CJW: The almost globular egg sac has a diameter of 3.5mm, is hanging on half a dozen threads, and is masked with particles of detritus and excrement as well as stellate hairs. Inside some first instars are observable. Some Theridiidae mask their egg sac in a similar way, see PÖTZSCH (1963: Fig. 49).

F1140/BB/AR/CJW: This globular egg sac has a diameter of 4.5mm, is partly cut off and is masked with particles of detritus. It is hanging in a capture web; at the outer margin remains of an exuvia are hanging. The producer of the egg sac is unknown. 4.5mm away from the egg sac a beetle (family Elateridae) is hanging in the capture web, which has been a prey of a spider.

F1149/BB/AR/CJW from the Bitterfeld deposit: The diameter of the globular egg sac is 4.5mm. It is masked on one side with particles of detritus and excrement as well as stellate hairs. The other side is partly cut off; about 20 eggs are well observable, their surface is shrunk, bears fissures and appears dried out. Probably the embryos did not develop because they were not fertilized.

F1150/BB/AR/CJW from the Bitterfeld deposit: The egg sac has a triangular shape and a size of 3.5-4mm. It is hanging in a web on threads mainly at the corners of the triangle and is masked with particles of detritus and stellate hairs. Inside few exuviae are observable.

F1151/BB/AR/CJW from the Bitterfeld deposit: The almost globular egg sac is hanging in a larger of an irregular capture web, its diameter is up to 3mm, it is masked with particles of detritus, tiny balls of excrement and stellate hairs. Inside remains of few exuvia are probably present. Remains of the surface of a second egg sac are preserved in the same piece of amber which may originate from a member of the family Theridiidae.

F1152/BB/AR/CJW from the Bitterfeld deposit: The size of the almost globular egg sac is 3-3.5mm. It is hanging in a capture web and is masked with particles of detritus and excrement as well as stellate hairs; the outer layer consists of wiry threads. The egg sac is marginally cut off and thickly filled with probably more than 30 instars.

F1153/BB/AR/CJW from the Bitterfeld deposit: The egg sac has a slightly triangular shape, the size is 3-4mm; it is thickly masked with particles of detritus and stellate hairs. I find no eggs or instars inside.

F1278/BB/AR/CJW is somewhat flattened, has a diameter of 4.5-5.5mm, is partly cut off and masked with particles of detritus; remains of few tiny exuviae are present outside the margin of the egg sac. Nearby preserved are dissected remains of an ant.

F1302/BB/AR/CJW: An egg sac - 7 x 3.5 x 3mm - is hanging in a capture web incl. droplets; it is masked by detritus and the 7mm long anterior wing of a beetle. The remains of a tiny exuvia and a preyed spiderling (cannibalism) are also preserved. The beetle's wing is most probably the remains of a prey of a larger spider which may be a member of the genus *Eustaloides* PETRUNKEVITCH, the family Zygellidae.

F1313/BB/AR/CJW: A larger egg sac, up to 9mm long, slightly cut off on one side, not flattened and with an irregular surface, is masked with particles of detritus and stellate hairs, and is hanging in a spider's web which has no droplets. Exuviae and

instars are absent.

F1320/BB/AR/CJW: A smaller egg sac which is partly cut off on one side, almost globular, diameter 3.2 x 3.8mm, weakly masked with stellate hairs and few small particles of bark, is hanging in an irregular web of thin threads without droplets. Inside present are more than 20 remains of egg covers and exuviae as well as numerous hyphae which most probably were decomposing the egg covers and exuviae.

Coll. M. KUTSCHER, no. EK1 from the Bitterfeld deposit: This egg sac has a globular shape, a diameter of 3mm and is hanging on several threads. The outer layer consists of wiry threads and is masked with tiny particles of detritus and striking stellate hairs. Inside about 1 dozen eggs are present which have a diameter of 0.6mm.

Coll. M. KUTSCHER, no. EK2 from the Bitterfeld deposit: The egg sac has a globular shape and a diameter of 3.5mm; it is hanging on several threads and is masked with splinters of amber, particles of detritus, excrement and liverworts (Hepaticae) as well as stellate hairs. Inside some exuviae are observable.

Coll M. KUTSCHER, no. EK3 from the Bitterfeld deposit: The globular egg sac has a diameter of 4mm and is masked with pieces of detritus which are held together by only few threads on one side. The other side is partly cut off, so that remains of some exuviae are observable.

Die Spinnen *Eugen Roth*

Die *Spinnen* leben streng allein;
Auch wenn es manchmal hat den Schein,
Als sässen friedlich sie vereint:
Sie sind einander spinnefeind.
Zwei Arten wurden da gefunden:
Ansässige und Vagabunden.
Ja, manche schiffen sogar Luft;
Durch den Altweiber-Sommerduft
Ziehn, Liebesfäden jungen Mädchen,
Hold flatternd die Mariafädchen.
Den Fischern ist die Spinn verwandt,
Indem sie ihre Netze spannt
Und rennt gleich voller Eifer hin,
Sobald nur etwas zappelt drin.
Oft freilich wird vom fettesten Bissen
Das schöne, neue Netz zerissen,
Das sie, was den Betrieb verteuert,
Statt es zu flicken, ganz erneuert.
Es führt, aus diesem Grunde eben
Das Spinnenvolk ein Hundeleben,
Und hat, bedenkt man Zeit und Kräfte,
Wohl eins der kläglichsten Geschäfte,
Wobei ihr Leben, arg bedrängt,
Stets nur an einem Faden hängt.
Viel üppiger ihr Brot gewinnen
Die Arten, die *Intrigen* spinnen.
Schwer ist es ihnen zu entschlüpfen,
Weil leicht Verbindungen sie knüpfen.
Die Männchen – das wär noch zu melden –
Sind traurige Pantoffelhelden.
Kaum naht eins, die Braut zu grüssen,
Auf allen seinen Freiersfüssen,
Frisst es (welch tolles Liebesspiel!)
Das Weibchen auf mit Stumpf und Stiel.

THE PREY AND PREY CAPTURE BEHAVIOUR OF THE FOSSIL SPIDERS (DIE BEUTE UND DAS BEUTEFANG-VERHALTEN DER FOSSILEN SPINNEN)

Photos 621-685.

See also the chapters on the capture webs, moulting behaviour, the relationships between spiders and ants, cannibalism, Eresoidea: Archaeidae and Mimetidae in these volumes.

Introduction

All spiders are predators, almost all members are poisonous; only in the Uloboridae and the Heptathelidae venom glands are absent. They feed mainly on insects and other arthropods, see BRISTOWE (1941: 262-330). Most species are generalists, but various species are specialized on certain groups of arthropods, e.g., ant-eaters are most Zodariidae, many Theridiidae as *Dipoena*, certain Oecobiidae as *Oecobius*, Thomisidae (Aphantochilinae), Corinnidae, Gnaphosidae and Salticidae. Surprisingly about half of the fossil spider's prey in amber is ants, see below and the chapter on the relationships between spiders and ants in this volume. Specialized spider-eaters are e.g. most members of the Archaeidae and Mimetidae. According to NENTWIG (1987) the potential prey of epigeous spiders consists mainly of Collembola, Diptera (Brachycera), Coleoptera, Hymenoptera (Formicoidea), Araneae and, to a lesser extent, Aphidina and Auchenorrhyncha. Spiders hunting on vegetation have a potential prey spectrum of mainly Aphidina, Auchenorrhyncha, Diptera, Coleoptera, Araneae and Collembola. Web-building spiders in higher strata of the vegetation capture mainly Diptera (Nematocera), Aphidina, Thysanoptera, Auchenorrhyncha, Hymenoptera and Coleoptera. Capture webs can be regarded as "selective filters". According to FOELIX (1996: 241) "Pollinating insects (bees, wasps, certain flies, and beetles) are rarely found trapped in the space webs of theridiids and linyphiids,...". The prey spectrum of fossil spiders in Baltic and Dominican amber is quite different, see below.

Members of numerous groups of arthropods feed on spiders, e.g. some Myriapoda, beetles, ants, wasps, mites and spiders. How can we recognize a fossil arthropod as a spider's prey?

(a) An arthropod which is held by a spider (figs. 3, 5) is undoubtedly a prey of the spider; if spider and arthropod are associated we need a closer study.

(b) An arthropod which is attached to a spider's web may be at least a possible prey. Some threads of a capture web - of a member of the superfamily Araneoidea (e.g. of the Theridiidae) or of the Pholcidae - may bear droplets. We have to look for injuries and bite marks on the prey (fig. 4) and whether the arthropod is sucked out. Bite marks can be seen on the head incl. an eye of an extant beetle by FOELIX (1996: Fig. 36a); such marks are hard to observe in fossils, I recognized only 7 of such pie-

ces: On the eyes of a Trichoptera, coll. V. ARNOLD no. 1340, dorsally on a Blattaria larva, F111/CJW, on the abdomen of an ant (F127/CJW) (fig. 4), ventrally on a member of the Auchenorrhyncha (F1205/CJW), dorsally on the right wing of a beetle (Cerambycidae) (F106/CJW), dorsally behind the head of a Trichoptera (F1297/CJW) and on the case of a Psychidae (Lepidoptera), F1319/CJW, see below. Bite marks may be absent because - e.g. in most Araneidae and Theridiidae - the bite occurs after the spinning in of the prey.

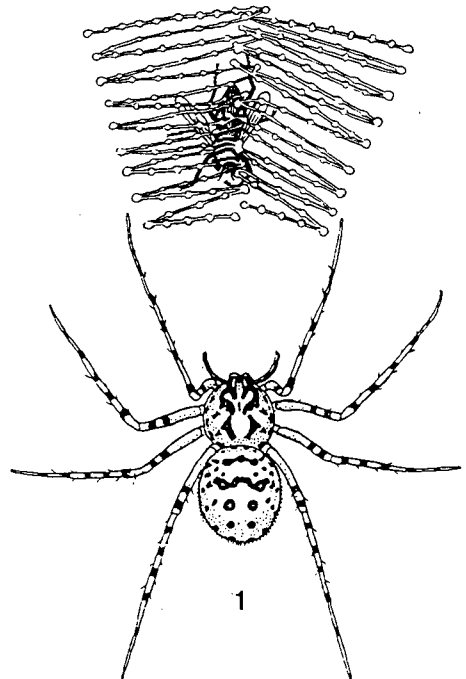
Spiders digest the substance of their prey partly outside their body. I observed a spider's prey which may be covered by remains of digestive enzyme of a spider, coll. GRABENHORST no. AR-100, and also the member of the Diptera (F1299) may be covered with digestive fluid, see below. Usually the spiders inject their digestive enzymes e.g. through the biting mark and suck them out later on through this opening, see fig. 4. Several spiders as Mimetidae (they do not spin in their prey) and most Theridiidae suck out their prey through the biting mark and so the prey may look as if not injured. Other spiders - most often large ones and hunting spiders which possess large cheliceral teeth, e.g. Araneidae, Mygalomorpha and Lycosidae - chew their prey and dissect it. - Photos 639, 676.

(c) An arthropod which is spun in in threads (figs. 1-2) - inside or outside a capture web - is usually a spider's prey. But one has to exclude the fine hyphae of fungi which may look similar to spider's threads but have numerous branches and blind ends. Both occur occasionally together. - "...web spiders do not usually feed at the capture side but carry their prey to a safer place (into a retreat or to the hub of an orb web)." (FOELIX (1996: 167). An example of such a "parcel of food" may be preserved in Baltic amber, F1299/CJW; see below and the photo.

(d) Not rarely egg sacs are masked with remains of spider's prey, e.g. fig. 6.

(e) Most difficult - and frequently unsure - is the assessment of arthropods which are more or less dissected and have no contact to a spider or its threads. The prey of hunting spiders as Corinnidae, Salticidae and Zodariidae may be strongly deformed and dissected but not spun in in threads. Besides the spiders certain beetles and ants (e.g.) are common predators of arthropods.

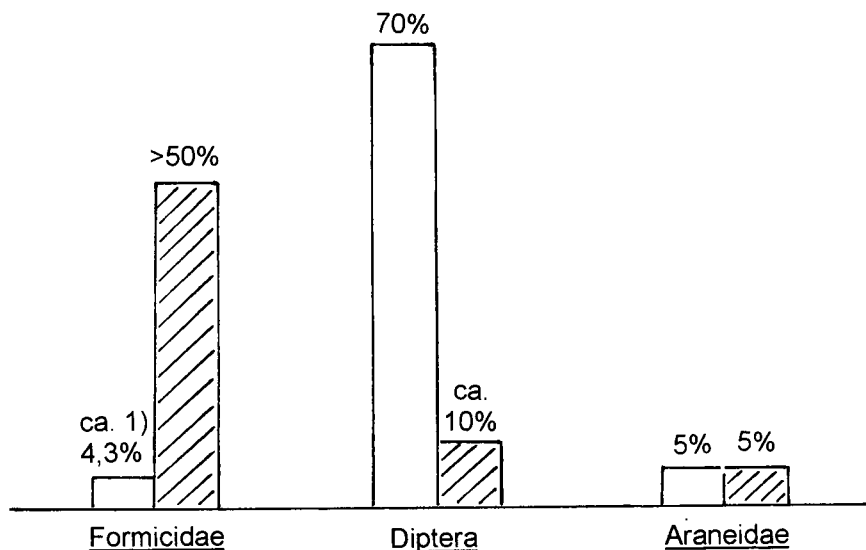
Fig. 1) An extant female of the Spitting spider (Scytodidae), *Scytodes thoracica* (LATREILLE 1802), body length about 5mm, which is distributed worldwide today, has fixed its prey (a fly) at the bottom, with the help of sticky threads which are ejected by its fangs (!). Related fossils are known from Baltic and Dominican amber. - Taken from WIEHLE (1953), after BRISTOWE (1947).- Abb.1) Eine Speispinne (Familie Speispinnen), der Gattung *Scytodes*, Körper-Länge etwa 5mm, die heute weltweit verbreitet ist, hat ihre Beute (eine Fliege) am Untergrund mit Hilfe klebriger Fäden fixiert, die aus den Giftklauen (!) geschleudert wurden. Verwandte fossile Spinnen sind vom Baltischen und Dominikanischen Bernstein bekannt.



I have seen more far than a hundred pieces with prey of fossil spiders in amber, and I have studied most of them. Some of the ants were determined by Dr. BARONI URBANI.

Observations, results and discussion. The prey spectrum, with remarks on special capture behaviour, special prey and selected predator-prey relationships:

I found Arachnida, Diplopoda and Insecta as the prey of fossil spiders in Baltic amber.



Specimens of three selected taxa of the Arthropoda in Baltic amber (left bars) and specimens of these taxa as the prey of fossil spiders (right bars)

The prey concerning the remaining orders is less than 10% each.

The frequency of Formicidae is taken from C. & H. W. HOFFEINS (unpubl.).

It is surprising that ants as the spider's prey is about ten times overrepresented compared with the specimens which are preserved in Baltic amber. Roughly the reverse is the case in specimens of the Diptera, which are preserved in Baltic amber seven times more than as the prey of spiders; so Diptera in Baltic amber as the prey of spiders are strongly underrepresented. The reason: Certain Diptera as Syrphidae are known to recognize and avoid spider's webs.

Remark: Spiders as spider's prey in this list is overrepresented because I studied relatively more spiders than prey of other orders; dealers selected more spiders for me than other arthropods.

1. Arachnida - Spinnentiere. I found members of four orders.

Araneae - Spinnen: Two *Custodella* sp. indet. (Linyphiidae) near a Mimetidae (potential prey), F1206/CJW, one Theridiidae indet. held by an Archaeidae indet., F713/CJW, two Theridiidae indet. near an Archaeidae (potential prey), e.g. F567/CJW, one *Acrometa* (Synotaxidae), one *Insecutor* sp. indet. (Insecutoridae), F645/CJW, one questionable *Eomatachia* sp. indet. (Zoropsidae), one Salticidae indet. and three Araneae indet., e.g. F1247/CJW.

Opiliones - Weberknechte: Three specimens, F1336, F1337 and F1338/CJW.

Acari - Milben: A specimen indet., F405/CJW.

Pseudoscorpiones - Pseudoskorpione: Three specimens indet..

2. Chilopoda - Hundertfüßer

A questionable Lithobiomorpha, F1317/CJW.

3. Diplopoda - Doppelfüßer

Two Polyxenidae indet. and one Diplopoda indet.

4. Insecta - Insekten

I found members of 17 orders; some are questionable. Members of the orders Lepidoptera (Schmetterlinge) and Orthoptera (Heuschrecken und Verwandte) are not so rare in Baltic amber but a sure prey of a spider is unknown to me except one larva of the Lepidoptera, F1319/CJW.

Collembola - Springschwänze: Few specimens indet., e.g. F17/CJW and F133/CJW; most specimens are questionable prey.

Thysanura - Borstenschwänze: Three specimens indet. as questionable prey, e.g. F1313/CJW.

Embioptera - Embien, Tarsenspinner: A single specimen indet., F500/CJW.

Blattaria - Schaben: A larva indet., F111/BB/AR/CJW and an adult questionable prey, F1316/CJW.

Isoptera - Termiten: Two winged specimen are attached to spider's threads, F1265, F1326/CJW, and a potential prey, F1325/CJW.

Megaloptera - Schlammfliegen: A single specimen as a potential prey, F1312/CJW.

Psocoptera - Staubläuse: A single specimen with *Segestria*.

Thysanoptera - Fransenflügler: A single specimen indet. (questionable).

Auchenorrhyncha - Zikaden: Three specimens.

Hemiptera - Wanzen: A single larva, F133.

Aphidina - Blattläuse: Five non-winged specimens - one is the prey of a juvenile Thomisidae - and a questionable prey.

Coccina - Schildläuse: Specimens were the prey of spiders indet., see KOTEJA (1998: 215).

Coleoptera - Käfer: 7 or 8 specimens, among them a larva, a member of the Curculionidae as a questionable prey, a member of the Cerambycidae with a bite mark, and the anterior wing of a beetle indet. on a masked egg sac of a spider (fig. 6).

Hymenoptera: Formicidae (ants - Ameisen) are frequent in Baltic amber: I saw more than 50 specimens, figs. 2-3, photos; two thirds of these are spun in in threads. Except two winged specimens (F142/CJW) all ants are workers.

Surprisingly more than 50% of the spider's prey in Baltic (as well as in Dominican amber) is ants. The explanation: (a) Ants are frequent in both kinds of amber, (b) ants are known as the prey of extant Theridiidae (mainly of the genera *Dipoena* and *Episinus*) and Zodariidae; Theridiidae are frequent in Baltic amber and Zodariidae are not rare, see below. Furthermore I occasionally found fossil ants as the prey of members of the family Trochanteriidae (*Sosybius*), e.g. fig. 3 and F948/CJW, and as potential prey in the web of the Segestriidae (*Segestria*); members of both families are not rare in Baltic amber. According to BRISTOWE (1941: 315) *Segestria senoculata* LATREILLE 1804 accepted ants of different genera as their prey in experiments.

Hymenoptera: Braconidae: One specimen, coll. KERNEGGER.

Trichoptera - Köcherfliegen: Four specimens, e.g. F1326/CJW.

Diptera - Zweiflügler (Mücken und Fliegen) are very frequent in Baltic amber: I found only about 20 specimens as the prey of spiders; few of them are flies. Members of the genus *Orchestina* SIMON (Oonopidae), which are frequent in Baltic amber, captured mainly Diptera, three pieces in which spider and Diptera are in contact, e.g. F196/CJW.

Insect's larvae - Insekten-Larven: Five specimens indet., e.g. 1319/CJW.

Insecta indet.: Few specimens, e.g. F1317/CJW.

Remarks on spiders which are specialised on certain prey and have a special capture behaviour:

(1) Extant Archaeidae feed usually on spiders and build no capture webs. Besides the questionable prey of a male *Archaea* sp. indet. near a male of the family Theridii-

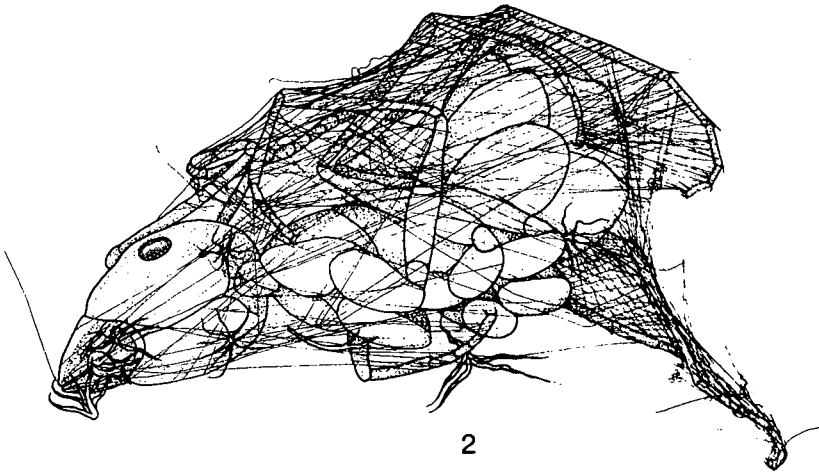


Fig. 2) A dissected fossil ant in Baltic amber which is spun in in spider's threads, its head at the left side. - Abb. 2) Eine zerlegte fossile Ameise im Baltischen Bernstein, die in Spinnfäden eingesponnen ist, links der Kopf. - Taken from WEITSCHAT & WICHARD (1998: Fig. 37).

dae indet., CJW, and a male *Archaea paradoxa* near a female of the family Theridiidae indet., F567/CJW, there is a juvenile ?*Archaea* sp. indet., F713/CJW, which holds a juv. Theridiidae as a prey in its legs, fig. 5, see below. This is the first sure report of a fossil member of the family Archaeidae preying on a spider. - Note: The fig. 51 in the book of BACHOFEN-ECHE (1949) shows a member of the genus *Archaea* with an ant near its chelicerae, but the spider is not in contact with the ant. I saw these specimens and in my opinion the combination of these arthropods is nothing else but an accident.

(2) Also most extant members of the Mimetidae feed on spiders and build no capture web. They may imitate the prey of web-building spiders as Linyphiidae and enter their web. F1206/CJW is a remarkable piece of amber - size 0.8 x 1.8 x 1.8cm - which contains two females of the genus *Custodella* sp. indet. (Linyphiidae) with a part of their capture web incl. droplets, and in contact with the web a juvenile member of the family Mimetidae, probably of the genus *Succinero* n. gen. . Web and spiders are preserved in the same layer of amber. Apparently the spiders and the web were captured in the moment in which the Mimetidae tried to capture one of the Linyphiid spiders. This is the first fossil report of a member of the family Mimetidae trying to capture a spider.

(3) Almost all members of the superfamily Araneoidea - e.g. Araneidae, Cyatholipidae, Linyphiidae, Synotaxidae, Theridiidae and Zygeliidae - use a capture web incl. sticky droplets. Most web spiders occur in higher strata of the vegetation and are therefore the most frequent specimens in amber (besides members of the genus *Orchestina* SIMON in Baltic amber which is also frequent but build no capture web). Nume-

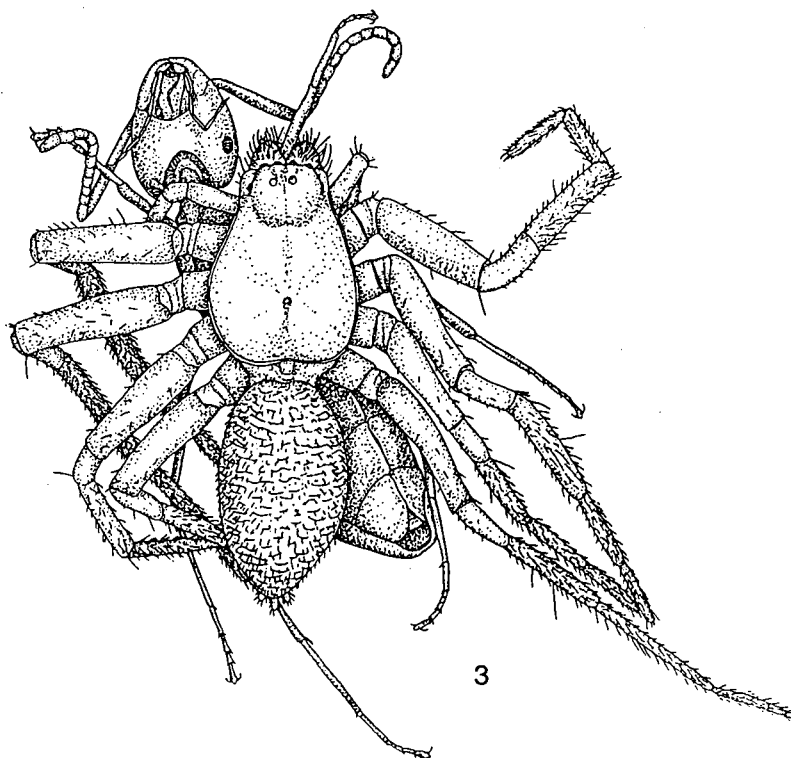


Fig. 3) A juvenile spider of *Sositybius* sp. indet. (Trochanteriidae), body length 3.7mm, erroneously published as a member of the family Dysderidae by WEITSCHAT & WICHARD (1998: Fig. 36), ventrally holding an ant indet. and biting in a leg of its prey. - Drawing by G. LIEDTKE; slightly modified: I added the outlines of the lenses of the posterior median eyes. - Abb. 3) Jungspinne der Gattung *Sositybius*, Familie Trochan-teriidae, Körper-Länge 3.7mm, im Buch von WEITSCHAT & WICHARD (1998: Abb. 36) irrtümlich als Vertreter der Familie Dysderidae publiziert, die unter sich eine unbestimmte Ameise hält und in eines der Beine ihrer Beute beißt. - Zeichnung von G. LIEDTKE; leicht verändert: Ich habe die Umrisse der Linsen der hinteren Mittelaugen hinzugefügt. Photo 630.

rous extant and fossil members of the family Theridiidae capture ants, a capture web is most often present but it may be absent, a retreat is usually present. Numerous spiders of this family use a special tangled web incl. sticky droplets at the "trap threads" to capture ants, see FOELIX (1996: Fig. 106a). Members of *Episinus* LATREILLE 1809 and several *Dipoena* THORELL 1869 build a reduced capture web, members of *Euryopis* MENGE 1868 (extant) capture ants without a web. Such an intact capture web of a fossil Theridiidae is unknown to me, but "trap threads" - with sticky droplets - in the same piece of amber with a member of the Theridiidae are frequently preserved, occasionally a Theridiid spider is kept with its prey which is usually an ant. About a dozen specimens of the family Theridiidae - most often members of the genus *Dipoena* THORELL (e.g. F657/ CJW and F1212/CJW), and *Episi-*

nus WALCKENAER 1809 - are preserved near an ant as its prey or even in contact with an ant; most are kept in my private collection, see below. Extant members of *Dipoena* are known which first bite into a leg of an ant. Numerous ants which are spun in in threads which may come from a theridiid spider are preserved in Baltic and Dominican amber. So the capture behaviour of Theridiidae - and ants as their prey - was apparently already not different from extant relatives as early as in the Early Tertiary. Most specimens of spider's prey which I studied - probably 40% - may be the prey of a Theridiid spider.

(4) Most extant members of the family Zodariidae feed on ants, to my knowledge they capture workers; a capture web is absent, a retreat is present. They may first bite near the base of the antennae (near to the brain!), wait for a while and then feed on its prey. Did Zodariidae of the Early Tertiary Baltic amber forest already hunt ants? (a) The female of Zodariidae indet. 2, F187/CJW, body length ca. 3.3mm, holds an ant in its fangs as its prey, a second ant lies below the first one, and a third ant is preserved somewhat in front of the spider; its body length is ca. 1.7mm, it is weakly dissected. All specimens are preserved in the same layer of the amber. (b) The female of a Zodariidae gen. indet. 3, coll. F. EICHMANN, body length 2.8mm, ventrally holds an ant indet., as its prey with its left legs I and II; its body length is 2mm. The ant's legs are strongly bent. Both arthropods are apparently not injured. These are the first proofs of fossil ant-hunting members of the family Zodariidae; members of this family fed on ants already in the Early Tertiary. (c) A male of *Adorator hispidus* (KOCH & BERENDT 1854), F184/CJW, body length almost 4mm, fights with two ant workers, *Liometopum goepperti* (MAYR), BARONI URBANI det., body length ca. 4mm; see the paper on the family Zodariidae in these volumes. The aggressor is unknown in this case. Extant spiders may be a common prey of ants, usually less than 5%, but in some cases up to 39%, see KIRCHNER (1990). (d) A male Zodariidae, gen. indet. 4, body length 4.2mm, is in contact with an ant of *Formica* sp. indet., body length ca. 4.6mm. A second worker ant, *Liometopum oligocenicum* WHEELER is preserved nearby. Both ants are apparently not injured and may be possible prey of the spider. (e) The male of *Anniculus balticus* PETRUNKEVITCH 1942, coll. F. EICHMANN, is preserved in front of an ant which may have been a potential prey. Photos.

(5) Most members of the family Salticidae do not build a capture web and hunt different arthropods, spiders and ants, too, so do especially their plesiomorphic taxa, and such members are present in the Baltic amber. The large eyes and strong legs in the fossils - as in the extant spiders - indicate that these spiders orientated themselves mainly in an optical way and captured their prey by jumping in the same way as the extant spiders already in the Early Tertiary. The observation of a preying fossil Salticidae is wanting; certain prey, e.g. ants, which is not covered by spider's threads, may be the prey of a member of the Salticidae. Certain Salticidae are spider eater, see FOELIX (1996: 244).

(6) A special prey capture behaviour is used by the members of the genus *Scytodes*, family Scytodidae (fig. 1), which are known from Baltic and Dominican amber. They fix their prey on the ground with the help of sticky threads which are ejected by their fangs (!). According to the domed prosoma the fossil spiders already used in the same prey capture behaviour as the extant spiders already in the Early Tertiary, but observations of this unusual behaviour in the fossils is wanting.

Einleitung

Alle Spinnen leben räuberisch und fast alle besitzen Giftdrüsen; bei den Kräuselradnetzspinnen (Uloboridae) und den Heptathelidae fehlen sie. Sie fressen überwiegend Insekten und andere Gliederfüßer. Die meisten Arten sind Generalisten, einige sind in ihrer Ernährung auf bestimmte Gruppen von Gliederfüßern spezialisiert, so sind die meisten Ameisenjäger (Zodariidae), viele Kugelspinnen (Theridiidae) wie *Diplocephala*, manche Scheibennetzspinnen (Oecobiidae) wie *Oecobius*, Ameisen-Sackspinnen (Corinnidae), Plattbauchspinnen (Gnaphosidae), Krabbenspinnen (Thomisidae: Aphantochilinae) und Springspinnen (Salticidae) auf Ameisen spezialisiert. Überraschenderweise ist etwa die Hälfte der fossilen Beutetiere der Spinnen im Bernstein Ameisen, siehe unten und das Kapitel über die Beziehungen zwischen Spinnen und Ameisen in diesem Band. Von Spinnen ernähren sich z. B. die meisten Urspinnen (Archaeidae) und Spinnenfresser-Spinnen (Mimetidae). Nach NENTWIG (1987) besteht die mögliche Beute der am Boden lebenden Spinnen überwiegend aus Springschwänzen (Collembola), Fliegen (Brachycera), Käfern, Hautflüglern (Ameisen), Spinnen und seltener Blattläusen und Zikaden. Das mögliche Beutespektrum von Spinnen, die in der Vegetation leben, besteht nach NENTWIG überwiegend aus Blattläusen, Zikaden, Mücken und Fliegen, Käfern, Spinnen und Springschwänzen. Netzspinnen in höheren Vegetations-Schichten erbeuten überwiegend Mücken, Blattläuse, Fransenflügler, Zikaden, Wespen und Käfer. Fangnetze können als selektive Filter bezeichnet werden. Nach FOELIX (1996: 241) werden Pollen sammelnde Insekten (Bienen, bestimmte Wespen, Fliegen und Käfer) selten in Raumnetzen von Kugelspinnen und Baldachinspinnen gefunden. Das Beutespektrum fossiler Spinnen im Baltischen und Dominikanischen Bernstein ist ganz andersartig.

Vertreter zahlreicher Gruppen von Gliederfüßern ernähren sich von Spinnen, z. B. einige Tausendfüßer, Käfer, Ameisen und Spinnen. Woran können wir einen fossilen Gliederfüßer als Beute einer Spinne erkennen?

(a) Ein Gliederfüßer, der von einer Spinne festgehalten wird (Abb. 3, 5), ist zweifellos ihre Beute; sofern beide nahe beisammen liegen, ist eine gründlichere Untersuchung nötig.

(b) Hängt ein Gliederfüßer im Netz einer Spinne, so ist er zumindest eine mögliche Beute. Einige Fäden eines Fangnetzes tragen - wenigstens bei den meisten Vertretern der Radnetzspinnen-Verwandten - klebrige Tröpfchen (siehe die Fotos) (Vertreter der Zitterspinnen benutzen ebenfalls Klebtröpfchen). Wir haben auf Verletzungen und Spuren von Bissen der Spinne an der Beute zu achten (Abb. 4) und ob der Gliederfüßer ausgesaugt ist. Bißspuren am Kopf wie auch an den Augen (hier ist die Kutikula dünn) eines heutigen Käfers bildet FOELIX (1996: Abb. 36a) ab. Derartige Spuren sind bei Fossilien schwer zu erkennen; ich fand lediglich sieben Stücke, z.B.: In beiden Augen einer Köcherfliege in der Slg. V. ARNOLD Nr. 1340, auf dem Hinterkörper einer Ameise (Abb. 4), an der Bauchseite einer Zikade, oben auf dem rechten Vorderflügel eines Bockkäfers und oben hinter dem Kopf einer Köcherfliege.

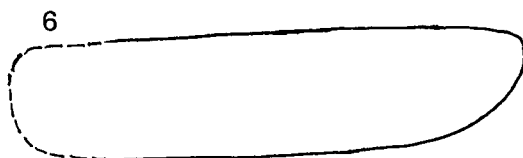
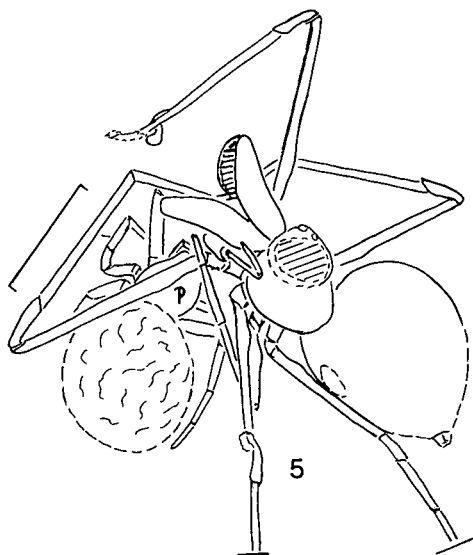
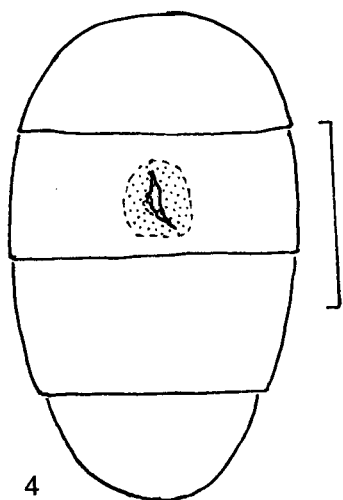


Fig. 4) Abdomen of an ant, Dolichoderinae indet. in Baltic amber, with a bite mark of the spider which captured the ant, dorsal aspect, F127/CJW, M = 0.5. - Abb.4). - Hinterkörper einer Ameise im Baltischen Bernstein von oben, mit einer Bißspur der Spinne, die die Ameise erbeutet hat. F127/CJW.

Fig. 5) ?Archaea sp. indet. (Archaedidae), ?juv. ♀, holding a ?juv. member of the family Theridiidae (at the left side) as its prey. Note the folds on the dorsal surface of the Theridiid opisthosoma. The dorsal part of the "head" of the Archaea is cut off. F713/CJW. - M = 1mm, P = prosoma of the Theridiid spider. - Abb. 5) Eine möglicherweise juvenile Spinne der Familie Urspinnen (Archaedidae), vermutlich Gattung *Archaea*, hält eine vermutlich juvenile Spinne der Familie Kugelspinnen (linke Seite) als Beute. Beachte die Falten des Hinterkörpers der Kugelspinne. Der obere Teil des "Kopfes" der Urspinne ist abgeschliffen. F713/CJW. - M = 1mm, P = Vorderkörper der Kugelspinne.

Fig. 6) Outline of a 7mm long anterior wing of a beetle, Coleoptera indet., ventral aspect, as the remains of a prey and part of a masked spider's egg sac, F. 1302/CJW. The basal part of the wing is hidden. - Abb. 6) Umriß eines 7mm langen Vorderflügels eines Käfers als Beuterest einer Spinne und Teil eines getarnten Kokons, F1302. Der basale Abschnitt des Flügels ist verdeckt.

Bißspuren an der Beute können deshalb fehlen, weil sie bei zahlreichen Radnetzspinnen und Kugelspinnen erst nach dem Einspinnen erfolgen.

Spinnen verdauen ihre Nahrung teilweise außerhalb des Körpers. Ich fand ein Beutestück, das möglicherweise mit Resten von Verdauungssaft bedeckt ist, Slg. GRABENHORST AR-100, und auch die Mückenreste (F1299) könnten mit Verdauungssaft bedeckt sein, siehe unten. Gewöhnlich injizieren Spinnen der Beute ihre Verdauungsenzyme z. B. durch die Öffnung des Giftbisses und manche saugen sie durch diese Öffnung später aus (Abb. 4). Verschiedene Spinnen wie die Spinnenfresserspinnen (Mimetidae) (sie Spinnen ihre Beute nicht ein) und die meisten Kugelspinnen (Theridiidae) saugen ihre Beute durch die Bißstelle aus, und so mag die Beute unverletzt erscheinen. Andere Spinnen - meist große und/oder frei jagende Spinnen, deren Kiefer (Cheliceren) große Zähne tragen, etwa Radnetzspinnen, Vogelspinnen und Wolfspinnen - zerkauen ihre Beutetiere und zerlegen sie auf diese Weise.

(c) Ein Gliederfüßer, der gefesselt und eingesponnen ist (Abb. 1-2), innerhalb oder außerhalb eines Fangnetzes, ist gewöhnlich die Beute einer Spinne. Allerdings muß ausgeschlossen werden, daß es sich um Pilzfäden (Hyphen) handelt, die Spinnfäden ähneln können, aber zahlreiche blinde Enden und Gabelungen besitzen. - "...Netzspinnen verzehren ihre Beute gewöhnlich nicht im Fangnetz, sondern transportieren sie zu einem sichereren Platz (zum Versteck oder zur Nabe des Radnetzes." (FOE-LIX (1996: 167)). Ein derartiges "Freßpaket" ist möglicherweise im Baltischen Bernstein erhalten, F1299/CJW, siehe unten und das Foto.

(d) Kokons von Spinnen sind gelegentlich mit Beuteresten getarnt, siehe Abb. 6.

(e) Höchst schwierig und oft unsicher ist die Beurteilung fossiler Gliederfüßer, die mehr oder weniger stark zerlegt sind, aber keinen Kontakt zu einer Spinne oder einem Netzteil besitzen. Die Beutetiere etwa von Ameisen-Sackspinnen, Ameisenjägern und Springspinnen können stark deformiert und zerlegt sein, ohne daß sie eingesponnen sind. Neben Spinnen sind z. B. manche Käfer und Ameisen häufige Freßfeinde von Gliederfüßern.

Ich habe weit mehr als einhundert Stücke mit Beutetieren fossiler Spinnen und die meisten von ihnen näher untersucht. Einige Ameisen hat Dr. BARONI URBANI bestimmt.

In the following I describe the pieces which contain prey of fossil spiders:

Compare the photos 621-685.

Remark: A probable spider's prey is an arthropod which is hanging in few spider's threads but is apparently not injured, and probably no spider had the opportunity to feed on this specimen. A potential spider's prey is an arthropod which is dissected, but not covered with spider's threads nor hanging in a spider's web. This arthropod may be, e.g., the prey of a beetle, even in the case that it is preserved in the same piece of amber as a spider.

(1) Inclusions in Dominican amber:

A dozen pieces of prey are present (only about 1/10 of the specimens in Baltic amber), five ants, among them four which are covered by spider's threads and two are combined with a member of their predator, a Theridiid spider. The remaining prey consists of an Isoptera, a Diptera, a Psocoptera, a larva of the Auchenorrhyncha, an insect indet., and two spiders, one of them is a member of the family Pholcidae.

F1198/DB/AR/CJW: A dissected and incomplete member of the Psocoptera, body length less than 2mm, spun in and hanging in the part of a capture web which has droplets.

F1199/DB/AR/THE/CJW: *Dipoena* sp. indet. (Araneae: Theridiidae), body length 2mm, with its fairly dissected prey, an ant, Pheidole sp. indet. (Myrmecinae), det. BARONI URBANI, which is spun in in spider's threads; see WUNDERLICH (1986: Fig. 29).

F1200/DB/AR/CJW: Two dissected pieces of spider's prey which are spun in in spider's threads: (a) the larva of an Auchenorrhyncha, body length 3mm, and (b) remains of a member of the spider family Pholcidae.

F1201/DB/AR/CJW: Two partly dissected ants indet., body length ca. 1.8mm, are spun in and hanging in a spider's web without droplets. Another thread nearby possesses droplets.

F1264/DB/AR/CJW: An ant, Dolichoderinae indet., BARONI URBANI det., body length ca. 1.2mm, dissected (the abdomen is loose), is kept in a spider's web incl. droplets, which probably originates from a member of the family Theridiidae.

F1265/DB/AR/CJW: A winged and partly dissected termite, body length 3mm, is kept in the part of a spider's capture web which has droplets, and which probably originates from a member of the Araneidae.

F1266/DB/AR/CJW: A juvenile member of the spider family Theridiidae, body length 1.4mm, with its possible prey, which is located directly in front of the spider, a tiny Diptera: Nematocera, body length 1mm. The body of the midge is dissected, its abdomen is almost empty.

F1267/DB/AR/CJW: Remains of an insect indet. (or few insects), diameter 2mm, as a potential prey of a spider. Threads are absent.

F1275/DB/AR/CJW: Remains of a strongly dissected spider indet. in a spider's web; its length is 2mm.

F1286/DB/AR/CJW: A dissected ant indet., body length ca. 1.5mm, has probably been the prey of a spider; spider's threads are absent. The dissection of the ant may be the result of decomposition.

(2) Inclusions in Baltic amber

I found the prey of 19 families: Anapidae, Araneidae, Archaeidae, ?Clubionidae, Corinnidae, ?Linyphiidae, Liocranidae, Mimetidae, Oonopidae, ?Philodromidae, Segestriidae, Synotaxidae, Tetragnathidae, Theridiidae, Theridiosomatidae, Thomisidae, Trochanteriidae, Zodariidae, ?Zygiellidae.

The list starts with material from museums and private collections:

Coll. V. ARNOLD, no. 1340: A dissected and incomplete Trichoptera (the addomen is missing) is partly in contact with spider's threads without droplets. Its length incl. wings is 4.3mm. Small holes in both eyes are most probably bite marks through which the spider probably sucked out its prey.

Coll. F. EICHMANN: A male spider, *Anniculus balticus* PETRUNKEVITCH 1942 (Zodariidae), body length ca. 5mm, is preserved in front of an ant indet., body length probably 3mm, from which the left half is cut off. The ant may have been a potential prey of the spider.

Coll. F. EICHMANN: A female of the family Zodariidae, gen. indet. 3, body length 2.8 mm, is holding ventrally at the left side an ant indet., body length 2mm, as its prey in its left legs I and II. The ant's legs are strongly bent. Both arthropods are seemingly not injured.

Coll. F. EICHMANN: A juvenile member of the superfamily Clubionoidea indet., body length 3mm, is holding ventrally with its legs a fly as its prey, body length ca. 2.5mm; the fly is slightly deformed.

Coll. GRABENHORST, no. AR-100: In contact to the left leg I of a possible member of the genus *Episinus* WALCKENAER 1809 (Araneae: Theridiidae), a subad. ♂, body length 2.3mm, an ant indet., body length 2.7mm, is lying. Apparently the ant is covered by a spider's digestive fluid, and the spider was disturbed before it was able to feed on its prey. Threads on the prey are not observable. Bitterfeld deposit.

Coll. GRABENHORST, no. AR-104: A male of the genus *Orchestina* SIMON (Oonopidae), body length 1.1mm, is preserved with its prey, a Diptera: Nematocera, body length 1.3mm, which is apparently sucked out. Bitterfeld deposit.

Coll. F. KERNEGGER, no. 326/1994: A Hymenoptera: Braconidae, body length 1.6 mm, is included in a probably sticky droplet, which is attached to spiders threads. I consider this specimen as a potential prey of a spider.

Coll. J. KOTEJA: Coccinea as prey of spiders, see KOTEJA (1998: 215).

Coll. LIEDKE, no. 418 (fig. 3): A juvenile member of the genus *Sosybius* PETRUNKEVITCH 1942 (Araneae: Trochanteriidae), body length 4mm, is preserved with its prey below, an ant indet., body length 5mm. The ventral part of the ant is in contact

to the ventral opisthosomal part of the spider. The left leg I of the ant is held by a fang of the spider. The ventral part of the spider and the dorsal part of the ant are covered by a white emulsion.

Coll. Mus. Naturkunde in Magdeburg, no. 5471: An ant which is spun in in spider's threads is preserved in a distance of 4mm near a member of the genus *Episinus* WALCKENAER 1829 (Theridiidae).

MNHN Paris, no. 463: A female of *Segestria ?tomentosa* KOCH & BERENDT 1854 (Araneae: Segestriidae), body length 7.8mm with a small crumpled ant indet., body length ca. 3mm, as its prey, which is preserved directly beneath the mouth parts of the spider.

Coll. VAHLIDIEK, no 4960 in 29693 Böhme: A fly is captured in a spider's web with droplets.

Mus. Ziemi, no. 8835: Two ants indet., body length ca. 2mm, are partly dissected and weakly covered by spider's threads. They are in ventral contact of a female spider, probably of the family Theridiidae, body length 1.1mm, which was apparently the predator of the ants.

F15/BB/AR/LIN/CJW: A Collembola was the potential prey of a female of the genus *Succinea* n. gen. (Araneae: Linyphiidae) in the same piece of amber.

F17/BB/AR/LIN/CJW: A Collembola, body length 0.5mm, and a Diptera, body length 1mm, are the prey of a male of the genus *Custodea* PETRUNKEVITCH 1942 (Linyphiidae), body length 2mm, in a web with droplets.

F102/BB/AR/CJW: A member of the Araneae: Zodariidae gen. indet. 4, body length 4.2mm, is in contact with an ant worker of *Formica* sp. indet., body length ca. 4.6mm. A second worker ant, *Liometopum ?oligocenicum* WHEELER, is preserved nearby. Both ants are apparently not injured and may have been the potential prey of the Zodariid spider (most Zodariidae are ant-hunters).

F106/BB/AR/CJW: A beetle (Coleoptera: Cerambycidae), body length 10.5mm, is spun in in spider's threads. An almost circular hole in its right anterior wing is probably the bite mark of a spider. Hyphae cover parts of the beetle, and about 20 phoretic mites are present on the beetle's body.

F111/BB/AR/CJW: A no-dissected larva of the Blattaria, body length 2.2mm, weakly spun in inspider's threadns, is held by a female spider of the genus *Acrometa* PETRUNKEVITCH 1942 (Synotaxidae), body length 1.75mm by its anterior tarsi. Some indistinct spider's threads without droplets are present. So apparently the Blattaria was captured in the web of *Acrometa*, but was probably not sucked out. A bite mark of the spider, size 0.03 x 0.05mm - is present dorsally on the second abdominal segment of the Blattaria.

F127/BB/AR/?LIO/CJW: A male member of the superfamily Clubionoidea (Araneae: Liocranidae), body length 4mm, is holding an ant ventrally, Formicidae: Dolichoderinae, BARONI URBANI det., body length 3mm, which was captured by the spider. Both arthropods are ventrally covered by a white emulsion. The left leg III of the spi-

der is autotomized and is lying beneath the spider's opisthosoma. The dorsal side of the ant has a depression and a bite mark, which is 0.2mm long fig. 4.

F133/BB/AR/CJW: The prey of a female of *Acrometa* sp. indet. (Araneae: Synotaxidae), a partly dissected Collembola, is hanging at a spider's thread, a partly dissected bug larva is located at the margin of an egg sac, a beetle: Curculionidae is hanging at a thread and has probably been a prey of the spider; it is not dissected.

F135/BB/AR/CJW: A strongly dissected juvenile female spider, probably a member of the genus *Eomatachia* PETRUNKEVITCH 1942 (Zoropsidae), body length probably more than 4mm, is preserved in a web of a spider. This spider was the prey of a spider. Also preserved are two spider's exuviae.

F141/BB/AR/CJW: A larger part of an orb web which is partly oxidated, with two Diptera hanging in it; the Diptera is ca. 1mm long and is not dissected.

F142/BB/AR/CJW: In a large part of a tube-shaped web, 3cm long, probably originating from a Segetriid spider, the dissected remains of a winged ant indet., body length 3mm, are preserved; it is weakly spun in in spider's threads.

F143/BB/AR/CJW: Remains of 1 1/2 ants indet., body length ca. 3.5mm, are spun in in spider's threads and are partly covered by a white emulsion. The larger ant is hanging in a 4cm long part of an irregular spider's web without droplets.

F145/BB/AR/CJW: A member of the Aphidina indet., body length 1mm, is preserved in contact with a three-lined spider's thread which is bearing numerous stellate hairs. The Aphidina is not dissected, so it was probably not the prey of a spider.

F146/BB/AR/CJW: On a ca. 2 1/2cm long spider's thread an ant indet., body length 1.5mm, is hanging in contact to the thread with its abdomen. The ant is not dissected and was probably not the prey of a spider.

F155/BB/AR/CJW: A non-dissected ant indet., body length 3.2mm, is weakly spun in in spider's threads. Close to the ant a juvenile possible member of the spider genus Sosybius PETRUNKEVITCH 1942 (Trochanteriidae), body length 1.9mm, is preserved, and its (?) exuvia below the spider. The large ant was probably not the prey of the small spider.

F156/BB/AR/THE/CJW: A non-dissected ant indet., body length ca. 1.5mm, is weakly covered by spider's threads. Most probably it was captured by a female Theridiid spider indet., body length ca. 2.3mm, which is preserved 3mm away from the ant. The spider's exuvia is also present in the piece of amber.

F184/BB/AR/CJW: A male of *Adorator hispidus* (KOCH & BERENDT 1854) (Araneae: Zodariidae), body length almost 4mm, is fighting with two ants, *Liometopus goepperti* (MAYR), BARONI URBANI det., body length ca. 4mm. See the paper on the family Zodariidae in these volumes.

F187/BB/AR/CJW: A female of the Araneae: Zodariidae gen. indet. 2, body length ca. 3.3mm, is holding an ant in its fangs, a second ant is lying below the first ant, and a third ant is preserved somewhat in front of the spider and is partly dissected. All spe-

cimens are preserved in the same layer of the amber. See the paper on the family Zodariidae in these volumes.

F196/BB/AR/OON/CJW: An indet. female of the spider genus *Orchestina* (Oonopidae), body length 1.4mm, is holding a fly in its legs, body length 2mm. The fly is not dis-sected and not spun in in threads. Both arthropods are completely and well preserved.

F375/BB/AR/CJW: A Diptera: Nematocera, body length 1.6mm, probably not injured, is hanging on a spider's web as a potential prey of a spider.

F377/BB/AR/CJW: A Diptera: Nematocera indet., body length 1.4mm, is hanging in an irregular spider's web without droplets. The midge is not injured, and its abdomen is swollen, so it was not sucked out, and is regarded only as a potential prey of a spider.

F383/BB/AR/TRO/CJW: A dissected Diptera: Nematocera indet., body length 0.8mm, was probably the prey of a spider. In the distance of 1.2cm a juvenile spider is preserved in the same layer of the amber, body length 2.2mm, a questionable member of the genus *Sosybius* PETRUNKEVITCH 1942 (Trochanteriidae), which probably was the predator of the midge.

F405/BB/AR/CJW: A probably not injured mite indet., body length 0.35mm, is spun in in spider's threads, and is hanging in a capture web with tiny droplets closely in front of a male of *Eoepeirotypus* sp. indet., body length 1.2mm. I consider the mite as a probable prey of the spider.

F456/BB/DIP/CJW: A member of the Diptera: Culicidae, body length less than 4mm, is in contact with a single spider's thread. The head and the abdomen have shrunk. The insect was probably not the prey of a spider, and the contact to a thread may be an accident. An autotomized leg of the biting midge is preserved behind/beneath its body.

F465/BB/AR/CJW: A male spider of the genus *Insecutor* PETRUNKEVITCH (Insecutoridae) is spun in in spider's threads and was the prey of a spider; its prosoma and legs are dissected, the opisthosoma is lost.

F479/BB/AR/CJW: A partly dissected ant, body length almost 2.5mm, is weakly covered by spider's threads. The ant is not hanging in a web, its abdomen has broken off.

F500/BB/EM/CJW: A distinctly deformed member of the Embioptera, indet., body length ca. 9mm, is spun in in spider's threads and was probably sucked out by a spider. 1.25cm away from the Embioptera a small part of a spider's thread incl. a droplet is preserved on remains of plants.

F657/BB/AR/THE/CJW: The anterior part of a female *Dipoena* sp. indet. (Araneae: Theridiidae), body length 1.15mm, is in contact with a dissected ant, body length ca. 2mm, which is weakly spun in in spider's threads without droplets.

F567/BB/AR/CJW: A female member of the spider family Theridiidae indet. is a questionable prey of a male of *Archaea paradoxa* KOCH & BERENDT 1854.

F658/BB/AR/SAL/CJW: A male spider of the family Salticidae, prosomal length 1.5 mm, has been the prey of a spider; it is spun in in several spider's threads which are lacking droplets. The prosoma is complete, but only shrunken remains of the opisthosoma are present.

F690/BB/AR/OON/CJW: A male spider of the genus *Orchestina* SIMON (Oonopidae), body length 1.2mm, is holding a Diptera: Nematocera indet., body length 1.2mm, and is probably biting into a leg of its prey. The midge has apparently been sucked out, the abdomen is ventrally strongly depressed. The piece of amber was heated.

F691/BB/AR/CJW: A polyxenidae-shaped beetle larva indet. is preserved on a spider's web without droplets. Syninclusions in the web are stellate hairs, detritus and insect's excrement particles.

F709/BB/AR/CJW: A dissected ant indet., body length 3mm, is spun in in spider's threads. Nearby a part of a spider's web without droplets is preserved.

F713/BB/AR/ARC/CJW: A juvenile questionable member of the spider genus *Archaea* KOCH & BERENDT 1854 (Archaeidae), body length 2.5mm (the caput is partly cut off), is holding directly left of its body a juvenile spider which may be a member of the family Theridiidae, body length 1.8mm (fig. 5). Both spiders are only fairly well preserved and partly covered by a white emulsion; the opisthosoma of the Theridiidae, which most probably was a prey of the *Archaea*, is distinctly shrunken; its right metatarsus and tarsus I are injured, broken and shortened.

F765/BB/AR/THO/CJW: An Aphidina indet., without wings and not dissected, body length 0.85mm, is preserved below the sternum and the mouth parts in contact to a juvenile spider of the family Thomisidae indet., body length ca. 1.3mm. Most probably the Aphidina was captured by the spider.

F883/BB/AR/CJW: A dissected member of the Diptera: Nematocera, body length 2mm is not spun in in threads and may have been the prey of a spider (Salticidae?).

F948/BB/AR/TRO/CJW: A member of the spider genus *Sosybius* PETRUNKEVITCH (Trochanteriidae), body length 2.1mm, is in contact with an ant as its prey, body length ca. 2.5mm; one of the ant's legs is held by the spider's chelicerae.

F1108/BB/AR/CJW: A member of the Formicidae indet., body length 3mm, is spun in in spider's threads. The ant is partly dissected, the head is partly broken off; the specimen was most probably sucked out by a spider which may have been a member of the family Theridiidae.

F1146/BB/AR/CJW: A dissected ant indet., body length 4.7mm, is spun in in spider's threads.

F1202/BB/AR/CJW: A member of the beetle family Curculionidae, body length 3.5 mm, was captured in a spider's web; its body is covered by a white emulsion and not dissected.

F1203/BB/AR/CJW: A member of the Diptera: Nematocera, body length almost 1.5 mm, is held by some spider's threads. It is not injured and so it was probably not the prey of a spider.

F1204/BB/AR/CJW: A dissected ant, Lasius sp., K. DUMPERT det., body length 2.3 mm, is spun in in spider's threads, and is hanging in a spider's web without droplets; see WUNDERLICH (1986: Fig. 28).

F1204a/BB/AR/CJW: Remains of a dissected member of the Pseudoscorpiones indet., body length ca. 2mm, are hanging on a thick spider's thread. Apparently the pseudoscorpion was the prey of a spider.

F1205/BB/AUC/CJW: A member of the Auchenorrhyncha, body length 7mm, is spun in in spider's threads, a prey of a spider. The specimen is well and completely preserved, and dorsally weakly covered by a white emulsion. Ventrally, between the 2. and 3. pairs of legs are circular holes, which may be bite marks.

F1208/BB/AR/CJW: In a large irregular spider's web without droplets a dissected ant indet., body length ca. 1.5mm, is hanging, and nearby a dissected pseudoscorpion indet., body length ca. 1mm. The ant is spun in in spider's threads. Furthermore the remains of a Polyxenus sp. indet. (Diplopoda), 0.8mm long, is hanging in a spider's thraed as a spider's prey.

F1209/BB/AR/CJW: Four non-winged Aphidina, body length 1.2-4.5.mm, and two beetle's larvae (Dermestidae?), body length 1.1 and 2mm, as well as an ant are hanging in an irregular spider's capture web. The ant and the beetles' larvae are not dissected.

F1210/BB/AR/CJW: An insect larva, cover of a puparium, body length 4mm, is hanging in an irregular spider's web without droplets. This was not the prey of a spider because the puparium is empty and the larva is missing.

F1211/BB/AR/CJW: Strongly dissected remains of a spider indet., prosomal length 1.8mm, are spun in in some spider's threads. The spider is only fairly well preserved and partly covered by a white emulsion. A second spider indet., a male, body length 3.3mm, is preserved directly behind the first spider, and was probably its predator.

F1212/BB/AR/THE/CJW: A female spider of the genus Dipoena THORELL (Theridiidae), body length 1.5mm, is holding an ant indet. with its legs, body length 1.5mm, as its prey. The ant is not dissected and spun in with few spider's threads. The piece of amber was heated.

F1213/BB/AR/CJW: A 4mm long part of the Diplopoda indet. is hanging in some strong spider's threads. The Diplopoda was probably the prey of a spider; according to the thick threads the predator may have been a member of the family Segestriidae.

F1215/BB/AR/CJW: A member of the Thysanura, body length 3mm, is preserved on some spider's threads without droplets as a probable prey of a spider.

F1246/BB/AR/ANA/CJW: The female of the spider family Anapidae (Anapinae), body length 1mm, is holding a prey ventrally, probably an insect's larva, which is not dissected, and is at least 1mm long. The spider has probably bitten in the anterior-ventral part of the larva.

F1247/BB/AR/CJW: A member of the Araneae indet., body length 3.3mm, is dissected and densely spun in in a spider's web without droplets as the prey of a spider.

F1253/BB/AR/CJW: The right half of a female of the spider family Theridiidae (the left half is cut off), body length probably 2.2mm, is preserved together with dissected remains of at least two ants indet., body length ca. 2mm. Although the ants are not covered with threads they may be the prey of the spider. There are numerous syninclusions.

F1257/BB/AR/CJW: A dissected and probably juvenile female of the Araneae indet., whose opisthosoma is missing, prosomal length 1.5mm, is spun in in some spider's threads, and was the prey of a spider.

F1262/BB/AR/OON/CJW: A Diptera: Nematocera, body length 1.3mm, which has probably been sucked out as the prey of a female spider, *Orchestina* sp. indet. (Oonopidae), body length 1.3mm. Both arthropods are separated by 0.7mm.

F1263/BB/AR/CJW: Four ants, Dolichoderinae and questionable Formicinae, BARONI URBANI det., body length 2-3mm, are partly dissected but not covered with threads, and were probably the prey of a member of the family Zodariidae. A juvenile of the spider family Mimetidae indet. is preserved in the same piece of amber.

F1265/BB/AR/CJW: A winged termite is spun in in spider's threads with droplets. The predator was probably a member of the Araneidae, Tetragnathidae or Zygellidae.

F1268/BB/AR/CJW: A non-dissected and indet. ant, body length 2mm, weakly spun in in spider's threads, was the prey of a spider. In the same piece of amber a beetle is preserved which was not a prey of a spider.

F1269/BB/AR/CJW: Two ants, Dolichoderinae indet., body length ca. 4mm, which are weakly spun in in spider's threads, were the prey of a spider. One of the ant is dissected and its abdomen is partly cut off.

F1270/BB/AR/CJW: An ant indet., body length ca. 4mm, which is spun in in spider's threads, dissected and partly covered by a white emulsion, is preserved together with some threads of a spider's web.

F1271/BB/AR/CJW: Remains of a dissected ant indet., diameter 1mm, is spun in in spider's threads; it was probably the prey of a member of the ant-eating family Zodariidae. Furthermore are preserved: A non-dissected ant, a juvenile member of the spider family Linyphiidae indet., spider's threads, an Acari, an Collembola, a stamen, numerous particles of insect's excrement and detritus as well as stellate hairs.

F1272/BB/AR/CJW: Remains of a dissected and clumped ant indet., diameter 1.2mm is weakly spun in in spider's threads as a spider's prey.

F1273/BB/AR/CJW: A dissected ant, probably of the subfamily Dolichodinae, BARONI URBANI det., body length ca. 3.3mm, is weakly spun in in spider's threads.

F1274/BB/AR/SYN/CJW: A male of *Acrometa* sp. indet., Araneae: Synotaxidae, body length ca. 2.4mm, is injured and weakly spun in in spider's threads; the petiolus is torn off from the prosoma, only remains of the shrunken opisthosoma are present. This spider was probably the prey of a member of the spider family Salticidae.

F1277/BB/AR/CJW: A dissected ant indet., body length ca. 2mm, is spun in in spider's threads and is captured in a larger part of an irregular web without droplets.

F1278/BB/AR/CJW: Two dissected ants indet. are not covered with threads, one is well preserved and 2.8mm long. Both may be the prey of a member of the ant-eating spider family Zodariidae. In the same piece of amber an egg sac is preserved.

F1279/BB/AR/CJW: In a large part of an irregular spider's web with tiny droplets three not dissected Diptera are hanging which I consider the potential prey of a spider. A strongly dissected arthropod is preserved outside the spider's web; it is 0.5mm long and may be the prey of a spider.

F1280/BB/AR/CJW: A member of the Auchenorrhyncha, body length ca. 9mm, is spun in in spider's threads. The cicada is not dissected.

F1281/BB/AR/CJW: A strongly dissected ant indet., body length ca. 3.1mm, is weakly spun in in spider's threads.

F1282/BB/AR/CJW: An ant indet., body length about 3.5mm is not dissected, spun in in spider's threads, and is hanging in a spider's web without droplets.

F1283/BB/AR/CJW: Two ants, *Liometopum ?oligocenicum* WHEELER, det. BARONI URBANI, body length ca. 2.2mm, are well preserved closely together. They are covered by spider's threads and only weakly dissected.

F1284/BB/AR/CJW: Remains of a Diptera indet., body length ca. 1.5mm, is hanging in a spider's web without droplets.

F1285/BB/AR/?PHI/CJW: A questionable male member of the spider family Philodromidae indet., body length ca. 4.3mm, has captured a small Diptera: Nematocera, body length 1.5mm, which is held by the spider's legs under its sternum.

F1287/BB/AR/CJW: A pincer of a pseudoscorpion indet. ca. 1.5mm long, is captured in a part of a spider's web.

F1288/BB/?AR/CJW: A strongly dissected ant indet., body length originally probably 4mm, was probably the prey of a spider. Spider's threads are absent.

F1289/BB/AR/CJW: A non-dissected ant, Dolichoderinae, body length 3mm, not spun in in spider's threads, is hanging in a spider's web in which few droplets are present. I consider the ant a potential prey.

F1290/BB/?AR/CJW: A strongly dissected ant indet., body length ca. 4mm, was probably the prey of a spider; threads are absent.

F1291/BB/AR/CJW: Two strongly dissected insects, probably ants, 2mm long, are spun in in spider's threads. 1.1cm away from these insects an ?adult spider is preserved, body length 1.2mm, which is probably a member of the family Theridiidae. Another spider, family indet., body length 3.5mm, a subad. male, is preserved 6mm away from the prey. The spiders and the prey are preserved in different layers of the amber.

F1292/BB/AR/CJW: A non-dissected ant indet., body length 2.8mm, is spun in in spiders threads without droplets; it was surely the prey of a spider.

F1294/BB/AR/CJW: A non-dissected ant, Formicinae indet., body length 2.5mm, a Diptera: Nematocera, body length 2.1mm and remains of a tiny Acari are hanging in a part of a spider's web without droplets. I consider these arthropods the potential prey of a spider.

F1295/BB/AR/CJW: Prey of a spider which is only slightly dissected and spun in in spider's threads: (a) A member of the Auchenorrhyncha indet., body length 6.7mm, (b) an ant of the genus *Geomyrmex* (Formicinae), body length 2.6mm. Both insects are well preserved.

F1296/BB/AR/CJW: A completely dissected ant, probably Dolichoderinae, BARONI URBANI det., body length ca. 2.5mm, is preserved on the sheet of a spider's web and spun in. Bitterfeld deposit.

F1297/BB/AR/CJW: A slightly dissected Trichoptera indet., body length 4mm, is preserved as the prey of a spider in contact to spider's threads, but is not spun in. There is a white injury behind the head, probably remains of a bite mark.

F1298/BB/AR/THS/CJW: A subadult male of the spider family Theridiosomatidae indet., body length 1.8mm, is preserved in a distance of 2mm from an ant indet., body length 1.3mm, which is weakly dissected and is not spun in in spider's threads. The ant was probably the prey of a spider. The amber piece was heated.

F1299/BB/?AR/CJW: A lump of legs and wings, most probably from a Diptera, weakly spun in in spider's threads, size 3 x 4.5mm, is probably covered with digestive fluid of a spider. One side is showing a heated surface. This may be a "parcel of food" of a member of the spider family Zygellidae. Members of several groups of spiders transport their prey to a safer place before they feed on it. The prey was probably not sucked out and is not so strongly destroyed as I would expect after it has been chewed by a predator for a longer time.

F1300/BB/AR/?SEG/CJW: A strongly dissected questionable Diptera indet., is held below a spider of the questionable genus *Segestria* LATREILLE 1804 (Segestriidae), body length ca. 6mm.

F1301/BB/AR/CJW: A weakly dissected ant indet., body length 3mm, is weakly spun in in spider's threads; its abdomen is loose.

F1302/BB/AR/CJW: The wing of a beetle (fig. 6), 7mm long, apparently the remains of a spider's prey, is preserved as part of the mask of an egg sac, which is hanging in a spider's capture web with droplets. The web may originate from a member of the spider families Araneidae or Zygellidae; the large beetle - body length more than 10mm - indicates a large predator, probably a member of the genus *Eustaloides* PETRUNKEVITCH (Zygellidae), which is not rare in Baltic amber.

F1304/BB/AR/CJW: A weakly dissected ant indet., body length 2.5mm, is preserved in an irregular spider's web without droplets as a spider's prey.

F1305/BB/AR/CJW: A dissected ant indet., body length ca. 2mm, and a questionable Thysanoptera, body length 1mm, are hanging in a spider's web without droplets. The ant's abdomen is preserved 7mm away from its remaining parts.

F1306/BB/AR/CJW: An apparently not dissected ant indet., *Formica ?flori* MAYR, BARONI URBANI det., body length ca. 4.5mm, is spun in in spider's threads, and is hanging in a web without droplets. The amber piece was heated.

F1307/BB/AR/CJW: A strongly dissected ant indet., body length ca 1.5mm, is hanging in a spider's web with enlarged droplets near the part of a larger leg of a beetle.

F1308/BB/AR/CJW: A strongly dissected midge, Diptera: Nematocera: Mycetophilidae, det. HOFFEINS, body length 3.7mm, is weakly spun in in spider's threads, and was the prey of a spider.

F1310/BB/AR/CJW: A female Araneae indet., body length 6.3mm, dissected (the opisthosoma is missing) and spun in in spider's threads without droplets, was the prey of a spider.

F1311/BB/AR/CJW: A Coleoptera: Elateridae, body length 5.7m, and a Diptera: Brachycera, body length 1.3mm, are attached to spider's threads without droplets. Both arthropods are not dissected and are the potential prey of a spider.

F1312/BB/AR/CJW: A member of the Megaloptera indet., body length 5.2mm, not dissected, is attached to spider's threads without droplets as a potential prey of a spider.

F1313/BB/AR/CJW: Part of a capture web without droplets incl. a masked egg sac, with (a) an ant indet., body length 3.6mm, dissected and most probably sucked out, which is located next to spider's threads as a spider's prey, (b) dissected remains of a Coleoptera indet., an anterior wing is 1.2mm long, and (c) a non-dissected Thysanura is attached to spider's threads as a potential prey of a spider.

F1314/BB/AR/CJW: An anterior leg of a beetle indet., 3.6mm long, is hanging in a spider's web without droplets. The beetle was probably the prey of a spider.

F1315/BB/AR/CJW: Remains of a beetle, part of a leg and an anterior wing which is incomplete and 3mm long, are hanging in a spider's capture web without droplets.

F1316/BB/AR/CJW: A member of the Blattaria indet., body length 8mm; the head and the right leg I are attached to spider's threads without droplets. The potential prey has apparently not been sucked out.

F1317/BB/AR/CJW: Remains of an almost globular Myriapoda: Lithobiomorpha, diameter 2.7mm, spun in in spider's threads as a spider's prey, is hanging in a spider's web. It is partly covered by a white emulsion as well as questionable hyphae or bacteria, which probably decompose the prey; such questionable hyphae or bacteria (or remains of cribellar threads?) are also present on some of the spider's threads; they build numerous tiny "capitulae".

F1318/BB/AR/CJW: An ant indet., body length 4mm, is preserved in a spider's web without droplets. The ant is partly dissected, weakly spun in in spider's threads, and was the prey of a spider.

F1319/BB/AR/CJW: The case of an insect larva indet., probably of the family Psychidae (Lepidoptera), size 2.5 x 0.9mm, is hanging in a spiders web without droplets. Remains of the larva are not observable. An oval opening in the middle of the case (photo) has the largest length of 0.16mm; I consider this as a bite mark of a spider. The surface of the case consists of particles of detritus and is weakly spun in in spider's threads. The case was doubtless captured in the spider's web, and the bite mark results most probably from a spider, the owner of the web, but it is unknown that in fact the spider ate the larva. This is the first fossil report of such kind of a potential prey of a spider. BRISTOWE (1942: 286) reports caterpillars as rare prey of extant spiders, but an insect's larva in its quiver (case) as a (potential) prey of a spider has been unknown to me.

F1325/BB/AR/CJW: A winged termite, body length 5.5mm, is preserved near a spider's web without droplets as a potential prey of a spider.

F1326/BB/AR/CJW: A dissected Trichoptera, body length at least 2mm, and a non-dissected winged termite, body length 5mm, are attached to spider's threads. I consider the Trichoptera a prey of a spider and the termite a potential prey.

F1336/BB/AR/CJW: A strongly dissected member of the Opiliones indet., body length 1.5mm, is preserved with few spider's threads, and a Diptera: Nematocera, body length ca. 1.2mm, which is also strongly dissected. Both are the prey of a spider. A larger part of a spider's web is absent.

F1337/BB/AR/CJW: A strongly dissected Opiliones indet., body length ca. 1.6mm, weakly covered by spider's threads with droplets, was the prey of a spider.

F1338/BB/AR/CJW: A non-dissected Opiliones: Nemastomatidae, body length ca. 1.7 mm, is held by few spider's threads without droplets as a potential prey of a spider.

F1339/BB/AR/TET/CJW: A female of Corneometa sp. indet. (Araneae: Tetragnathidae), body length 6.2mm, is holding a female ?juv. spider of the family Theridiidae indet., body length ca. 2mm, with parts of the Theridiid web within her anterior legs. A beetle indet., body length 2mm, is preserved between the patellae I and dorsally

possesses a probable bite mark, which has a size of 0.05 x 0.12mm. I consider the beetle and the Theridiid spider a potential prey of the Tetragnathid spider.

F1340/BB/AR/CJW: A member of the Formicidae: Formicidae, *Camponotus* sp. indet., BARONI URBANI det., body length 3.6mm, is only slightly dissected, the left antenna is broken off at its base and is fettered by spider's threads without droplets.

F1346/BB/AR/CJW: A strongly dissected ant indet., body length ca. 3mm, has probably been the prey of a spider; it is weakly spun in in spider's threads. The opisthosoma and some leg articles are loose. A questionable and probably decomposing Nematoda indet., body length at least 0.5mm, is preserved ventrally on the abdomen.

F1347/BB/AR/CJW: A dissected winged ant indet., body length ca. 3mm, is weakly spun in in spider's threads and has the prey of a spider.

F1348/BB/AR/CJW: A questionable ant indet., body length ca. 2.8mm, and an unknown small arthropoda, are questionable prey of a spider. Both arthropods are strongly dissected; spider's threads are absent.

F1349/BB/AR/CJW: A strongly dissected Trichoptera indet., body length > 3mm, is weakly spun in in few spider's threads without droplets and has been the prey of a spider.

CJW (no no.): A female *Segestria* sp. indet. (Araneae: Segestriidae) with a member of the Psocoptera as its prey.

Addendum

Certain insects live more or less constantly in or near spiders' webs; for example decomposing Collembola or bugs may feed on prey remains. Midges may even use exposed spiders' threads as resting places or may feed as kleptoparasites in orb webs. A polistine wasp is able to walk on web threads, including sticky threads, owing to its special tarsal lobes. See NENTWIG & HEIMER (1987: 223-225). This kind of behaviour may be one of the reasons for the rarely preserved midges and wasps as the prey of fossil spiders.

CANNIBALISM IN FOSSIL SPIDERS (KANNIBALISMUS BEI FOSSILEN SPINNEN)

Photo 513.

According to BRISTOWE (1939: 214) "In some species the female is very liable to destroy her male after mating with him." Well-known is the genus *Latrodectus* = "widows" (in German "Witwen") of the family Theridiidae (Kugelspinnen), e.g. the Black widow (Schwarze Witwe) of America and its counterpart, the "Malmignatte" of the South of Europe. Both species possess a dangerous poison; the male is distinctly smaller than the female and is frequently eaten by the female after mating - the female makes herself a widow -, note the appropriate name of these spiders. Members of the genus *Latrodectus* are not known from fossils.

(The advantage of this sexual size dimorphism: The large females with their strong poison can overwhelm larger prey, and the smaller males can capture different (smaller) prey. So the intraspecific competition of the adult spiders is reduced and the prey spectrum of the species is enlarged).

Also females of numerous Araneidae feed on their - frequently dwarf - males after mating. A document of such a behaviour in fossil spiders is still wanting.

Furthermore it is wellknown that in certain spiders - e.g. in some orb-weavers of the family Araneidae which produce a large number of eggs - cannibalism occurs in the spiderlings; brothers and sisters may be the first prey of such spiders.

A male member of the genus *Dipoena* THORELL (Theridiidae, CJW) may have been the prey of a conspecific female. The reason for the injuries of several other fossil male spiders in Baltic amber (CJW) is quite unsure; some spiders may have been the prey of spiders of different species, see the chapter on prey and on enemies of fossil spiders.

Up to now I have not found a sure proof of an adult fossil spider feeding on a spider of the same species, but I found some indications of cannibalism in spiderlings in Baltic amber:

A piece of amber - F1140/CJW - contains remains of a spider's (indet.) web and an egg sac with some exuviae as well as a crumpled juvenile spider hanging in the web near a beetle (Elateridae). Apparently the juvenile spider has been the prey of another spiderling from the same egg sac. Another small and crumpled spiderling - body length ca. 0.7mm - F1302/BB/CJW -, and the exuvia of a spiderling are preserved near a masked egg sac. The shape of the remains of this juvenile spider indicates that it has been a prey. Together with the male holotype of *Eomatachia barbarus* n. sp. (Zoropsidae) two partly crumpled/dissected and probably conspecific juvenile spiders are preserved which have probably been the prey of the male spider.

Studies in fossils - science and nonsense

Modern (Brave) New World science
seems partly of a special kind:
Numerous "new discoveries"
are published in endless series:
DNA from inclusions in amber,
reanimated Bacteria in Dominican amber,
miraculous fossils in meteorites from Mars
and other miraculous "findings" and "stars" -
are mistakes and speculations
- or even falsifications -
for some authors glorifications,
to earn "fast money" and to serve
a clever "capitalistic science"
in the crazy sense
of producing "rubbish - or perish".
Spiders known from European ambers
- as Archaeids, Cyatholipids and Synotaxids -
are declared Gondwanan members,
Collembola are set beside Crabs -
nobody knows
the complete list of doodled crap(s).

J. W.

PARASITES, PARASITIDS AND OTHER ENEMIES OF FOSSIL SPIDERS AND THEIR EGG SACS (PARASITEN, PARASITENÄHNLICHE UND ANDERE FEINDE FOSSILER SPINNEN UND IHRER KOKONS)

Photos 589-605.

See the chapters on phoresy, kleptoparasites and egg parasitoids, as well as BRIS-TOWE (1941: 331-413) and WUNDERLICH (1986: 47).

Parasites and parasitoids of spiders and other arachnids are Viruses, Rickettsia, Bacteria, Protozoa, Fungi, Cestoda, Nematoda, Nematomorpha, Trematoda, insects (mainly larvae of: Wasps, midges, flies, rarely Planipennia (Neuroptera), Thysanoptera and beetles) and Arachnida: Acari, see COKENDOLPHER (1993) (on Opiliones). A - not complete - reference list of extant spider parasites was given by EASON et al. (1967). MOREL (1978) reports on diseases of Arachnida (p 477): "...rickettsial and virus diseases provide the main part of arachnid pathology."

Parasitoids - like fungi or larvae of ichneumonoid wasps on arthropods - feed on their hosts only once (continuously), and kill them slowly. (**Predators** kill their prey fast). Contrarily to parasitoids the **parasites** like fleas may feed on their hosts several times and usually don't kill them. Endoparasites like Bacteria, Fungi, Nematoda and certain insect larvae feed inside their hosts (eggs, larvae or adults), ectoparasites like fleas and certain insect larvae feed outside their hosts.

Observed fossil parasites and parasitoids of spiders are rarities; only very few examples have been documented, see below. Parasitic fossil Viruses, Rickettsia and Bacteria of spiders are unknown to me; certain other groups are treated in the following.

Translation into German: Schmarotzer (Parasiten) und Schmarotzerähnliche (Parasitoide) von Spinnen und anderen Spinnentieren sind Viren, Rickettsien, Bakterien, tierische Einzeller, Pilze, Bandwürmer, Fadenwürmer, Saitenwürmer, Saugwürmer, Insekten (überwiegend Larven von Wespen, Mücken, Fliegen, selten von Fransenflüglern, Netzflüglern und Käfern) und Spinnentiere: Milben, siehe COKENDOLPHER (1993) (bei Weberknechten). Eine - unvollständige - Liste heutiger Spinnen-Parasiten wurde von EASON u. a. (1967) veröffentlicht. MOREL (1978) berichtet über Krankheiten bei Spinnentieren (S. 477): "...Rickettsien und Viren verursachen die meisten Erkrankungen."

Parasitenähnliche - wie Pilze oder Larven von Schlupfwespen an Gliederfüßern - fressen lediglich einmal (andauernd) an ihrem Wirt und töten diesen langsam. (**Freßfeinde/Räuber** töten ihre Beute schnell). Im Gegensatz zu Parasitenähnlichen entnehmen **Parasiten** wie Flöhe ihrem Wirt mehrmals Nährstoffe und töten sie gewöhnlich nicht. Innenschmarotzer wie Bakterien, Pilze, Fadenwürmer und einige Larven von Insekten leben im Inneren ihrer Wirte (in Eiern, Larven und Geschlechtsreifen), Außenschmarotzer wie Flöhe und die Larven gewisser Insekten leben außerhalb ihrer Wirte.

Fossile Schmarotzer und Schmarotzerähnliche an Spinnen sind Seltenheiten; es sind erst sehr wenige Exemplare beschrieben worden, siehe unten. Parasitische fossile Viren, Rickettsien und Bakterien von Spinnen sind mir unbekannt; verschiedene andere Gruppen werden im folgenden beschrieben.

(1) **Nematoda** (Roundworms - Fadenwürmer)

Extant nematode parasites of spiders: See POINAR (1987), POINAR & POINAR (1986).- Besides the saprobiontic and occasionally phoretic Nematoda - the tiny Rhabditida - the parasitic members of the family Mermithidae occur in Baltic amber. Larvae of this family develop as endoparasites in the lungs and other parts of the opisthosoma of Arthropoda and Mollusca. Fossils are rare and mainly found with Diptera of the families Chironomidae and Culicidae. Only a single Mermithidae with a spider has been found in Baltic amber, see POINAR (2000) (fig. 1): "The smooth surface of the cuticle, curled position of the specimen, and shape of the head and tail demonstrate that the specimen is a post-parasitic juvenile mermithid nematode that just emerged from its spider host."..."Mermithid nematodes sometimes emerge from their hosts if the host accidentally perishes, as in this case when the spider fell into the sticky resin." (POINAR (2000: 388, 391)). - Tylenchida: See POINAR (1984).

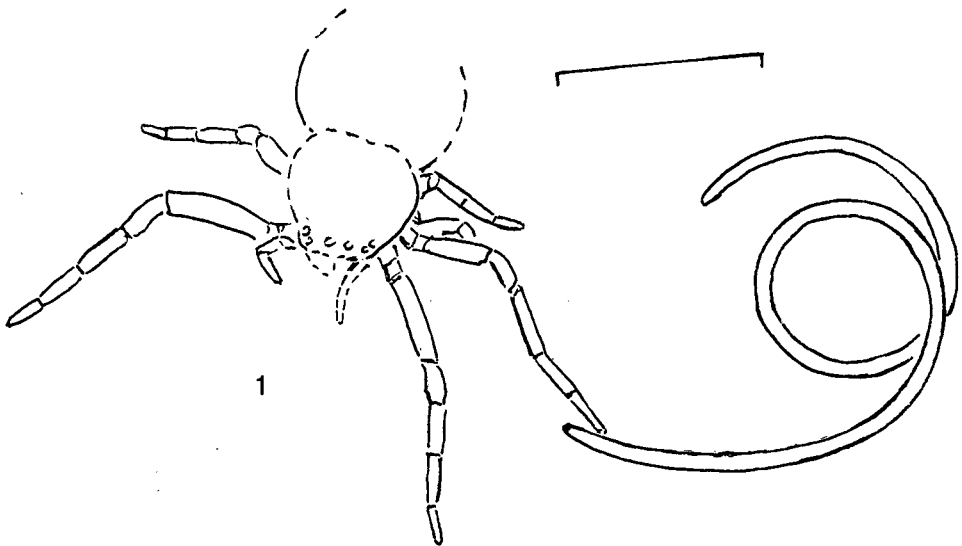


Fig. 1) A fossil post-parasitic roundworm (Nematoda: Mermithidae), *Heydenius araneus* POINAR 2000 adjacent to its spider host, a juvenile member of the family Thomisidae in Baltic amber, in anterior-dorsal aspect. Not all legs and eyes of the spider are shown, the posterior part of its opisthosoma is cut off. M = 0.33mm. - Drawn from a photo from POINAR (2000: Fig. 1). (Fossiler Fadenwurm neben einer jungen Krabbspinne im Baltischen Bernstein).

(2) Acari (Mites - Milben)

Fossil parasitic mites' larvae on midges and flies in Baltic amber are fairly rare, see EICHMANN (2002); numerous pieces are kept in the collection of the author, but fossil records of parasitized spiders are rare, see WUNDERLICH (2002). In extant spiders more than 20% of a population may be parasitized. At least five families of mites are known to parasitize spiders: Eutrombidiidae, Erythraeidae (e.g. *Leptus*), Laelapidae, Microtrombidiidae and Trombidiidae, see FAIN & JOCQUE (1996) and WELBOURN et al. (1988). Mainly members of the Erythraeidae and Trombidiidae parasitize fossil spiders in Baltic amber. Hexapod (six-legged) "*Leptus* larvae are ectoparasites of a wide range of arthropods...while the octopod (eight-legged) nymphs and adults are free-living predators of other arthropods", see BAKER & SELDEN (1997: 183).

Observations, results

Among more than 100 000 fossil spiders I found about 10 specimens in Baltic amber which may be parasitized by mites; these are members of the following seven families: Agelenidae (questionable), Corinnidae (questionable), Linyphiidae (*Custodella* sp. indet.), Liocranidae (questionable), Oonopidae (*Orchestina* sp. indet.), Salticidae (*Distanilinus pernutus*) and Theridiidae. Three specimens were determined to the genus level, one to the species level. One of the parasitized specimens - *Orchestina* - is an adult female, one - *Distanilinus* - is an adult male, the remaining ones are juveniles.

According to my studies most mites are attached on the anterior-dorsal part of the opisthosoma, which is soft in unarmoured spiders and difficult to clean with the legs; few are found at the soft part between sternum and the dorsal prosomal sclerite. I found one on the prosoma and one near the spinnerets:

F89/BB/AR/AGE/CJW (fig. 2): A six-legged parasitic mite larva with thin legs of the Trombidiidae or Microtrombidiidae (A. WOHLTMANN det.), body length 0.8mm, is attached antero-dorsally on the opisthosoma of a spider, probably of the family Agelenidae, body length 2.4mm. Both arachnids are well preserved. The mouth parts of the mite seem to be in direct contact to the spider, and its enlarged opisthosoma suggests that it had already been feeding for a while. The spider's spinnerets are not as long as in most spiders of this family, its posterior eye row is slightly recurved, its leg bristles are long. (Only few hairs are drawn).

F103/BB/AR/?FAM/CJW: A mite larva of the Trombidiidae or Microtrombidiidae, body length 0.8mm, is parasitizing a juvenile spider indet. (?Trionycha), body length 3mm. Both arachnids are only fairly well preserved, most parts are covered by a white

emulsion. The position of the mite on the spider, its shape and structure of the cuticula are similar to no. F89.

F282/BB/AR/ARA/CJW: Near the right side of the opisthosoma of the holotype of *Palaeonephila curvata* n. gen. n. sp. (Araneidae) a parasitic mite larva is preserved, which may have come from the spider.

F311/BB/AR/CJW: A parasitic mite larva, Trombidiidae (A. WOHLTMANN det.), body length 0.22mm, is situated directly behind the spinnerets and the anal tubercle of the holotype male of *Distanilinus pernutus* n. gen. n. sp., body length 3mm. Both arachnids are well preserved. Most probably the mite was originally fixed to the opisthosoma - or spinnerets, anal tubercle? - of the spider and was separated during the process of the embedding in the fossil resin.

F361/BB/AR/CJW: A parasitic mite larva, *Leptus* sp. indet. (Erythraeidae), body length 0.5mm is preserved 2mm above the male of *Succinero* sp. indet. (Mimetidae), body length 2.4mm. Most probably the mite was not parasitizing the spider because it is preserved in the next amber layer above the spider's layer.

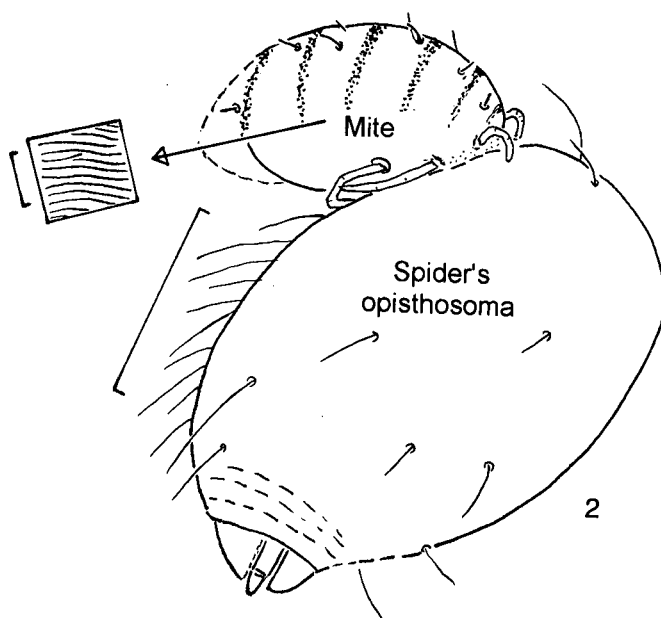


Fig. 2) A parasitic fossil mite (Acari: Trombidoidea) in Baltic amber, sucking body fluids from the opisthosoma of a juvenile spider (Araneae: ?Agelenidae), lateral aspect. M = 0.2mm. Enlarged: The structure of the cuticula of the mite's opisthosoma. Photo 594.

F381/BB/AR/CJW: A parasitic mite larva, Trombidiidae or Microtrombidiidae (A. WOHLTMANN det.), body length 0.37mm, is apparently sucking dorsally-frontally on the opisthosoma of a *Custodela* sp. indet. (Linyphiidae), body length 2mm. The mite is almost completely and the spider in several parts covered by a white emulsion. The opisthosoma of the mite is distinctly swollen, the opisthosoma of the spider is deformed.

F427/BB/AR/THE/CJW: A parasitic mite larva, Erythaeinae (A. WOHLTMANN det.), body length 0.37mm, is sucking between the left coxae I and II of a member of the Theridiidae indet., subad. male, body length 1.3mm. Most parts of the ventral side of the spider are covered by a white emulsion, the mite is freely observable. The mite's opisthosoma is strongly swollen. A droplet of excrement on the anal tubercle of the spider indicates that the arachnids were kept alive in the resin.

F745/BB/AR/LIN/CJW: A parasitic mite larva indet., body length 0.33mm is sucking on the left side dorsally-laterally on the opisthosoma of a male *Custodella* sp. indet. (Linyphiidae), body length 2.5mm. The opisthosoma of both arachnids is somewhat depressed dorsally, the mite's opisthosoma is fairly slender, white emulsions are absent, the piece of amber was heated.

F940/BB/AR/CJW: A parasitic mite larva indet., body length 0.4mm, is sucking frontally-dorsally on the opisthosoma of a juvenile of the questionable family Liocranidae, body length 2.4mm. The opisthosoma of both arachnids is somewhat deformed, the mite's opisthosoma is fairly thick, the ventral side of the spider is thickly covered by a white emulsion. The piece of amber was most probably heated.

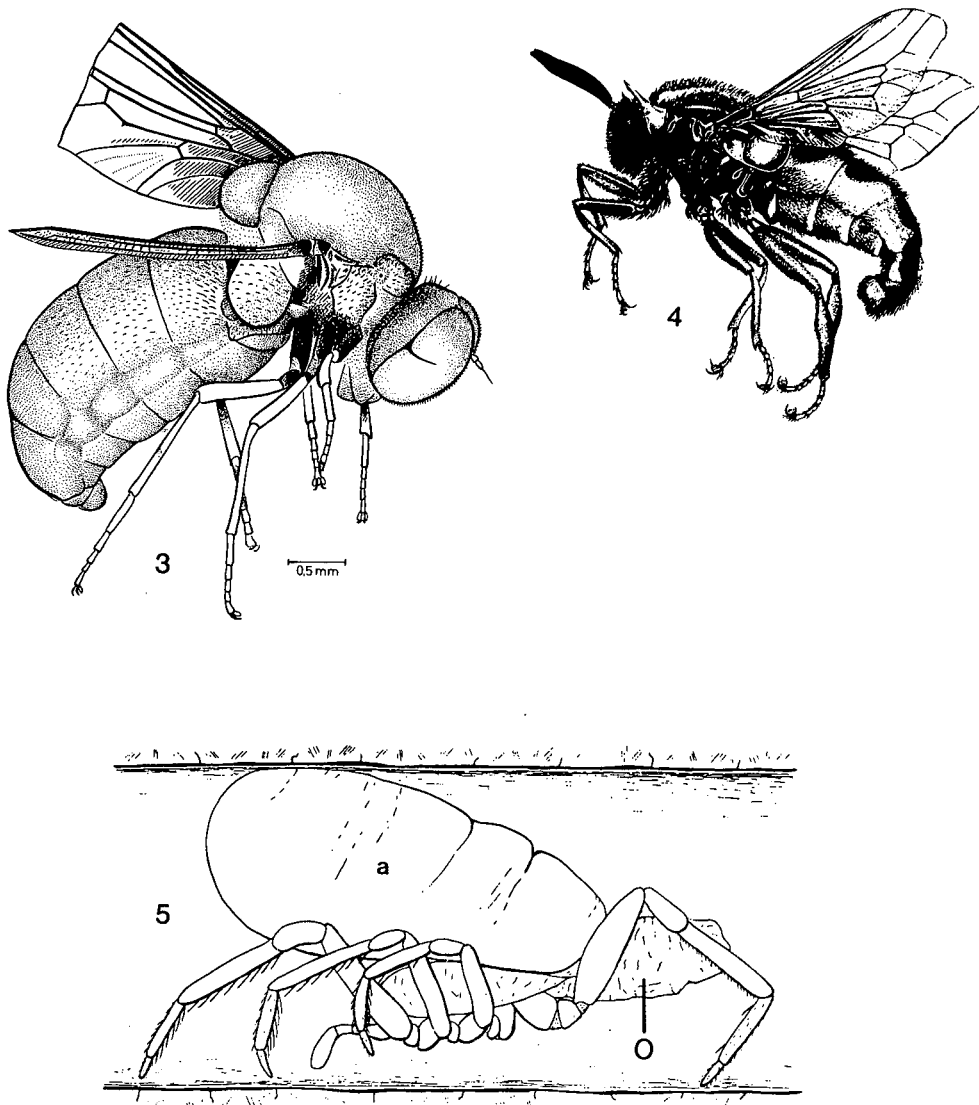
F1250/BB/AR/CJW: A parasitic mite larva indet., body length 0.14mm, is apparently sucking on the left side on the dorsal-posterior part of the prosoma near the petiolus of a juvenile member of the superfamily Clubionoidea indet., body length 3.5mm. The mite's opisthosoma is strongly swollen, some ventral parts of the spider are covered by a white emulsion.

F1355/BB/AR/CJW: A parasitic mite larva, *Leptus* sp. indet. (Erythraeidae), body length 0.45mm, is preserved 4mm right of a juvenile member of the genus *Sosybius* PETRUNKEVITCH (Trochanteriidae), body length 5.1mm. As the spiders' leg position shows the mite - and some hairs of the spider - have been drifted within a flow of the resin from the spider to its right side.

Coll. H. FLEISSNER no. BB 1172ACA: A parasitic mite larva, Trombidiidae or Microtrombidiidae indet., body length 0.19mm, is apparently sucking between the dorsal prosomal sclerite and the sternum near the left coxa IV of a female *Orchestina* sp. indet. (Oonopidae), body length 1.3mm. The mite's opisthosoma is slender, the right femur IV of the spider is deformed, some parts of the spider are covered by a white emulsion, the piece of amber was heated. Fig. 8, Photos 589-590.

(3) Coleoptera (beetles - Käfer)

The larva of a beetle (Coleoptera indet.), body length 1.8mm, is attacking a juvenile spider (indet.) in Baltic amber, body length 2.1mm, with its mouth parts dorsally between prosoma and opisthosoma and is probably sucking on the anterior part of the opisthosoma, see JANZEN (2002: Figs. 107-108). Coll. J. W. JANZEN. Photo.



Figs. 3-5: Members of the Diptera family Acroceridae, which are parasitoids of spiders. 3) *Villalites electrica* HENNIG 1966, habitus of the holotype in Baltic amber, lateral aspect. - Taken from HENNIG (1966: Fig. 34); 4) *Ocnaea boharti* SCHLINGER, an extant parasitoid of mygalomorph spiders, habitus, lateral aspect; 5) Mature, externally larva of the extant Acroceridae *Sphaerops appendiculata* (a) feeding on the opisthosoma (o) of the spider *Ariadna* sp. (Segestriidae). Both animals are inside the silken tube prepared by *Ariadna*. - Figs. 4-5 are taken from SCHLINGER (1987: Figs. 112, 114).

(4) Thysanoptera (Thripse, Fransenflügler)

A questionable - parasitic or phoretic? - Thysanoptera indet., F536/BB/AR/CJW, body length 0.3mm, is in close contact to a stellate hair and a subadult male of the family Theridiidae indet., body length 4.5mm. Both arachnids are partly covered by a white emulsion, the piece of amber was heated. According to G. MICKOLEIT (Univ. Tübingen) (person. commun.) the habitus of the Thysanoptera is similar to members of the family Aelothripidae, which may parasitize e.g. mites. Parasitic Thysanoptera of spiders are unknown to R. ZUR STRASSEN (SMF) (person. commun.). Therefore I do not want to exclude that the special position of these animals may be an accident.

(5) Diptera (Midges and flies - Zweiflügler, Fliegen und Mücken)

Four genera of Acroceridae flies (fig. 3) are known from Baltic amber, see HENNIG (1966), LARSSON (1978: 98). Larvae of extant Acroceridae (fig. 4) are obligatory parasitoids in or on spiders and parasitoids in or on spider eggs, see SCHLINGER (1987); they may attach their eggs to the spider's opisthosoma. In contrast to the larvae of mites they do not have legs, and fossil larvae may be easily mistaken for bubbles. Up to now I have not recognized such a parasitoidic fossil larva. According to HENNIG (1966: 20) the larvae of at least two fossil genera of the Acroceridae in Baltic amber were already parasitoids of spiders but a sure record is still wanting. According to NENTWIG (1985) females of extant Microphoridae are obligate klepto-parasites at spiders webs.

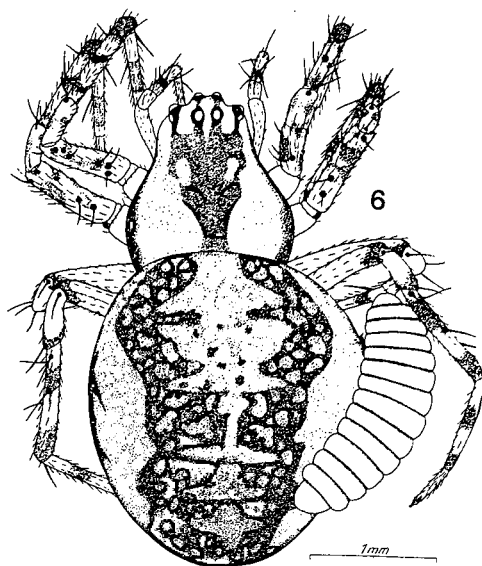
(6) Hymenoptera (Wasps and allies - Hautflügler)

Egg parasitism of a fossil spider by a wasp in Baltic amber: See the paper of POINAR in these volumes.

Parasitoidic Hymenoptera may attach their eggs to a spider's opisthosoma, see fig. 6. Mainly members of the families Ichneumonidae (in German: Schlupfwespen) with the genus *Pimpla*, and Sphecidae (in German: Grabwespen) with the "collective genus" *Crabro* were present in the Baltic amber forest. They may have attacked spiders in the Baltic amber forest. Up to now a direct wasp attack of a fossil spider is unknown, but a member of the Ichneumonidae is preserved near a fossil spider in Baltic amber, see below.

Fig. 6) The extant juvenile of a member of the family Tetragnathidae, *Meta* sp. indet., with attached parasitic larva of the genus *Polysphincta clypeata* (Ichneumonidae). - Taken from MÜLLER (1983: Fig. 1).

Abb. 6) heutige junge Strecker-spinne der Gattung *Meta* mit angehefteter parasitischer Larve einer Schlupfwespe.



Observations

F313/BB/AR/SAL/CJW: A member of the family Diapriidae indet., body length 1.8 mm, is situated 1mm left of a male spider, *Distanilinus paranutus* n. gen. n. sp. (Salticidae), body length about 3mm. The dorsal side of the wasp's body is directed to the spider. Diapriidae are parasitoids of arthropods including spiders.

F315/BB/AR/CJW: A member of the family Ichneumonidae, body length 4.2mm, is preserved in the same piece of amber as the holotype of *Eolinus insuriens* n. sp., body length about 4mm, but is situated in another layer of the amber. So the "community" of both animals may be an accident.

The holotype of the spider *Baltsuccinus flagellaceus* n. gen. n. sp. (Baltsuccinidae) is located in contact to a member of the Hymenoptera: Braconidae indet. - by an accident? Extant members of this family are parasitoids of caterpillars and certain other insects. EASON et al. - J. Kansas Entom. Soc., 40: 430 - list an extant larva of the family Braconidae (indet.) which - according to KOEWN (1936) parasitized a member of the spider *Latrodectus hasselti* THORELL (Theridiidae). So the location of these arthropods may be not an accident.

(7) Fungi (Mushrooms - Pilze)

Extant parasitotic fungi: See EVENS & SAMSON (1987), NENTWIG (1985, 1990), as well as COKENDOLPHER (1993) (fungi on Opiliones). NOORDAM et al. (1997) report fungi on spiders which "may involve a mild parasitism. Fungal parasitism of spiders is well known from the humid tropics. Its regular occurrence in temperate Europe seems poorly documented.". Fossils: I have not found a sure parasitotic fungus on a fossil spider; see the chapter on decomposing fungi.

Other - non-parasitic - enemies of fossile spiders; predators

Vertebrates as certain fishes, amphibians, lizards, birds and mammals prey on spiders, but I don't have a proof of such enemies in fossils spiders. The absence of such finds are a matter of the small and restricted "window to the past" of fossils in amber in which large animals are only rarely preserved.

In contrast to vertebrates there are numerous predatory arthropods of spiders as beetles, Diptera (Asilidae, Chloropidae), mites as Caeculidae and Labidostemmidae (fig. 7), see BRISTOWE (1942: 331ff). The most successful spider eaters among arthropods are probably ants and spiders themselves. According to KIRCHNER (1990) the percentage of ant's prey of spiders in Central Europe may be less than 5% up to 39%. See the chapter on the relationships between fossil ants and spiders in this volume, e.g. F184/BB/CJW.

Most spiders are not specialized on a certain prey, they feed on all arthropods which they are able to capture, including spiders. But members of certain spider taxa are specialized as spider's predators, e.g. members of the families Archaeidae and Mimetidae, as well as certain Salticidae, mainly of the Cocalodinae, see the papers on these taxa in these volumes and on the prey of spiders.

Observations:

F16/BB/AR/CJW: A fossil predatory mite (Labidostemmidae?) in Baltic amber, body length ca. 1mm, is attacking a female spider of the family Theridiidae in Baltic amber. Both arthropods are heavily armoured and have large dorsal opisthosomal scuta (fig. 7). See WUNDERLICH (2000).

F236/BB/AR/TRO/CJW: The ventral half of the opisthosomal cuticula of a *Sosybius* sp. indet. (Trochanteriidae), body length 6.3mm, is wanting. Apparently a predator has fed on the opisthosoma. A dorsal part of the opisthosoma has been broken off, one can observe remains of the cuticula; the opisthosoma has been filled with resin.

F713/BB/AR/CJW: A probably juvenile fossil female of the family Archaeidae is holding a probably juvenile member of the family Theridiidae as its prey; see fig. 5 in the chapter on the prey of fossil spiders. Extant Archaeidae are spider eaters.

F1206/BB/AR/THE/CJW: A *Dipoena* sp. indet. (Theridiidae, ♂, prosomal length 0.8 mm. The posterior part of the prosoma is strongly inclined; organic remains are present in the position of the opisthosoma which is lost. The spider has been injured or has been the prey of an unknown predator.

F1206/BB/AR/CJW: The piece of amber contains two females of the genus *Custodea* sp. indet. (Linyphiidae) with a part of their capture web including droplets, and -

in contact with the web - a juvenile member of the family Pirate Spiders (Mimetidae) (German name Spinnenfresser-Spinnen), probably of the genus *Succinero* n. gen. Web and spiders are preserved in the same layer of the amber. Extant Mimetidae are known to feed (e.g.) on spiders of the family Linyphiidae. This is the first fossil report of the family Mimetidae which apparently tried to capture a spider.

F1247/BB/AR/CJW: A 3.3mm long spider indet. which is spun in in spiders' threads was the prey of a spider.

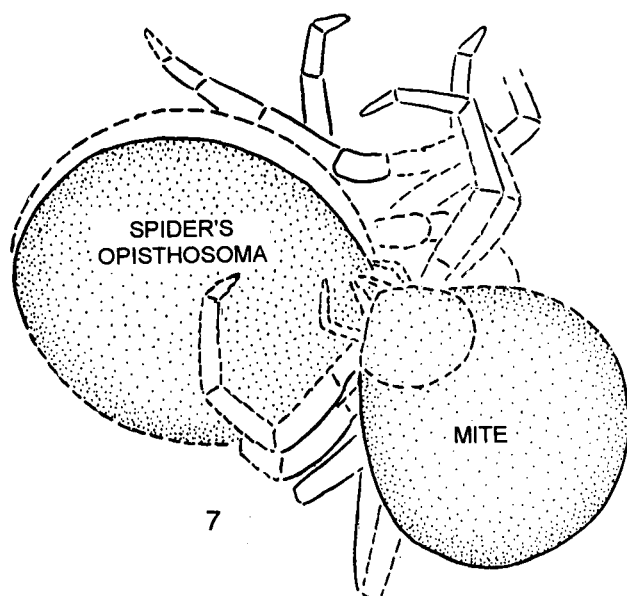


Fig. 7) A fossil predatory mite (Labidostommidae?) in Baltic amber, body length ca. 1mm, on the right side, is attacking a female spider of the family Theridiidae, dorsal aspect. Both arachnids are heavily armoured. (Eine fossile räuberische Milbe, rechts, ca. 1mm lang, attackiert eine Kugelspinne. Ansicht von oben. Beide Spinnentiere sind stark gepanzert). Photo 614.

F986/BB/AR/ANA/CJW: Male holotype of *Flagellapis voighti* n. gen. n. sp. (Anapidae: Anapinae): The opisthosoma of the spider is separated and situated two prosomal length behind and below the prosoma in a position which is turned by 90°. Behind the eyes the prosoma bears a larger opening which probably is caused by the bite of an unknown enemy.

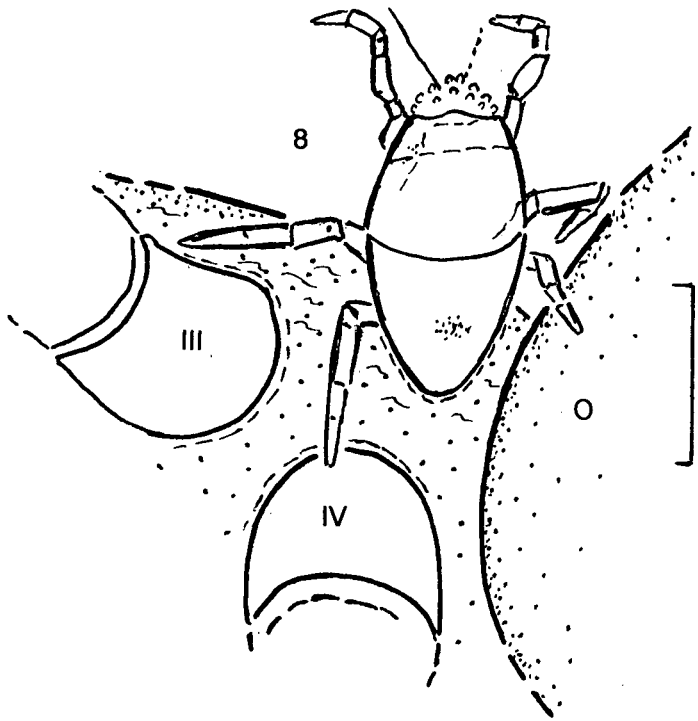


Fig. 8. A parasitic mite larva, Trombidiidae or Microtrombidiidae indet., coll. H. FLEISSNER, body length 0.19mm, is apparently sucking between the dorsal proso-mal sclerite and the sternum near the left coxa IV of a female of *Orchestina* sp. indet. (Oonopidae), body length 1.3mm. The mite's opisthosoma is slender, the right femur IV of the spider is deformed, some parts of the spider are covered by a white emulsi-on. M = 0.1mm. O = the basal part of the spider's opisthosoma. Photos 589-590.

KLEPTOPARASITES, COMMENSALES AND SOCIAL FOSSIL SPIDERS (DIEBS-SPINNEN, "MITESSER" UND SOZIAL LEBENDE FOSSILE SPINNEN)

Photos 143ff and 240.

Generally spiders live solitarily as "lone wolves" (in German: Einzelgänger); even cannibalism is widely spread in spiders. There are few exceptions: (a) Spiderlings may live together for some time - see the paper on eggsacs in this volume -; in Lycosidae they can be found on the opisthosoma of their mother even in great numbers, (b) kleptoparasites and commensals live together in a various number in webs of their hosts, and (c) social spiders may build common webs. Only few families - e.g. Araneidae and Theridiidae - and few genera are known in which social spiders are known.

Three requirements have to be fulfilled concerning the different grades of socially living spiders: (a) Tolerance against each other, (b) interaction(s) between the conspecific members, and (c) cooperation as building common webs, capturing prey and caring for the brood; see the book of FOELIX.

Kleptoparasites steal prey from their hosts; they live in or near the web of their hosts. Commensalism is reported from extant spiders, e.g. from *Mysmenopsis* SIMON 1897 (Anapidae: Mysmeninae), which feed on very small prey which is ignored by their hosts, see PENNEY (2000: 355).

The best known kleptoparasitic spiders are members of the genus *Argyroides* SIMON 1864 s. l. (Theridiidae) which may occur (e.g.) with Araneidae of the genera *Cyrtophora* SIMON 1864 and *Nephila* LEACH 1815, which build large capture webs. Members of the families Anapidae s. l. (Mysmeninae, Symphytognathidae and probably Comarominae (see below)), Dictynidae, Oonopidae, Salticidae, Sparassidae (= Heteropodidae) and Theridiidae have been recorded as kleptoparasites of web-building spiders, see RAMIREZ & PLATNICK (1999: 548-549).

The first fossil *Argyroides* was described by WUNDERLICH (1986: 39, 42, 47, fig. 355), (1988: 128-131, figs. 279-288, 732) from Dominican amber. A second genus of spiders in which the members of probably most species are kleptoparasites is *Mysmenopsis* SIMON 1897; spiders of the genus *Ischnothele* AUSSERER 1875 are known as hosts. According to PENNEY (2000: 355) "There is no reason to believe that the fossil species behaved in any other way;" (than kleptoparasites) "it is morphologically similar to the Jamaican species, and in addition, *Ischnothele* has been found in Miocene amber from the Dominican Republic (WUNDERLICH (1988))."

There is no sure report of kleptoparasitic spiders in Baltic amber. (Note: WUNDERLICH (1986: 47) erroneously reported a member of *Argyroides* from Baltic amber but this report was most probably based on a wrong determination). - Probably members of the genus *Balticoroma* n. gen. (Anapidae: Comarominae n. subfam.) of the Baltic amber forest had a kleptoparasitic behaviour, but I do not want to exclude that these fossils in Baltic amber were socially living; see the discussion on this matter in the paper on the family Anapidae s. l., the genus *Balticoroma*, subfamily Comarominae.

DECOMPOSITION AND INJURIES (ZERSETZUNG UND VERLETZUNGEN)

Photos 435, 473-494, 536 and 617.

See the chapters on autotomy, egg sacs, enemies, healing, palaeopathology and prey in this volume.

Decomposing - saprobiontic - organisms of extant and fossil spiders are e.g. some Acari, Bacteria, Collembola, Fungi and Nematoda. Occasionally a spider and various decomposers are preserved in the same piece of amber. Examples are the holotype of *Gerdiopsis infrigens* n. gen. n. sp. (Oecobioidea: Hersiliidae) (fig. 1) and the ?juvenile questionable member of the Theridiidae, F154/CJW (fig. 4), which have been entombed alive, see below.

Material (in the alphabetic order of the numbers; coll. HOFFEINS at the end. Only selected pieces are treated in this chapter):

Gerdiopsis infrigens n. gen. n. sp., holotypus ♂ with numerous syninclusions, F50/BB/AR/HER/CJW; a questionable Fungus on a loose metatarsus of the holotypus of *Mizalia spirembolus* n. sp., F54/BB/AR/OEC/CJW; ?*Eomatachia* sp. indet. (Zoropsidae), juv., as remains of a prey of a spider, also preserved are 2 spiders' exuviae (?Araneidae), the part of an irregular spiders' web and saprobiontic Fungi, F135/BB/AR/CJW; ?Agelenidae sp. indet., ♀ with saprobiontic Fungi, F144/BB/AR/CJW; ?Philodromidae sp. indet., subad. ♂, F152/BB/AR/?PHI/CJW; ?Theridiidae sp. indet., ?ad. ♀, F154(BB/AR/?THE/CJW; Araneae sp. indet., juv., F173/BB/AR/CJW; ?Agelenidae sp. indet., F177/BB/AR/CJW; Theridiidae indet.; JUV.; F179/BB/AR/THE/CJW; Araneidae indet., juv., F180/BB/AR/ARA/CJW; ?Trochanteridae sp. indet., ?exuvia with saprobiontic Fungi, F194/BB/AR/?TRO/CJW; ?Clubionoidea sp. indet., subad. ♂ with saprobiontic Fungi, F197/BB/AR/CJW; *Acrometa* sp. indet., ♀ with saprobiontic Fungi, F198/BB/AR/ SYN/CJW; Corinnidae sp. indet., ♀ with saprobiontic Fungi, F199/BB/AR/COR/ CJW; *Archaea* ?*paradoxa* KOCH & BERENDT 1854 (Archaeidae), juv., F203/BB/AR/ARC/CJW; Anapidae: Anapinae sp. indet., ?juv. ♀ with saprobiontic Fungi, the tiny amber piece will be preserved in glycerine, F208/BB/AR/ANA/CJW; Salticidae sp. indet., ♀, injured and with saprobiontic Fungi, F222/BB/AR/SALT/ CJW; *Acrometa* sp. indet. (Synotaxidae), ♂, injured and with saprobiontic Fungi, F223/BB/AR/SYN/CJW; some thin Fungi at the legs of *Priscometa capta* n. sp. as well as on the right leg I of a Diptera: Nematocera and nearby in the same amber piece, F227/BB/AR/TET/CJW; Salticidae indet., subad. ♂, exuvia, F591/BB/AR/SALT/CJW; *Eodictyna communis* n. gen. n. sp. (Dictynidae), ♂, paratype, F807/BB/AR/DIC/CJW; *Palaeomysmena hoffeinsoorum* n. gen. n. sp., holotype ♂ (Anapidae), F984/BB/AR/ANA/CJW, egg sac Ara-

neae indet., F1140/BB/AR/CJW; *Anniculus balticus* PETRUNKEVITCH 1942 (Zoropsidae), ♂, F1147/BB/AR/ZOD/CJW; Araneae indet., ?ad. ♀, F1165/AR/ CJW; spider-thread-shaped fungus, *Arachnomycelium*, F1207/BB/ICJW; Salticidae indet., ♂, with numerous hyphae ventrally, F1243/BB/AR/SAL/CJW; *Dipoena* sp. indet. (Theridiida), ♂, F1245/BB/AR/THE/ CJW; ?*Eomatachia* sp. indet. (Zoropsidae), ?juv. ♀, F1256/BB/AR/CJW; Mimetidae indet., juv. ♂, F1258/BB/AR/MIM/CJW; Myriapodae: ?Lithobiomorpha indet. (O. KRAUS det.) with the Fungus *Arachnomycelium*, F1317/BB/MYR/CJW; Araneae indet., egg sac, F1320/BB/AR/CJW; ?Gnaphosidae sp. indet., juv. with saprobiontic Fungi, coll. HOFFEINS in Hamburg no. 420.1; the amber piece has been embedded in artificial resin; *Orchestina* sp. indet. (Oonopidae), ♀ with saprobiontic hyphae, coll. HOFFEINS in Hamburg no. 420.2; the amber piece has been embedded in artificial resin.

(1) Bacteria (Bakterien)

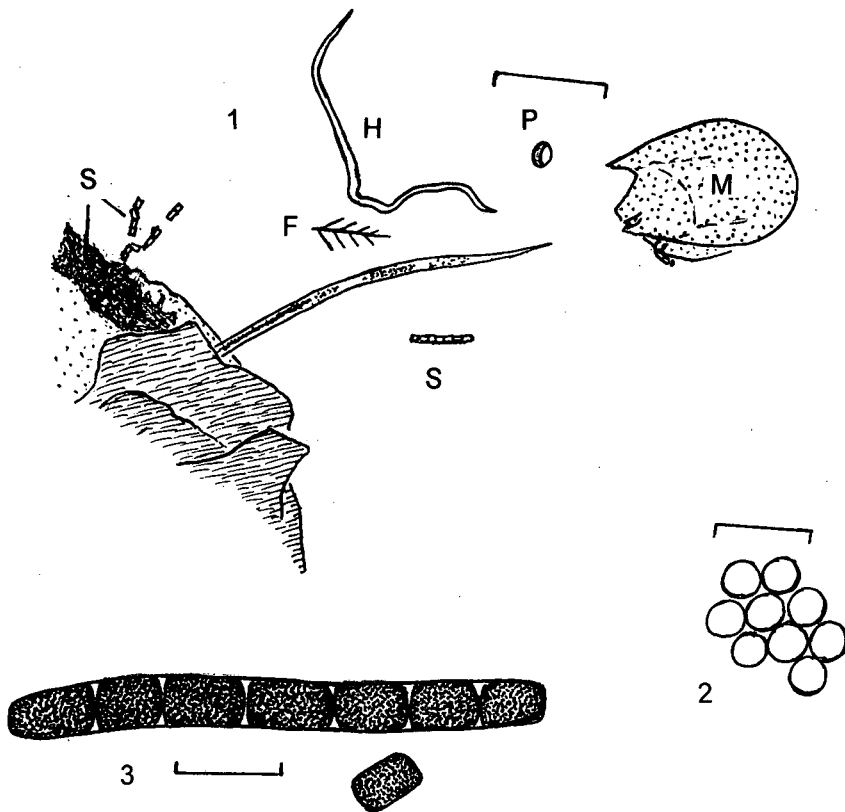
According to ANREE (1929: 146-147) DAHMS (1922) recorded the occurrence of gas bubbles on (e.g.) mouth parts, the anal area and the genital organs of spiders in Baltic amber, which are apparently products of decomposing. To these areas I will add the ventral surface of the opisthosoma. Occasionally the opisthosoma is swollen like a balloon, e.g. F984, photo 161.

Larger colonies of Bacteria are apparently preserved with certain decomposed fossil spiders in Baltic amber, see the photos, but must not be mistaken for haemolymph or for the white emulsion which is frequently preserved on the surface of arthropods in Baltic amber.

According to the white emulsion and the preserved remains of blood (haemolymph) on injured or autotomized leg articles all the spiders from my collection which are listed below were entombed in the resin shortly after their death or even alive, and the fungi were apparently growing within the resin. "Even after an insect is trapped in resin, bacteria and enzymes continue working in the gut, rotting the insect from the inside." (ROSS (1998: 33).

FOELIX (1992, 1996) does not mention Bacteria in his book "Biology of spiders". MOREL (1978) reports no pathenogenic/parasitic Bacteria but Rickettsia and Viruses. COKENDOLPHER (1993: 121) reports few taxa of extant Bacteria which parasite Opiliones.

We find only five lines about fossil Bacteria in the book of LARSSON (1978: 49). POINAR & POINAR (1992: 68) report fossil Bacteria in amber and wrote: "Owing to the difficulty of examination under the light microscope few studies have been performed on microorganism in amber." POINAR & POINAR (1999: 69, fig. 21) published the electronic micrograph of a Bacterial cell in Mexican amber.



Figs. 1-3: Syninclusions with the partly decomposed body of the holotype male of *Gerdiopsis infrigens* n.gen.n.sp. (Hersiliidae) in Baltic amber. - Syninklusen beim teilweise zersetzten Holotypus ♂ der Kreiselspinne *Gerdiopsis infrigens* im Baltischen Bernstein;

fig. 1) Syninclusions behind the partly decomposed opisthosoma (remains at the left side), dorsal aspect. F = a feathery hair of the spider, H = questionable twig of a stellate hair (similar to a Nematoda), M = a mite (Oribatei), P = pollen grain, S = questionable spores of a fungus, comp. fig. 3. M = 0.2mm. - Syninklusen hinter dem teilweise zersetzten Hinterkörper (Reste sind links erkennbar). F = ein Fiederhaar der Spinne, H = fraglicher Ast eines Sternhaares (er ähnelt einem Fadenwurm), M = Milbe, P = Pollenkorn, S = fragliche Pilzsporen, vgl. Abb. 3;

fig. 2) A lump of questionable Bacteria from the excavated and partly decomposed prosoma. M = 0.01. - Klumpen fraglicher Bakterien aus dem ausgehöhlten und teilweise zersetzten Vorderkörper;

fig. 3) a single spore and a thread of 7 questionable spores of a fungus behind the opisthosoma of the spider; comp. fig. 1. M = 0.01. - 8 fragliche Pilzsporen hinter dem Hinterkörper der Spinne.

Observations (see also below, descriptions of the Fungi):

F50 (figs. 1-3): Within the partly decomposed and excavated prosoma of *Gerdiosis infrigens* (Hersiliidae, holotype ♂, photo) a lump of tiny questionable Bacteria are preserved (fig. 2) which have a diameter of almost 0.005mm. I do not want to exclude that these "particles" are spores of a fungus. A dissection of the amber piece is probably needed for a closer study. Gas bubbles are present within the prosoma and within the opisthosoma, which may be a product of decomposition.

F154: A partly dissected questionable member of the family Theridiidae indet. is well preserved (fig. 5). This spider is remarkable because of its condition and its syninclusions, e.g. remains of a possible prey (an ant), a mite, remains of blood, and probably the twig of a stellate hair (it is similar to a Nematoda). The droplets of blood indicate that the spider was embedded alive in the fossil resin. While entrapped in the fossil resin, a predatory animal - probably a beetle - may have fed on the spider's body on the surface of an amber layer. Bacteria may also be present.

F179: A large gas bubble is included in the opisthosoma of a juvenile Theridiidae.

F180: A movable gas bubble in liquid is preserved in the opisthosoma of a juvenile questionable Araneidae.

F807 (photo): The right side of the body of *Eodictyna communus* (♂) has largely been cut off within the fossil resin at an inner layer. A large bubble of decomposing gas and probably Bacteria has come out and has been covered by the next flow of the resin.

F984: The opisthosoma of the holotype of *Palaeomysmena hoffeinsorum* is strongly swollen probably by gas from decomposition.

F1245: A male of *Dipoena* sp. indet. (Theridiidae) is injured: The opisthosoma is deformed, some legs - e.g. the right leg II - are deformed or even broken (photo), the body is thickly covered by a white emulsion. Probably decomposing Bacteria are preserved on the body within the white emulsion.

F1258: The right femora I and II of a juvenile male of the Mimetidae indet. are deformed; within a white emulsion on the mouth parts questionable Bacteria are preserved.

(2) Fungi (Pilze) Photos 475ff

Decomposing (saprobiontic) Fungi ("mould Fungi") are frequent on rotten Baltic amber inclusions, also on most injured/deformed spiders. Old arthropods may be attacked and killed by pathogenic Fungi, more often one can observe dead arthropods covered with hyphae of saprobiontic fungi which decompose dead animals, e.

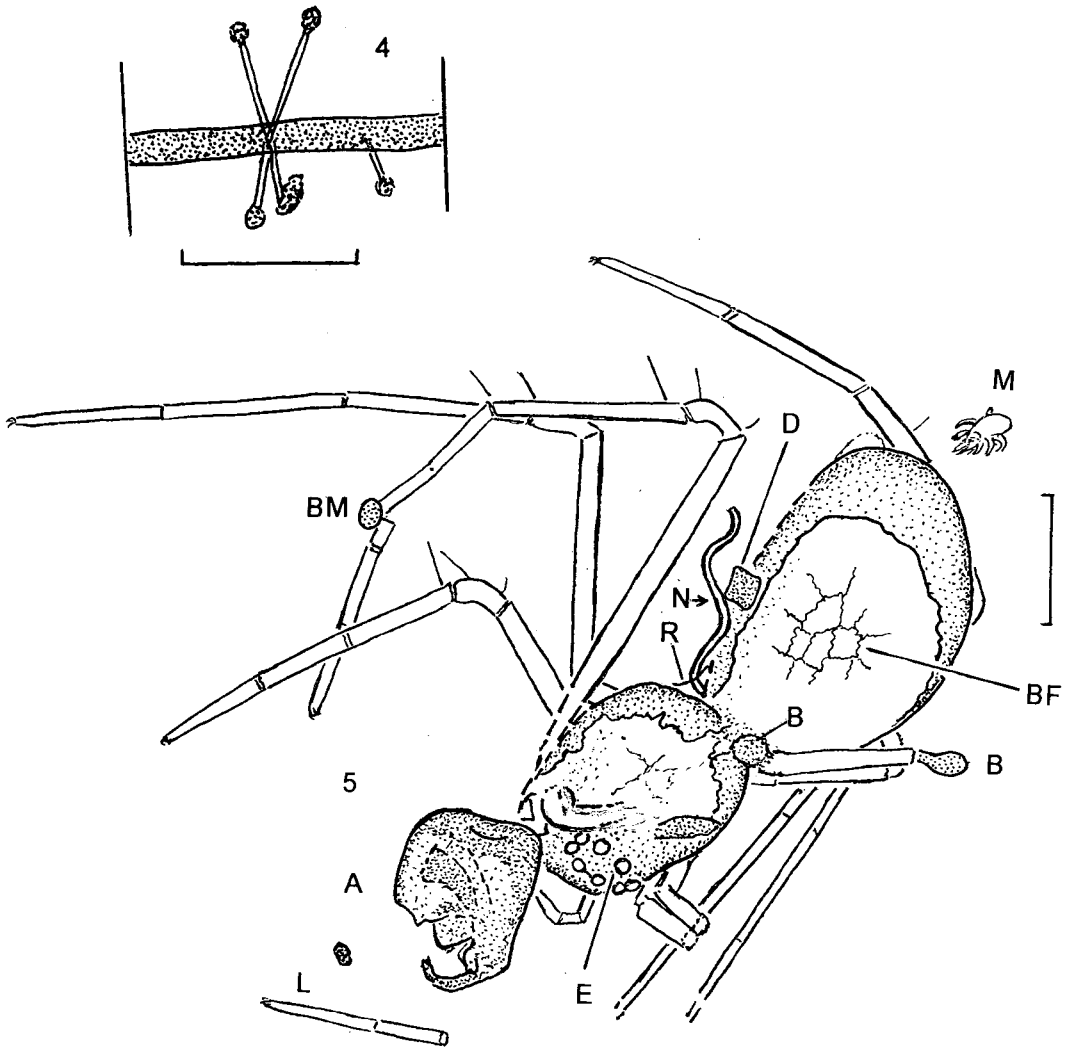


Fig. 4) Questionable fungal sporangia (*Arachnomycelium*) with growing on a questionable spider's thread in Baltic amber (only a short section is shown), F1140/CJW, see the text. M = 0.02. - Fragliche Pilzfäden mit "Köpfchen" (Sporangien?) auf einem Spinnfaden (?); "Spinnfadenpilz" (*Arachnomycelium*) im Baltischen Bernstein, siehe den Text;

fig. 5) Partly dissected body of a fossil spider, ?Theridiidae indet., F154/CJW, see the text. A = remains of an ant's head (a prey of the spider?), B = blood, BF = a droplet of blood at the end of the right femur I, BM = a droplet of blood on the broken right metatarsus II, D = questionable particle of dust, E = eye field, F = fissures of the opisthosoma which has been "opened" and dried out, L = distal articles of the right leg I, M = mite, N = questionable Nematoda, R = remains of a liquid (water?). M = 0.5. - Teilweise zersetzter Körper einer fossilen Spinne; siehe den Text.

g. mycels/hyphae on the "dead fly at the window". Apparently the limit between pathogenic and saprobiontic fungi is not clear in all taxa, and transitional stages exist. Fungi which grow with numerous hyphae on living spiders may be pathogenic. The body of such fossil spiders is not deformed/injured (e.g. fig. 6), and there are indications that these spiders were captured alive in the resin. Most Fungi which grow on dead spiders are saprobiontic. The body of such fossil spiders shows - usually strong - deformations, which are caused by mechanic influences, see the photos, they exist on spiders which have been a prey, e.g. F135, and furthermore hyphae are growing on spiders' exuviae as well as on spiders' eggs. Furthermore some Fungi use the cuticula of Arthropods simply commensally as a substratum, see NOORDAM et al. (1998). Such hyphae of a Fungus have probably grown on the cuticula of the prosoma of the holotype of *Gerdiopsis infrigens* n.gen.n.sp. (Hersiliidae), F50, fig. 1. Similar hyphae have grown on a splinter of amber in the same amber piece. Apparently even after a spider has been trapped in the resin the growing of the Fungus continued for a while, see the shape of the hyphae in the photos, figs. 6-7, and see also ROSS (1998: 33). Some hyphae on the right side of the female of an Anapidae indet. (F208) were growing away from the spider, and upwards into the next (!) layer of the amber, too. VOIGT (1937: 42, t.2, fig. 4) published conidia of a Fungus growing on the remains of a fossil insect in Baltic amber.

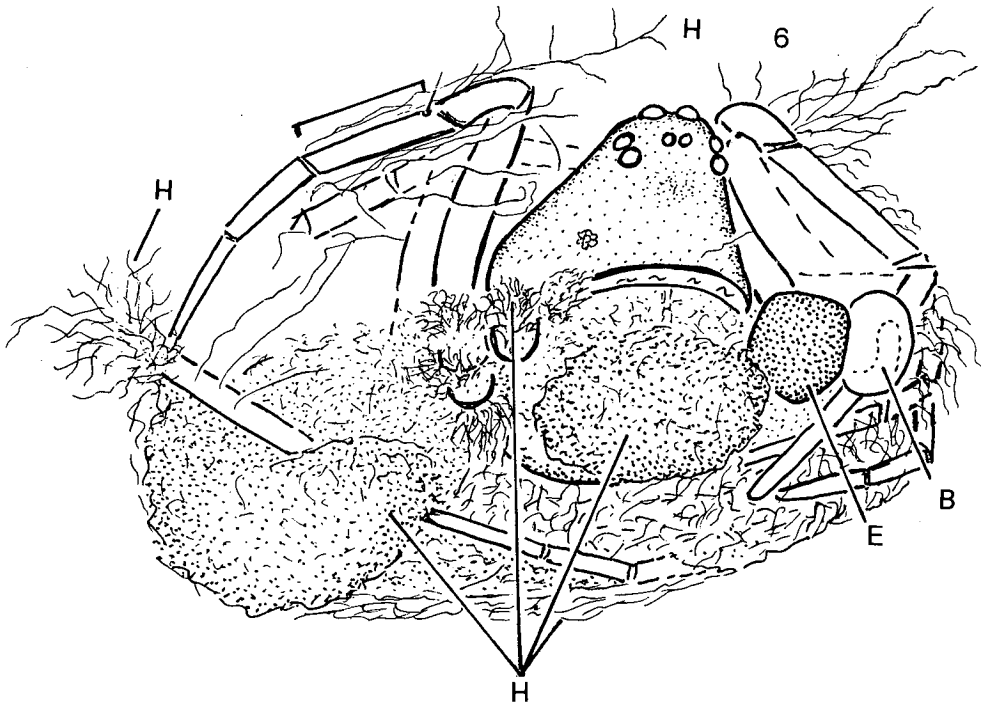


Fig. 6) Dense decomposing hyphae (H) on body and legs of a fossil spider in Baltic amber, family Anapidae: Anapinae indet., F208. B = bubble, E = small excrement. M = 0.2. - Dichte zersetzende Pilzfäden an Körper und Beinen einer fossilen Zwerg-Kugelspinne im Baltischen Bernstein, Ansicht von rechts vorn;

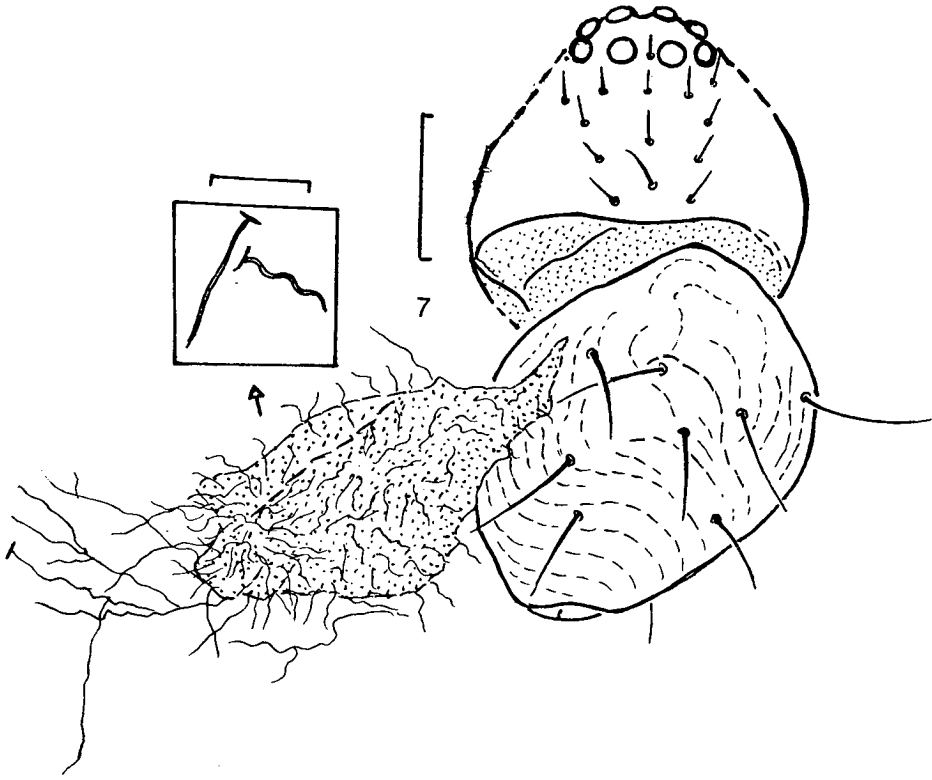


fig. 7) Dorsal aspect of the body of *Acrometa* sp. indet. (Synotaxidae), F198/CJW. Note the strongly deformed/injured prosoma which bears a deep posterior depression. Besides the injured opisthosoma: Numerous hyphae on a flow of blood (dotted). Only few hyphae and few of the long body hairs are drawn. Square: Two enlarged hyphae. M = 0.5. - Aufsicht auf Körper und Beine einer fossilen Kugelhöhlenspinne (*Acrometa* sp. indet.). Beachte den stark deformierten/verletzten Vorderkörper, der hinten eine tiefe Depression trägt. Neben dem verletzten Hinterkörper: Zahlreiche Pilzfäden auf einem Blutfluß (punktiert), im Quadrat sind sie vergrößert dargestellt. Foto 477.

WUNDERLICH (1986: 47, fig. 327) shortly describes hyphae on a fossil male of the spider *Nephila breviembolus* WUNDERLICH 1986 (Araneidae) in Dominican amber, which have been decomposing or pathogenic. NENTWIG (1985) regards the Fungus *Nomuraea* (= *Spicularia*) (Hyphomycetes) on extant spiders of *Nephila clavipes* (LINNAEUS) as parasitic.

Differences between spiders' threads and thin Fungus hyphae like relatives of *Aspergillus* (there are also thick and articulate Fungus hyphae which cannot be mistaken for spiders' threads): Most often the hyphae have numerous branches, are ending blind, are usually very thin, short and dense, the shape is often undulatory (the wiry hairs of spiders' egg sacs are thicker), see the photos. On the surface of some inclusions we find both - hyphae and spiders' threads as well -, see F135 and 194 below.

Occasionally - e.g. F807/CJW, F1140/CJW (see below and fig. 4), F1207/CJW, F1317/CJW - I found threads in Baltic amber which I regard as spider's threads which were decomposed by a Fungus which bears sporangia (fig. 4, photo). According to RIKKINEN (person. commun.) these structures may be Bacteria or fungal sporangia growing from the surface of probable spider's threads. GRÜSS (1931: 66, fig.7) published a strange "fungus", *Arachnomycelium filiforme* GRÜSS 1931, in which the basal thread looks extremely similar to a spider's thread which bears sporangia. Are these structures in fact originating from fungi? Closer studies are needed. See the paper on spiders' webs and threads (addendum).

I rarely found a hair-shaped questionable saprobiontic Fungus, e.g. on a loose metatarsus of the holotype of the Oecobiidae *Mizalia spirembolus* n. sp., F54 (similar in F216).

I found a single Fungus growing on questionable spiders' excrement, F1164; see the chapter on spiders' excrement.

In the following I describe shortly selected fossil spiders in Baltic amber, which are partly dissected, are covered with hyphae, and which got into the resin injured and/or dead:

F50: See above (Bacteria).

F135: The juvenile spider - ?*Eomatachia* sp. (Zoropsidae) - has been the prey of another spider. The body length may have been 3mm. The remains of the body's and legs' cuticula is strongly dissected, the spider is covered by numerous spiders' threads as well as short and thin hyphae. Remains of such prey is known from pre-dating Araneidae.

F144: A female of the family ?Agelenidae, body length 2.7mm. The prosoma and - especially - the opisthosoma are strongly deformed and covered by hyphae. The legs are complete.

F154: See above (Bacteria).

F194: The ?exuvia - or prey of a spider? -, probably of the family Trochanteriidae (genus ?*Sosybius*) - is partly covered by thin and branched hyphae as well as spiders' threads. The length of a tibia of the spider is 3.9mm.

F197: A subad. male of the superfamily ?Clubionoidea, body length about 4mm. The prosoma is laterally compressed on both sides, the opisthosoma has dorsal folds, its tip is cut off, the legs are complete, some articles are compressed. Most of the hyphae are present on the sternum and the pedipalpi. - Photo.

F198 (fig. 7): An adult female of *Acrometa* sp. (Synotaxidae), body length 2.1mm. The legs are complete, the body is deformed, the posterior part of the prosoma has a deep depression. The left side of the opisthosoma has been injured, a flow of haemolymph and probably parts of organs and excrements is situated on the left femur IV. Because of the loss of pressure the legs are strongly bent under the body

and the haemolymph apparently flowed into the resin. Therefore the spider has been captured just after its death or during dying in the resin and most probably the hyphae grew after their embedding in the resin. This haemolymph flow is covered by numerous thin hyphae; other parts of the spider are free of hyphae. The diameter of the hyphae is about 0.002mm. Photo.

F199: An adult female of the family Corinnidae, body length 2.3mm. The spider is complete, a white emulsion is absent, the opisthosoma has a deep dorsal and a deep ventral depression, the legs are strongly bent under the body. The ventral part of the body is covered by numerous thin hyphae, the remains of two Collem-bola are also present in this piece of amber.

F208 (fig. 6): An indet. ?juvenile spider of the family Anapidae: Anapinae. Measurements (in mm): Body length about 0.8, prosomal height above the chelicerae 0.22, leg I: Femur 0.26, tibia 0.29, metatarsus 0.24, tarsus 0.26. Colour dark red-brown. 8 eyes, anterior medians the smallest. The opisthosoma bears a large dorsal scutum, the ventral side is hidden. The spider has been partly decomposed by a Fungus and partly destroyed: Both pedipalpi are missing, some leg articles are loose, the opisthosoma is largely blown up (best observable from above), a small excrement ball and a gas bubble are preserved besides the left part of the prosoma, some detritus particles are not drawn in the figure. The Fungus is growing under the body and some leg articles, especially on the stump of the right leg I and on some skinny parts between various leg articles. The hyphae are often branched, their diameter is about 0.003 mm.

F222: The body length of this female Salticidae is 4.5mm. The legs are strongly bent under the body. Most probably the amber piece has been heated in an autoclave. The ventral side of body and legs is covered by a white emulsion, the dorsal part of the opisthosoma has been cut off at a resin layer and later on excavated; in the opisthosoma a large and a small bubble are preserved. On the surface of the large bubble some tiny and branched hyphae, some large - up to 1.2mm long - and not branched ?Fungi are present. - Photo.

F223: The body length of this *Acrometa* sp. male is about 2.6mm. The legs are bent under the body, prosoma and opisthosoma are dorsally distinctly depressed - by a blow? So the spider has been captured alive in the resin. Probably the amber piece has been heated in an autoclave. The ventral side of the opisthosoma is covered by a white emulsion, a large white bubble covers dorsal parts of the body. A dense brush of thin hyphae has grown on the left legs I and II. - Photo

F591: The exuvia of a subadult male Salticidae indet. is preserved within numerous hyphae which probably were not dissecting the exuvia.

F1140: Near the remains of an egg sac and exuvia of an Araneae indet. a double thread of questionable spiders' silk is present which possesses swellings in some parts, and bears numerous ?mould fungi which have tiny "capitula" (sporangia?) as shown in fig. 4. Did this fungus decompose the spiders' threads and/or the exuvia? See above: *Arachnomycelium*.

F1143: A male Salticidae indet. has a deformed opisthosoma, and ventrally bears numerous hyphae.

F1147: A male of *Acrometa balticus* PETRUNKEVITCH 1942 (Synotaxidae) is injured and covered with hyphae. Acari indet. are present in the same piece of amber.

F1165: A probably adult female Araneae indet. is incompletely preserved, it is injured, and mainly dorsally covered by numerous hyphae.

F1256: A probably juvenile female of ?*Eomatachia* sp. indet. (Zoropsidae) is widely surrounded by numerous hyphae which are in contact with the legs and the body which is 4.5mm long. The prosoma is dorsally deformed, both sides are inclined.

F1258: A juvenile male of the family Mimetidae indet., injured and in decomposition.

F1320: An egg sac which has a diameter of 3.5mm and in which exuviae and egg covers are present. Probably some egg covers were partly decomposed by hyphae.

Coll. HOFFEINS no. 420.1: A juvenile spider probably of the family Gnaphosidae. The body length is 2mm. Prosoma and opisthosoma are strongly deformed, the right leg IV is missing after the coxa. Body and legs are covered with thin hyphae; ?another Fungus has grown on the right legs I and II in a nearly spherical shape of the mycel. Photo.

Coll. HOFFEINS no. 420.2: An adult female of the genus *Orchestina* SIMON (Oonopidae). The body length is 1.5mm. The spider is completely preserved, the legs are strongly bent under the body, the opisthosoma is dorsally totally excavated, the prosoma is dorsally completely covered and hidden by a dense mycel.

(3) Nematoda (Fadenwürmer)

There are two taxa of fossil "worm" *larva* of the phylum Nematelminthes: Nematoda with spiders in amber: (a) Saprobiotic members of the order Rhabditida - see the notes on the family Anguillidae in LARSSON (1978: 117) - which may be phoretic, and (b) endoparasites - or parasitoids - of the order Trichosyringida, members of the family Mermithidae. (Some authors place Mermithidae within the Dorylamida, others have proposed a new order, Mermithida).

Some probably saprobiotic fossil members of the order Rhabditida are present in the CJW, but the determinations are quite unsure, some may be Fungi or branches

of stellate hairs. An example is the questionable Nematoda which is in contact with the opisthosoma of a fossil spider (fig. 5).

(4) Acari (Milben)

Certain groups of mites are important decomposers. A study of fossil decomposing Acari is still wanting. Fossil phoretic mites must not be mistaken for decomposing or parasitic specimens.

Observations of fossils in Baltic amber:

F50: A member of the Oribatei is preserved near the partly decomposed opisthosoma of *Gerdiopsis infrigens* n. gen. n. sp. (Hersiliidae), (fig. 1).

F154: A tiny mite larva (indet.), is present behind a questionable member of the family Theridiidae which is partly dissected (fig. 5).

F883: An injured juvenile spider of the family Agelenidae (questionable), body length 3.5mm has a depressed prosoma. Probably decomposing mites of the family Anoetidae are preserved on the spider's body and nearby.

F1147: Numerous probably decomposing Acari indet., are preserved with a male of *Acrometa baltica* PETRUNKEVITCH 1942 (Synotaxidae). The spider is injured and covered with hyphae.

MOULTING AND EXUVIAE (HÄUTUNG UND HÄUTUNGSRESTE)

Photos 452-472

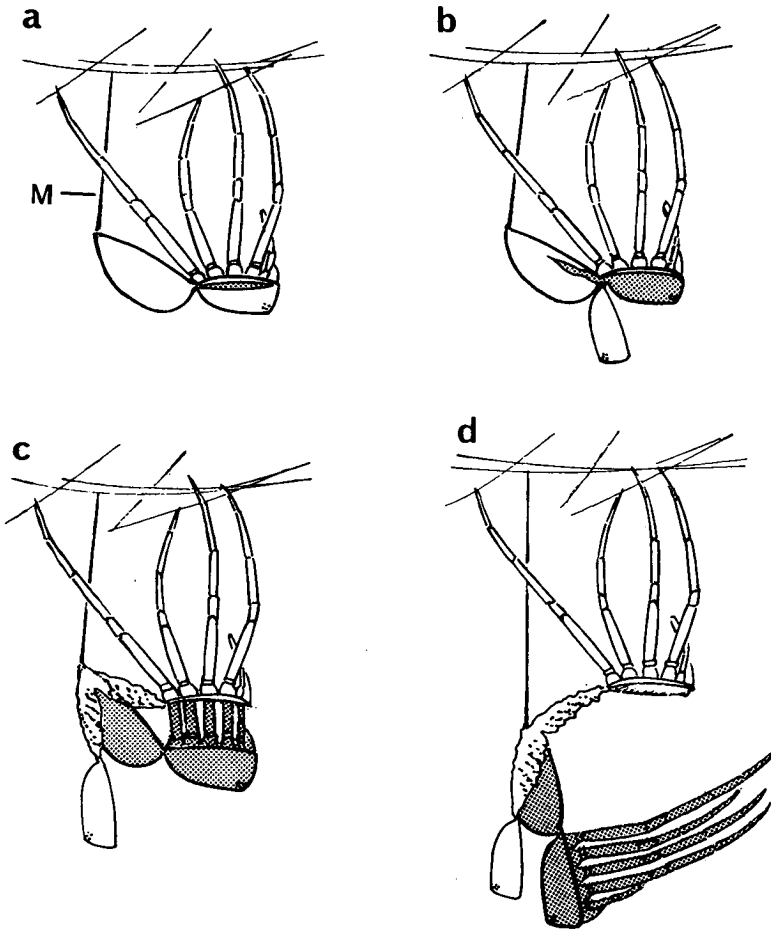
See also the chapters on prey, a retreat,..., capture webs, egg sacs, the Mygalomorpha and the Pisauridae in these volumes.

Introduction

Most parts of the spider's body possess a more or less hard exoskeleton which protects against enemies and against drying out, it functions also as a starting point of muscles, bears hairs, spines, openings of glands, sensory organs, and parts of the respiratory system and of the genital organs. The opisthosoma can be soft or armoured. Because of its hardness the exoskeleton cannot grow with the spider and the spider has to moult and to leave behind its old "skin" like a shirt, which may be blown away by the wind e.g. to fossil resin, and be decomposed by fungi. The new exoskeleton is still soft and thus can grow now. Most spiders moult about seven times until they are adult (reproductive). Certain spiders - the first instars - moult for the first time already in their egg cover within the egg sac, see FOELIX (1996). The last stage before being adult is the subadult stage in which the epigynal sclerotization is still weak and the tarsus of the male pedipalpus is large, balloon-shaped (see the photos) and possesses no sclerites like the cymbium, tibial and bulbus apophyses, embolus. During moulting the old "skin" of the pedipalpal tarsus is left behind like mitten. The eye lenses, spinnerets, hairs and most parts of the respiratory system are moulted, too; the hairy "skin" of the opisthosoma is shrunk, strongly deformed and usually located between the dorsal sclerite of the prosoma and the remaining parts (the chelicerae, sternum and legs), see fig. d and the photos. Most spiders do not moult any more as adults, but females of long-living and more "primitive" spiders as Mesothelae, Mygalomorphae and the cribellate Filistidae and Eresidae moult as adults, too; the short-living adult males moult only exceptionally. The old cuticula, lost hairs etc. are replaced, but these spiders do not grow any more. - The regeneration of legs is connected with the moult. Moulting is a complicated procedure; if a leg does not loosen from the old "skin" it may be autotomized and left within the exuvia.

Most spiders - except the Mesothelae and the Mygalomorpha - spin a special "moulting thread" or even a "moulting web", which may be preserved with the fossil spiders, see the photos. According to FOELIX (1996: 223) "In all spiders...three successive phases of the molting process can be distinguished: (1) lifting of the carapace" (prosoma) "; (2) liberation of the abdomen" (opisthosoma) "; and (3) extraction of the extremities." First the anterior and lateral parts of the prosoma burst, and then the dorsal cover of the prosoma flaps backwards as can be observed in most of the photos. Finally the spider fixes a thread on the exuvia and may rope down, see the figs. a-d below, fig. 1.

The fossil spiders: PETRUNKEVITCH (1950: 261, Fig. 169, 172, 179) described exuvia of fossil spiders in Baltic amber (*Eocryphoea*, *Segestria*) and the moulting web of an *Eocryphoea* specimen.



Figs. a-d: Moulting in araneomorph spiders. a) Spider suspended on the moulting thread (M); frontal and lateral tearing of the prosoma. b) Lifting of the dorsal prosomal sclerite and lateral fission of the opisthosomal cuticle. c) Freeing of legs and opisthosoma, continuing flapping backwards of the dorsal prosomal sclerite. d) Complete liberation from the exuvium. - After BONNET (1930); taken from FOELIX (1992).

Abb. a-d: Häutung bei höher entwickelten Spinnen. a) Aufhängen am Häutungsfaden (M); vorderes und seitliches Aufreißen des Vorderkörpers. b) Hochklappen der Decke des Vorderkörpers und Einreißen am Hinterkörper. c) Befreien der Beine und des Hinterkörpers, weiteres Umlappen der Decke des Vorderkörpers nach hinten. d) Vollständige Befreiung aus der alten "Haut" (Exuvie).

Einleitung

Die meisten Körperteile der Spinnen besitzen ein mehr oder weniger hartes Außenskelett, das gegen Feinde und Austrocknung schützt; außerdem dient es als Ansatzstelle für Muskeln, trägt Haare, Stacheln, Öffnungen von Drüsen, Sinnesorgane sowie Teile des Atmungssystems und der Geschlechtsorgane. Der Hinterkörper kann weich oder gepanzert sein. Weger seiner Härte kann das Außenskelett nicht mit der Spinne mitwachsen, die Spinne ist gezwungen, sich mehrfach zu häuten und die alte "Haut" wie ein Hemd als "Häutungsrest" zurückzulassen. Dieses kann vom Wind davongebblasen werden, z. B. zu fossilem Harz, und es kann von Pilzfäden zersetzt werden. Das neue Außenskelett ist noch weich und kann daher jetzt eine Zeitlang weiterwachsen. Die meisten Spinnen häuten sich etwa sieben mal bis sie erwachsen (fortpflanzungsfähig) sind. Manche Spinnen häuten sich bereits innerhalb der Eihülle im Eikokon zum ersten Mal, siehe FOELIX (1996). Das letzte Stadium vor der Reifehäutung ist das subadulte Stadium, bei dem die Verhärtungen der weiblichen Geschlechtsplatte (Epigyne) noch schwach ausgebildet sind und das Endglied des männlichen Pedipalpus ungewöhnlich groß ist, ballonförmig (siehe die Fotos), Cymbium und Apophysen fehlen noch. Während der Häutung wird die alte "Haut" der Pedipalpen wie Fäustlinge zurückgelassen. Die Linsen der Augen, die Spinnwarzen, die Haare und die meisten Teile des Atmungssystems werden ebenfalls abgestreift. Die haarige "Haut" des Hinterkörpers der Exuvie ist nun stark deformiert und enorm geschrumpft; sie befindet sich gewöhnlich zwischen der Decke des Vorderkörpers und den übrigen Teilen (Cheliceren, Sternum, Beinen), siehe Abb. d und die Fotos. Die meisten Spinnen häuten sich nicht mehr, sobald sie geschlechtsreif sind, aber die Weibchen lang-lebender und ursprünglicher Spinnen - wie der Gegliederten Spinnen (Mesothelae), der Längskieferspinnen (Mygalomorpha) sowie der cribellaten Sternnetzspinnen (Filistatidae) und der Röhrenspinnen (Eresidae) - häuten sich auch weiterhin; die kurzlebigen geschlechtsreifen Männchen häuten sich dagegen nur noch ausnahmsweise. Die alte "Haut", verloren gegangene Haare usw. dieser Spinnen werden ersetzt, aber die Spinnen wachsen nicht mehr. - Die Regeneration der Beine steht in Zusammenhang mit der Häutung. Häutung ist ein komplizierter und störanfälliger Vorgang; wenn ein Bein sich nicht aus der alten Haut löst, kann es abgestoßen (autotomisiert) und in der alten "Haut" zurückgelassen werden. - Fig. 1.

Die meisten Spinnen - mit Ausnahme der Gegliederten Spinnen und der Längskieferspinnen - spinnen einen besonderen "Häutungsfaden" oder sogar ein "Häutungsnetz", das bei fossilen Spinnen konserviert sein kann, siehe die Fotos. Nach FOELIX (1996: 223) lassen sich bei der Häutung der Spinnen drei Phasen unterscheiden: 1. Ein Anheben der Decke des Vorderkörpers, 2. Die Befreiung des Hinterkörpers und 3. das Herausziehen der Extremitäten. Dabei reißen zuerst die vorderen und seitlichen Teile des Vorderkörpers auf und dann wird die Decke des Vorderkörpers zurück geklappt; diesen Zustand zeigen die meisten Fotos. Schließlich fixiert die Spinne einen Faden (M) an der Exuvie, an dem sie sich herunterläßt, siehe die Abb. a-d.

In the following I describe selected moultings, exuviae and moulting webs of spiders in Baltic incl. Bitterfeld amber:

Exuviae of fossil spiders in Baltic amber are not rare, I have seen hundreds of pieces in numerous collections, more than 50 pieces are kept in my private collection. Specimens which are preserved during the moulting are rare, e.g. F138/CJW, F1170/CJW, coll. GRÖHN in Hamburg no 3947 and Museum Ziemi no. 21705 (just after the moulting). Occasionally a spider and its exuvia can be found in the same piece of amber, e.g. in the coll. GRABENHORST in Celle no. AR-19 and in F156/CJW. - The determination of exuviae may be difficult and is frequently impossible even to the family level.

As most adult spiders in Baltic amber also most of the exuviae are from species of the superfamily Araneoidea, e.g. Araneidae, Linyphiidae (*Custodea*), Synotaxidae (*Acro-meta*), Theridiidae (*Dipoena*) and Zygellidae, but also members of the families Salticidae (*Eolinus*, *Gorgopsis*), Segestriidae (*Segestria*), and Zoropsidae (*Eomatachia*) are not rare. Furthermore I have found exuviae of Clubionoidea (Corinnidae, Liocranidae), Ctenizidae, Dipluridae, ?Ephalmatoridae, ?Pisauridae, Thomisidae and Trochanteriidae. Surprisingly I did not identify a single member of the genus *Orchestina* (Oonopidae); specimens of this genus are very frequent in Baltic amber. The small exuviae of members of the family Ctenizidae are by far more frequent than the large and - in amber - extremely rare adults of this family. A moulting thread (a dragline) is preserved e.g. with a member of the Clubionoidea, F1173, see below, some threads or even moulting webs are present e.g. with a member of the families Synotaxidae and Theridiidae, F138/CJW, F139/CJW, F156/CJW; sticky droplets indicate parts of capture webs, e.g. F1191, 1196.

Twenty-three pieces with exuviae are kept in my private collection, F1218/BB/AR/CJW; most of them are not determined to the family level.

Description of the remaining specimens:

Coll. GRABENHORST AR-19: *Acrometa cristata* PETRUNKEVITCH 1942 (Synotaxidae), ♂ and exuvia nearby, in amber from the Bitterfeld deposit, body length ♂ ca. 2.3mm. Both are almost complete. The ventral side of the spider is covered by a white emulsion. Parts of the tarsi II-IV of the exuvia are cut off. There is only an indistinct thread at the exuvia.

Coll. GRÖHN no 3947: A male of *Eolinus* sp. indet. (Salticidae) during moulting. See the chapter on camouflage and the photo.

Mus. Ziemi no. 21705: *Gorgopsina* sp. indet., ♂ and its exuvia just after moulting. The body length of the male is 3mm, its ventral side is covered by a white emulsion; the dorsal sclerite of the exuvia is situated directly behind the prosoma of the male and covers its opisthosoma. The right leg III of the male is deformed, some leg articles of the prosoma are missing, threads are absent.

F138/BB/AR/THE/CJW from the Bitterfeld deposit: A probably juvenile female of the family Theridiidae indet. during moulting, body length of the female almost 2mm. Most leg articles of the exuvia are cut off. Some threads of silk are present in the sa-

me piece of amber, and probably remains of a globular egg sac. The tips of some tarsi are not yet removed from the exuvia.

F139/BB/AR/?SYN/CJW: ?*Acrometa* sp. indet. (Synotaxidae), exuvia, prosomal length 1.2mm, spiders (moulting?) threads, and more than 100 Nematoda: Rhabditida. The exuvia is complete, the remains of the opisthosoma and the inverted dorsal sclerite of the prosoma. Some Nematoda: Rhabditida are situated near to the spider but not in contact with it.

F156/BB/AR/THE/CJW: A female of the family Theridiidae indet., body length 2mm, which is thickly covered by a white emulsion, and its exuvia is preserved in its (moulting?) web. Nearby preserved is a prey of this (?) spider, a tiny ant.

F194/BB/AR/TRO/CJW from a locality in Denmark: Remains of a large exuvia, probably of the family Trochanteriidae (*Sosybius?*), the length of a tibia is 4mm. Several leg articles and the dorsal sclerite of the prosoma are missing, the chelicerae are present; numerous spider's threads and hyphae are preserved, too.

F376/BB/AR/CJW: ?Zygiellidae indet., exuvia, prosomal length 1.5mm, the dorsal sclerite of the prosoma is missing, a part of the left leg IV is loose and is lying behind the exuvia, threads are absent. A particle of excrement of an insect is preserved dorsally on the sternum.

F542/BB/AR/CJW: *Segestria* sp. indet. (Segestriidae), an incomplete exuvia, the sternum is 1.25mm long, the dorsal sclerite of the prosoma is missing, both legs IV are cut off, the legs I-III are stretched forwards as in adult spiders of this family. Threads of silk are absent.

F578/BB/AR/CJW: Tibia and tarsus of a subadult male exuvia of a spider indet. are preserved in a stretched position (photo), the prosoma is turned back and is 3mm long; few threads are present.

F822/BB/AR/DIP/CJW: Parts of a large exuvia of the family Dipluridae, several leg articles and a loose leg, length of its tibia 9.7mm.

F1109/BB/AR/SEG/CJW: Most parts of an exuvia of a *Segestria* sp. indet. (Segestriidae) are preserved in a stretched position (photo) on a layer in the amber, the dorsal sclerite of the prosoma is turned back and is 3mm long.

F1143/BB/AR/CJW: A complete exuvia of a probable member of the family Theridiidae. The remains of the opisthosoma connect the dorsal sclerite of the prosoma, which is 0.8mm long, and the remaining parts of the exuvia. Threads are absent.

F1167/BB/AR/CJW: A complete exuvia of ?*Ephalmator* sp. indet. (Ephalmatoridae) is stretched out on a layer in the amber. The remains of the opisthosoma connect the dorsal sclerite of the prosoma, which is 0.8mm long and weakly rugose, with the remaining parts of the exuvia. Threads are absent.

F1168/BB/AR/ZYG/CJW: An almost complete exuvia of a probable subadult female which may belong to the family Zygiellidae, prosomal length 2.3mm. In this unusual case the dorsal sclerite of the prosoma is present in its natural position, because this

sclerite flapped back after moulting. The anterior spinnerets are well preserved, threads are absent.

F1170/BB/AR/CJW: A specimen of the "Trionycha", indet., a male during moulting, in a heated piece of amber from the Bitterfeld deposit, body length 2mm. The prosoma and some leg articles are distinctly deformed. The moult of most parts is finished, but the pedipalpi are still fixed within the old exoskeleton. The tarsus of the right pedipalpus possesses a large distal outgrowth which is directed backwards. A large fissure is present at one side of both objects, threads are absent.

F1171/BB/AR/SEG/CJW: Most parts of an exuvia of *Segestria* sp. indet. (Segestriidae), prosomal length 2mm. The prosoma and small parts of the opisthosoma are lying away from the remaining parts of the exuvia. Threads are absent.

F1172/BB/AR/?ARA/CJW: A complete exuvia of a subadult male which may belong to the family Araneidae, prosomal length 1.7mm. The dorsal sclerite of the prosoma is lying in an inverse position on the opisthosoma, the sternum possess a light median band, the spinnerets are well preserved, a short dragline (moulting thread?) originates at the anterior spinnerets. The annulation of the legs is preserved.

F1137/BB/AR/CJW: An almost complete exuvia of a probably subad. female of the superfamily Clubionoidea indet. The prosoma and the tibia II are both 4mm long. The ventral side of the dorsal prosomal sclerite is situated beneath the sternum. The spinnerets are well preserved, and a dragline (moulting thread?) is present. Some leg articles are cut off or strongly oxidated. A larva of the Aphidoidea and a branch, 1.2cm long, of a Gymnospermae are preserved near the exuvia.

F1191/BB/AR/CJW: An incomplete exuvia of a member of the Araneidae or Zygeliidae in its capture web with sticky droplets, prosomal length 2.5mm. The dorsal sclerite of the prosoma is somewhat separated from sternum and legs, and partly covers the remains of the opisthosoma. A Nematoda: Rhabditida is preserved very close to the left margin of the dorsal prosomal sclerite, an insect larva is present 4mm away from the exuvia.

F1196/BB/AR/CJW: 7 exuviae of juvenile spiders - probably second or third instars - of an Araneae: Trionycha indet. are preserved in their webs, sticky droplets are present, their body length is about 1.5mm. Several Acari are preserved in the same piece of amber.

F1216/BB/AR/CJW: A complete exuvia of a juvenile male of the Araneae: Trionycha is hanging in the larger part of a probably tube-shaped web. The dorsal prosomal sclerite is 1.8mm long and flapped backwards by 180°.

F1219/BB/AR/LIN/CJW: It contains a female exuvia of a Linyphiidae indet., the dorsal prosomal sclerite is 1.0mm long and flapped up, some leg articles are cut off, few spider's threads are present.

F1220/BB/AR/?ZOR/CJW: An exuvia and part of a web of a ?*Eomatachia* sp. indet. are preserved in a piece of amber from the Bitterfeld deposit. The length of the loose dorsal prosomal sclerite is 2.2mm, most leg articles are missing.

F1221/BB/AR/ZOR/CJW: A female exuvia of *Eomatachia* sp. indet. (Zoropsidae) is hanging in its web, the incomplete dorsal prosomal sclerite is 1.3mm wide, several leg articles are cut off, e.g. all tarsal claws; on a single complete metatarsus II I found only a single trichobothrium. The posterior eye row is distinctly procurved, the labium is not rebordered as in most Araneoidea. Only parts of the spinnerets are preserved. Furthermore two juvenile and probably conspecific spiders - body length about 1.5mm - and remains of two more juveniles are present as well as ecribellate and probably cribellate spider's threads. The smell during dry cutting indicates that the piece of amber was heated.

F1222/BB/AR/CJW: An almost complete exuvia of a subadult male of the Araneae: *Trionycha* indet. is preserved in its web. The dorsal sclerite of the prosoma is 2mm long and situated behind the legs and above the shrunken remains of the opisthosoma. The thick pedipalpal tarsi are shrunk. Tibial sutures are absent.

Syphax fuliginosus KOCH & BERENDT 1854 (Thomisidae), ♀, holotype (PIHUB) in Baltic amber during moulting, photo, fig. 1.

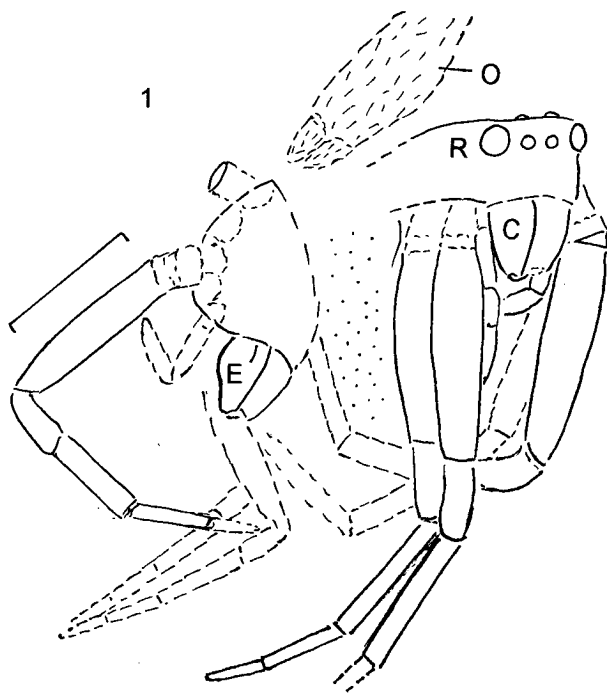


Fig. 1) Moulting of the holotype of *Syphax fuliginosus* KOCH & BERENDT 1854 (Thomisidae), ♀ in Baltic amber. Exuvia at the left side. M = 2mm. E = right chelicera of the exuvia, C = right chelicera of the moulted ♀, O = remains of the exuvial opisthosoma. Only few legs and no hairs are drawn. - Abb. 1) Häutung beim Holotyp ♀ der Krabbenspinne *Syphax fuliginosus*, links die Exuvie. Photo 470.

See the chapters on decomposition, injuries and parasites. Photo 89.

FOELIX (1992, 1996) does not mention Bacteria. MOREL (1978) reports no pathogenic/parasitic Bacteria but Rickettsia, Viruses and Fungi (Ascomycetes and Hyphomycetes). COKENDOLPHER (1993: 121) reports few taxa of extant Bacteria which parasitize Opiliones. NENTWIG (1985, 1990) reports on extant pathogenic/parasitoid (1985 sub "parasitic") - or saprobiontic? - Fungi of extant spiders. NOORDAM et al. (1998) regard an Hyphomycet as probable "mild" parasite of Linyphiid spiders. - Fossils: We find only five lines about fossil Bacteria in the book of LARSSON (1978: 49). POINAR (1992: 68) wrote: "Owing to the difficulty of examination under the light microscope few studies have been performed on microorganisms in amber."

Up to now I have not recognized any certain pathogenic Bacteria or Fungi on fossil spiders, but decomposing Bacteria and Fungi are not rare, see the chapter on injuries, healing and decomposition in this volume. A Fungus probably infected the holotype of the fossil spider *Gardiopsis infrigens* n. gen. n. sp. (Hersiliidae) which may have been injured above the anal tubercle; "wound parasitism" sensu HEITOR (1962). The gemmae of the Fungus behind the opisthosoma of the spider are similar to the gemmae of the pathogenic Fungus *Mucor hiemalis* (Zygomycetales), which is distributed cosmopolitically, see HEITOR (1962). The diameter of the cells of the fossil Fungus is less than 0.01mm. Extant Zygomycetales are known as saprobionts as well as pathogens, see NENTWIG (1990).

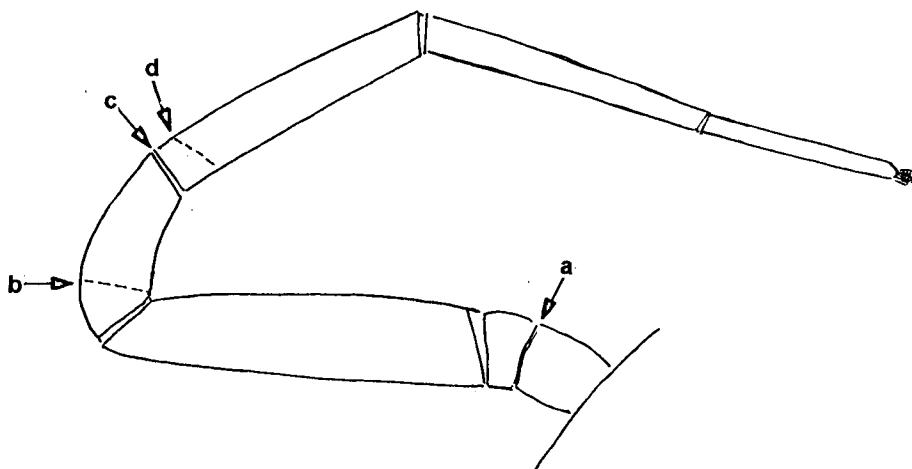
ON THE LEG AUTOTOMY IN SPIDERS - ZUR ABSTOSSUNG VON BEINEN BEI SPINNEN

Photos 89, 91, 95, 254-255, 461 and 674.

See ROTH & ROTH (1984) and FOELIX (1992: 229-230). A closer and systematic study in numerous spider taxa is needed. The sticky fossil resin induced leg autotomy of spiders; so the fossil spiders which are preserved in amber are optimal objects for the study of autotomy.

1. Definition: Autotomy is the separation/break of body appendages or their parts at a pre-determined locus of weakness caused by an external source. I use the well introduced term autotomy in a wide sense and subordinate the terms autospasy (as observed in most amber spiders the article is usually fixed and drawn away from the body) and autodilly; see various papers of GRISWOLD and the paper of ROTH & ROTH (1984).

2. Kinds of autotomy (see the fig. below and the photos): **(a)** By far the most frequent autotomy occurs between coxa and trochanter (e.g. in Oonopidae, Araneidae, Lycosidae, see below); **(b)** rarely through the patella: In some genera of the Agelenidae (?), see ROTH & ROTH (1984: 142) and *Diores* of the Zodariidae, see



Leg detachment points: (a) coxa-trochanter joint, (b) patellar detachment line, (c) patella-tibia juncture, (d) tibial detachment line.

JOCQUE & DIPPENAAR-SCHOEMAN (1992) and the below; **(c)** occasionally between patella and tibia (Filistatidae, Leptonetidae, Hersiliidae, Oecobiidae: Leban-oecobiinae and Oecobiini, Pimoidae and Linyphiidae); **(d)** rarely - not known by ROTH & ROTH (1984) - through the base of the tibia, only in males (in male juveniles, too): In Zoropsidae (s.l.) (in the extant Zoropsinae a brake is absent but a suture is present; see the paper on this family in this volume).

3. Occurrence and distribution of leg autotomy in spiders' taxa:

(A) In different taxa: From the Mygalomorpha I only know coxa-trochanter detachment, and autotomy seemingly is not frequent, e.g. it is absent in extant Atypidae, pers. observ., and in the Ctenizidae, pers. observ. in fossils, see ROTH & ROTH (1984: 143), but it is not rare in fossil juvenile Dipluridae: I found autotomy in more than 50% of the fossil specimens at one or several legs. - In the Araneomorpha autotomy is present in most families but usually absent in the cribellate taxa. Autotomy is present in the classical Haplogynae **(a)** between coxa and trochanter in the Oonopidae: Very frequent in amber fossils (pers. observ.), Segestriidae: Frequent in amber fossils (pers. observ.), Dysderoidea: E.g. in the Loxoscelidae and the Pholcidae; **(b)** between patella and tibia in the Filistatidae and the Leptonetidae. - In the Caponiidae and the Eresoidea autotomy seemingly is absent; in the fossil Dysderidae I found only rarely one leg broken off behind the coxa.

Araneioidea s. l. families: See no. 6.

In the families of the RTA-clade autotomy usually is present - probably as an autapomorphy of this clade - between coxa and trochanter; it is absent according to ROTH & ROTH (1984: 143) in few families only, e.g. in the Zodariidae (absent e.g. in all of the fossil taxa in Baltic amber, but present in *Diores*, see the paper on this family in these volumes) and Miturgidae.

(B) In juveniles' autotomy I found no difference to the adults.

(C) Sexual dimorphism: Only in the Zoropsidae autotomy occurs simply in males but not in females, see no. 2.

4. Frequency of autotomy in fossil Baltic amber spiders: I found it **(a)** usually in 30-35% of the specimens (e.g. in Salticidae) up to 55-60% e.g. in *Mizalia* (Oecobiidae) but exceptionally in all males studied by me in *Eoprychia* (Zoropsidae s.l.), see no. 3; in this case I call autotomy "frequent" or **(b)** up to about 10%, e.g. in Dictynidae, Dysderidae and Hahniinae; in this case I call autotomy "absent to rare", see no. 3. **(c)** In fossil *Mastigusa* (Dictynidae) I found autotomy in 20% of the specimens; here I call autotomy "not rare".

5. A remarkable result: The occurrence and the kind of autotomy are usually constant on family level, with few exceptions of a "multiple autotomy": **(A)** In the Oecobiidae: Autotomy is present (1) between coxa and trochanter in the Mizaliinae, (2) between patella and tibia in the Lebanocobiinae and the Oecobiinae: Oecobiini, (3) absent in the Oecobiinae: Urocteini and probably in the Uroecobiinae, **(B)** in the Araneidae: Present in taxa studied by me; according to ROTH & ROTH (1984: 143) "absent in some taxa" but these authors included erroneously the Tetragnathinae in this family - in which autotomy is absent (!); **(C)** in the Agelenidae: Usually autotomy occurs between coxa and trochanter but according to ROTH & ROTH (1984: 142) in few genera of - ?true - Agelenidae it occurs through the patella; **(D)** in the Zodarii-

dae: Autotomy is absent except in the genus *Diores* SIMON 1893, see JOCQUE & DIPPENAAR-SCHOEMAN (1992). - To my knowledge autotomy is also **constant (a)** on the **suprafamilial level**: In the Eresoidea leg autotomy is totally absent; **(b)** on the **genus level** different kinds of autotomy are present without exceptions e. g. in *Araneus*, *Custodela*, *Eomatachia*, *Eoprychia*, *Graea*, *Orchestina*, *Zoropsis* and *Zygiella* (pers. observ.).

6. Autotomy in the superfamily Araneoidea s. l. (personal observation): **(a)** between coxa and trochanter: In the „coxa-trochanter autotomy clade“ (frequent e. g. in the Araneidae and Zygiellidae; rare or probably absent in the Cyatholipidae); **(b)** between patella and tibia: In the Linyphiidae and Pimoidae (very frequent); **(c) absent** in most of the remaining taxa: Anapidae (probably rarely present), Deinopidae, Mimetidae (probably rarely present), Tetragnathidae, Theridiosomatidae, Uloboridae and probably in the extinct family Baltsuccinidae n. fam.

LEG REGENERATION IN FOSSIL SPIDERS (DIE REGENERATION VON BEINEN BEI FOSSILEN SPINNEN)

Photos 308, 448-451.

Leg regeneration is a widely spread phenomenon in arthropods, and well-known in extant spiders. Only in non-adult spiders one or more leg articles may regenerate and only if the autotomy occurred in the first quarter of the moultings. FOELIX (1996: 231) noticed: "When a juvenile spider loses a leg, it will often - but not always - be replaced at the next moult.... Apparently, regeneration is an all-or-nothing process that is controlled hormonally.... Regeneration of an autotomized leg cannot be observed directly because the leg grows inside the old coxa.... After ecdysis the regenerated leg appears a bit shorter and thinner than the original leg, but all leg segments are present in the right proportions. Even claws, spines, and sensory organs are regenerated, although the sensory organs are not always complete. ... the newly regenerated legs are often stretched out and held away from the body, and are not used for walking at all." Spines, bristles and hairs may be strongly reduced in number and size (fig. 1) or deformed (fig. 4) or even absent, a scopula may be absent.

Occasionally regenerated legs are present in the fossil spiders; I found regenerated legs in about 0.1% of the fossil spiders in Baltic amber which have been studied more closely by me. I will describe selected specimens of the families Corinnidae, Dictynidae: Cryphoecinae, Dysderidae, Oecobiidae, ?Liocranidae, ?Philodromidae, Salticidae, ?Trechaleidae and Trochanteriidae. Ten of twelve regenerated legs are first legs, one is from the third leg and one from the fourth leg. - Already PETRUNKEVITCH (1950: 261, figs. 169-170) reports on a regenerated spider's leg of a member of the family Segestriidae. According to PETRUNKEVITCH in this specimen the single-jointed (!) piece lacks claws. In the *Harpactea* sp. indet. (F581/CJW) (fig. 2) only a claw-less stump of the regenerated leg is present, and in a Dictynidae: Cryphoecinae only two or three segments are present (claws are absent) (fig. 3); so the "all-or-nothing" process" (see above) may have exceptions.

Description of the fossil material in Baltic amber

F53/BB/CJW: *Mizalia gemini* n. sp. (Oecobiidae), holotype ♂, body length 3.3mm. The left leg III is a slender regeneration (fig. 1), 2.1mm long, the coxa is 0.26mm wide, the tibia is 0.13mm wide (the right coxa III is 0.32mm wide, the right tibia III is 0.22 mm wide). All articles, three toothed tarsal claws and few hairs are present, a single short ventral tibial bristle is present.

F152/BB/CJW: ?Philodromidae (or Trochanteriidae?) indet., juv. ♂, body length 6.3 mm. The right leg I is a regeneration, the tibia is 1.4mm long and 0.4mm wide (the left tibia I is 2.4mm long and 0.52mm wide). All articles, toothed tarsal claws, shortened bristles and hairs are present.

F186/BB/CJW: A questionable male of *Custodela pseudokochi* n. sp. (Linyphiidae), CJW. The right leg I is distinctly shortened, the tibia is only 10mm long, the left tibia I is 17mm long. Bristles of the regenerated leg are present but small. - In some other specimens of the genus *Custodela* PETRUNKEVITCH 1942 shortened legs are present in which the number of bristles is reduced; see the paper on the family Linyphiidae.

F241/BB/CJW: *Sosybius* sp. indet. (Trochanteriidae), juv. ♀, body length 4.2mm. The right leg I is a regeneration, the tibia is 1.0mm long and 0.25mm wide (the left tibia I is 1.4mm long and 0.34mm wide). All articles and toothed tarsal claws are present, a scopula is absent, the hairs are reduced in number and size, the bristles are strongly reduced. Photo 451).

F264/BB/CJW: ?*Liocranidae* indet., juvenile. The left leg I (tibia, fig. 4) is a regeneration, compare the normal right leg (tibia, fig. 5). Measurements (in mm): Body length 3.5, prosomal length 1.4, right leg I: femur 1.2, tibia 1.2, left leg I (regenerate): Femur 0.9, tibia 0.8, ventral tibial bristles: Right tibia 0.6, left tibia: Up to 0.12. The right tibia I bears - besides short apical bristles - a short and 4 pairs of long ventral bristles; the left tibia I bears 4 pairs of short ventral bristles which most often are deformed (bent).

F265/BB/CJW: *Sosybius* sp. indet. (Trochanteriidae). The left leg I is a shortened and bristle-less regeneration. Measurements (in mm): Body length 3.7, prosomal length 1.6, left leg I: Femur 0.9, tibia 0.7, tibia II 1.05, right leg I 1.3.

F581/BB/CJW: *Harpactea* sp. indet. (Dysderidae), juv., body length 3.5mm. A blunt, claw-less and hairy stump of the left leg I is present (fig. 2) which is basally covered by a white emulsion. Apparently there is only a single segment; it is less than 0.3mm long and 0.15mm wide at the base (the base of coxa II is 0.35 mm wide).

Notes on further regenerated legs of fossil spiders in Baltic amber:

?*Agelenidae* sp. indet., juv., body length 3.5mm, F228/BB/CJW: The left leg III is a shortened regenerate; bristles and tarsal claws are absent. Photo 308).

?*Linoptes oculatus* MENGE IN KOCH & BERENDT (1854), ?subad. ♀ (Pisauridae or Trechaleidae): F11/BB/CJW, body length 6.2mm. The shortened left legs I and II are apparently regenerated, size and number of bristles are reduced, the trichobothria and tarsal claws are shortened. Photo 450).

Ablator sp. indet. (Corinnidae), ♂, F22/BB/CJW: The right leg I is a regenerate. *Trochanteridromus scutatus* n. gen. n. sp., ♂ paratype (Trochanteriidae), F240/CJW: The left leg I is a shortened regeneration.

Gorgopsina amabilis n. sp. (Salticidae), ♂ holotype: The shortened right leg I is most probably a regeneration.

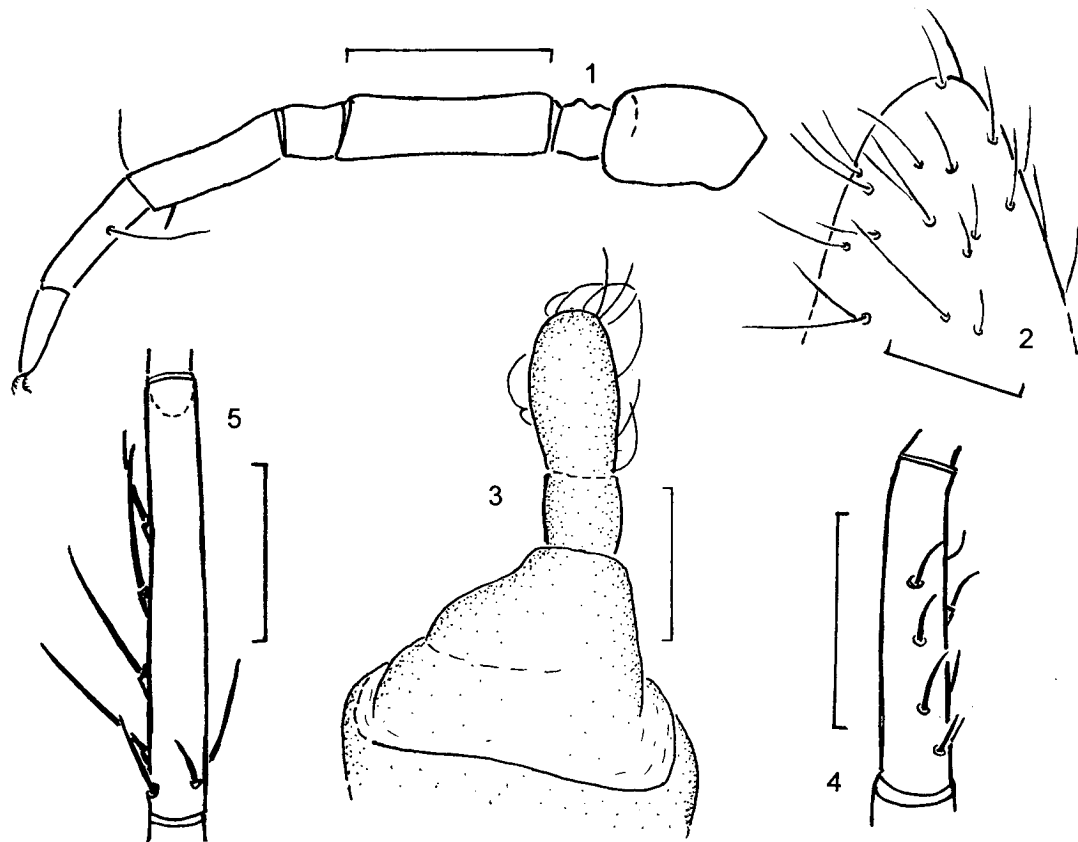


Fig. 1) Regenerated left leg III of *Mizalia gemini* n. sp. (Oecobiidae) in Baltic amber, holotype ♂, ventral aspect (hairs are not drawn). M = 0.5mm. (Regeneriertes linkes Bein III einer Kreiselspinne im Baltischen Bernstein).

Fig. 2) Regenerated stump of the left leg I of a juvenile of *Harpactea* sp. indet. (Dysderidae) in Baltic amber, lateral aspect. The basal part is hidden. M = 0.1mm. (Regenerierter Stumpf des linken Vorderbeins einer Sechsaugenspinne).

Fig. 3) A two- or three-segmented club-shaped regenerate of the left leg I of the holotype ♂ of *Eocryphoeca bitterfeldensis* n. sp. (Dictynidae: Cryphoecinae) in Baltic amber, ventral aspect. M = 0.1mm. (Ein zwei- oder dreigliedriges Regenerat des linken Vorderbeins der Kräuselspinne *Eocryphoeca bitterfeldensis*). Photos 448-449.

Figs. 4-5: Tibiae I of a questionable member of the family Liocranidae indet. in Baltic amber, juv., F264/CJW. M = 0.5. (Vordertibien einer fraglichen Feldspinne im Baltischen Bernstein).

Fig. 4) Regenerated shortened tibia I of the left leg with shortened and deformed ventral bristles, proventral aspect. (Regenerierte verkürzte **linke** Tibia des Vorderbeins mit verkürzten und deformierten Borsten der Unterseite).

Fig. 5) Non regenerated tibia I of the right leg with normal bristles, ventral aspect. Most of the proventral bristles are hidden. (Nicht regenerierte **rechte** Tibia I mit normalen Borsten, die teilweise verdeckt sind, von unten).

ASYMMETRY OF LEG USE IN FOSSIL SPIDERS? (EINSEITIGER GBRUCH VON BEINEN BEI FOSSILEN SPINNEN?)

The preference of parts of one side of the body - e.g. of organs, extremities - laterality/handedness - is well-known in mammals and other vertebrates. In contrast to mammals only few information is available on arthropods, but an asymmetry of leg use - handedness (or a "leggedness") - of such behaviour may not have been noticed or even been overlooked.

(Remark: The male "fiddler crabs" - German name "Winkerkrabben" - of the genus *Uca* (Ocypodidae) have a pair of pincers, one of which is enormously enlarged. This occurs on either side of these extremities in about the same percentage. To my knowledge in these arthropods we find no laterality.).

Does laterality of legs exist in spiders? From fossil spiders laterality has never been reported up to now (see c, results on amputated legs), but there exist observations on extant spiders.

(a) Leg use. ADES & RAMIREZ (2002) report on "Asymmetry of leg use during prey handling in the Spitting Spider *Scytodes globula* NICOLET 1849 (Scytodidae)". These authors found "a significant, overall bias towards the use of left legs." So at least one species of the family Scytodidae is left-handed.

(b) Autotomy. HEUTS & LAMPRECHTS (1998) report on significant left-biased extant members of *Zygiella x-notata* (CLERCK) (Zygiellidae) in their leg loss (autotomy). The same authors did not find laterality in *Araneus diadematus* (CLERCK) and *Larinioides sclopetarius* (CLERCK) of the family Araneidae. In fossil members of the family Linyphiidae (n = 100) I found no difference between both anterior legs. ADES & RAMIREZ (2002) found autotomy of *Scytodes globosa* in the left anterior legs significant more frequent than in the right anterior leg (15 : 4).

In about a dozen of fossil Scytodidae in amber and copal I found only very few legs autotomized, two on both sides of the anterior legs.

(c) Amputated legs. In members of the family Zodariidae in Baltic amber - except in the genus *Annicululus* PETRUNKEVITCH - I found a lower asymmetry in the number of amputated legs which I consider with some hesitation as an asymmetric leg use. Zodariid spiders hunt on ants; a fight of a fossil Zodariidae with two ants is documented in Baltic amber (F184/CJW, fig. 1), see the paper on this family in these volumes and the chapter on injuries. I found leg amputations - they are most probably caused by ants - in at least 5 fossil Zodariid genera, in about 20% of the specimens. 9 of 11 cases (= 82%) concern the first leg pair, 7 cases of these concern the right leg, 4 cases the left leg. Were most of the fossil Zodariidae "right-legged"? The difference may be an accident because the number of studied spiders is low. "Legged-

ness" is only rarely documented in spiders, see above. A larger number of fossil Zodariidae which have amputated legs is needed for further investigations, and also the study of extant material. Furthermore one has to check if the fossil ants - and not the spiders - were biased animals.

Final remarks:

(1) What members of the two families Scytodidae and Zodariidae have in common is the use of the anterior legs for something else than walking, namely for touching and defending themselves against their prey animals: The anterior legs of the Scytodidae may be very long, the anterior legs of the Zodariidae may bear special olfactory hairs. (There is a striking difference in the autotomy in both families: A coxa-trochanter autotomy is not rare in the Scytodidae in contrast to the Zodariidae in which autotomy is absent but a special "healing system" apparently is present).

(2) Concentration on one anterior leg may be an advantage in spiders as in numerous other animals, and a praedisposition for the favoured use of the left or the right anterior leg may exist in the brain of spiders.

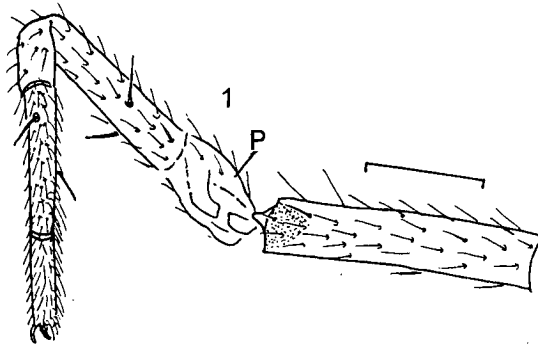


Fig. 1) The almost amputated posterior right leg of the ant-hunting spider *Adorator hispidus* (KOCH & BERENDT 1854) (Zodariidae) in Baltic amber, F184/CJW. Note the strongly injured patella (P). M = 0.5mm. - (Das nahezu amputierte rechte Hinterbein der Ameisenjäger-Spinne *Adorator hispidus* in Baltischem Bernstein. Beachte die stark verletzte Patella (P)).

INJURIES AND HEALING EFFECTS IN FOSSIL AND EXTANT SPIDERS (VERLETZUNGEN UND HEILUNGS-VORGÄNGE BEI FOSSILEN UND HEUTIGEN SPINNEN)

Photos 435, 473-494, 536, 542 and 617.

See the chapters on autotomy, decomposition, enemies, prey and regenerated legs.

Injuries (Verletzungen)

Injured fossil spiders in amber are occasionally be found: The Prosoma and/or the opisthosoma may be depressed by mechanical effects, the opisthosoma may be slit, a leg may be broken (F154/CJW, fig. 1) or autotomized (photos) or injured by an attack of an arthropod, e.g. an ant (figs. 2-5, photos), see below. If the flow of blood cannot be stopped - see fig. 1 and fig. 2 in the paper on decomposition - the spider has to die. An autotomized leg may regenerate. Probable "healing effects" of injured legs are discussed below.

Healing of injured legs (Heilungsvorgänge bei verletzten Beinen)

We have only very few informations about healing processes in extant spiders, and nothing is known about such effects in fossil spiders up to now. Healing mechanisms caused by elements of the blood of spiders and other arthropods is unknown to me and is not reported by FOELIX (1996); seemingly an injured area of the cuticula cannot "heal" in spiders, but see fig. 4 (!) and the discussion below. Healed leg (patellae) articles of an extant spider of the Mygalomorpha (Theraposidae) are reported by SCHMIDT (1980: Fig. 80). (Remark: According to SCHMIDT - person. commun. - the figured taxon is not a member of the genus *Acanthoscurria*). In another extant spider - a member of *Parazygiella* (n. gen.) *montana* (C.L. KOCH 1834) (Zygiellidae, CJW) - I found apparently scarred structures on the labium and the right gnathocoxa (fig. 7).

After the autotomy of a spiders' leg the flow of blood is stopped by closing movements of the sclerites, see FOELIX (1996: Fig. 190). Such an effect - most often after a coxa-trochanter autotomy as in the Oonopidae (*Orchestina*), Theridiidae (e.g. *Diploena*) and Zoropsidae (e.g. *Sosybius*), occasionally after a patella-tibia autotomy as

in the Linyphiidae (e.g. *Custodela*) - are not rare in the fossils, see the photos. In freshly autotomized legs - the leg articles are lost within the amber - a droplet of blood is frequently present on the stump, see the photos.

Injured and amputated legs. In the female holotype of *Pimoida liedtkei* n. sp. (Linyphiidae, Baltic amber) the right femur III has been broken at least two times; the sites of fracture have apparently healed, no blood is observable, see the photo and compare fig. 4. Thus healing mechanisms might be present at least in certain spiders.

Besides this Linyphiid spider I found healed leg articles only - and not rare! - in the family Zodariidae, see the paper on this family in these volumes. The Zodariidae which possess amputated legs did not bleed to death; so shows a broken patella of a Zodariid spider probably dry haemolymph (dotted in fig. 4) and there is no blood on the amputated stump at the end of the patella. Blood is also absent at a damaged coxa of this spider (fig. 3). In an extant Zodariid specimen of the genus *Malenella* RAMIREZ 1995 (CJW) I found four legs which are amputated through an article and are apparently healed - there is a stronger sclerotization at the stumps, and one femur was split up. According to my findings a special and striking "healing mechanism" is most probably present in members of the family Zodariidae (figs. 2-6). Most members of the Zodariidae are ant-hunters, but in reverse ants also may attack spiders.

The attack of a male Zodariid spider - *Adorator hispidus* (KOCH & BERENDT) - by two cooperating worker ants is preserved in Baltic amber, F184/CJW (figs. 2-5, photo). The Zodariid spider has a deformed opisthosoma, coxae I and II (fig. 3) and also the sternal area nearby are injured, the left leg I has been amputated behind the femur, the left leg II has been amputated behind the patella, the right leg IV has been dissected and almost amputated between femur and patella (there is no clear "cut" in an autotomized leg), and the distal articles are twisted about 90° (fig. 2). The left patella II is broken across (fig. 4). There is no blood at the ends of the left femur I and the patellae II and IV or the coxae. Therefore these wounds probably have been healed before the spider was entombed in the resin, and the spider was killed just before the embedding procedure or within the resin. One of the ants is biting in the base of the right tibia I of the spider (fig. 5) and probably tried to transport it to the ants' nest.

Another member of the Zodariidae - gen. indet. 2, F187/CJW, - has been attacked probably by an ant which is preserved in the same piece of amber; two further ants have been the prey of the spider. The right leg I of the spider has been amputated behind the distal part of the tibia (fig. 6). The apical margin of the tibia appears "splitted", no blood is observable; therefore the wound should have healed before the spider has been entombed in the resin.

Because of their powerful mouth parts (mandibles), and their large number, the co-working ants are dangerous to spiders: Injured and even amputated legs are not rare in fossil Zodariidae. Certain attacked opiliones and spiders may autotomize and leave a leg and thus they may escape. So it is remarkable - and not easy understandable - that in Zodariidae a leg autotomy is usually absent (the patellar detachment in the genus *Diores* is an exception). Leg autotomy is most expressed in long-legged spiders as Pholcidae, but most Zodariidae are not long-legged animals.

On the other hand I found leg amputations in at least five genera of fossil Zodariidae, in about 20% of the specimens (figs. 2-5) (the amputations are not restricted to a special area and go frequently through a leg article). I regard the absence of leg autotomy in the Zodariid spiders as connected with the presence of a healing mechanism of an unknown kind of operating, in which the haemolymph clump rapidly. Probably leg autotomy at a special area would make no sense in these ant-hunting spiders which are attacked by spiders at different leg articles and are even injured within leg articles (see figs. 4-6).

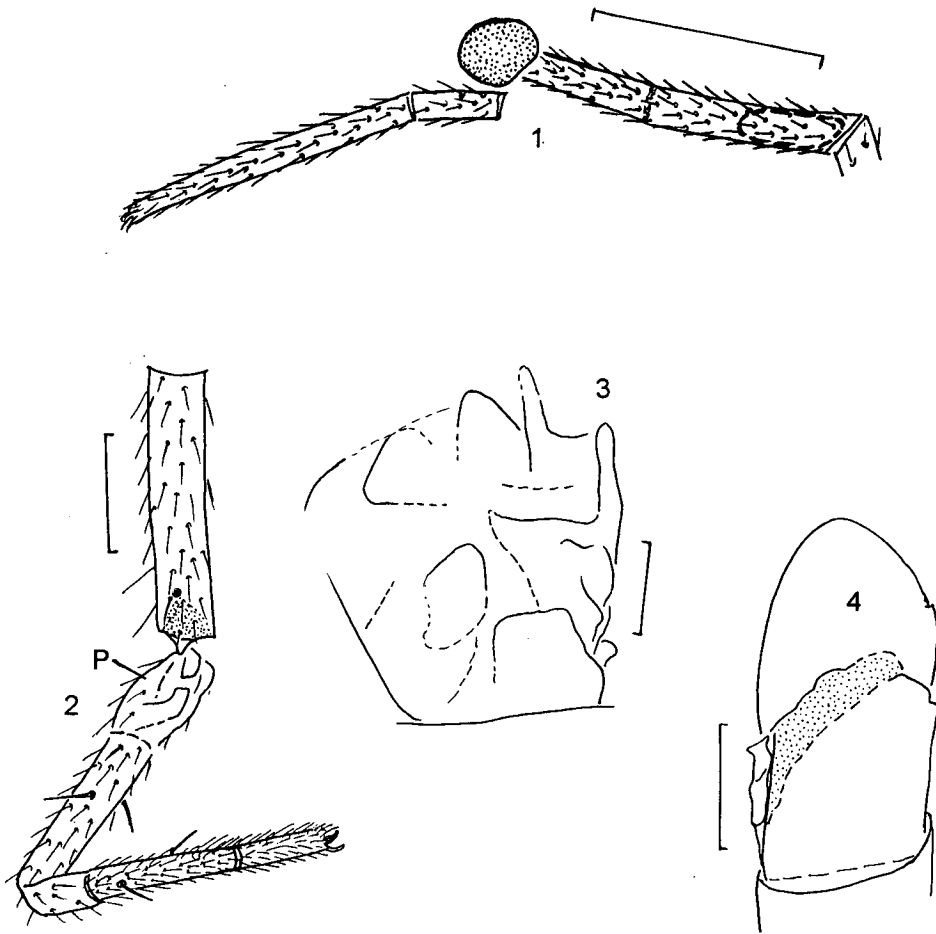


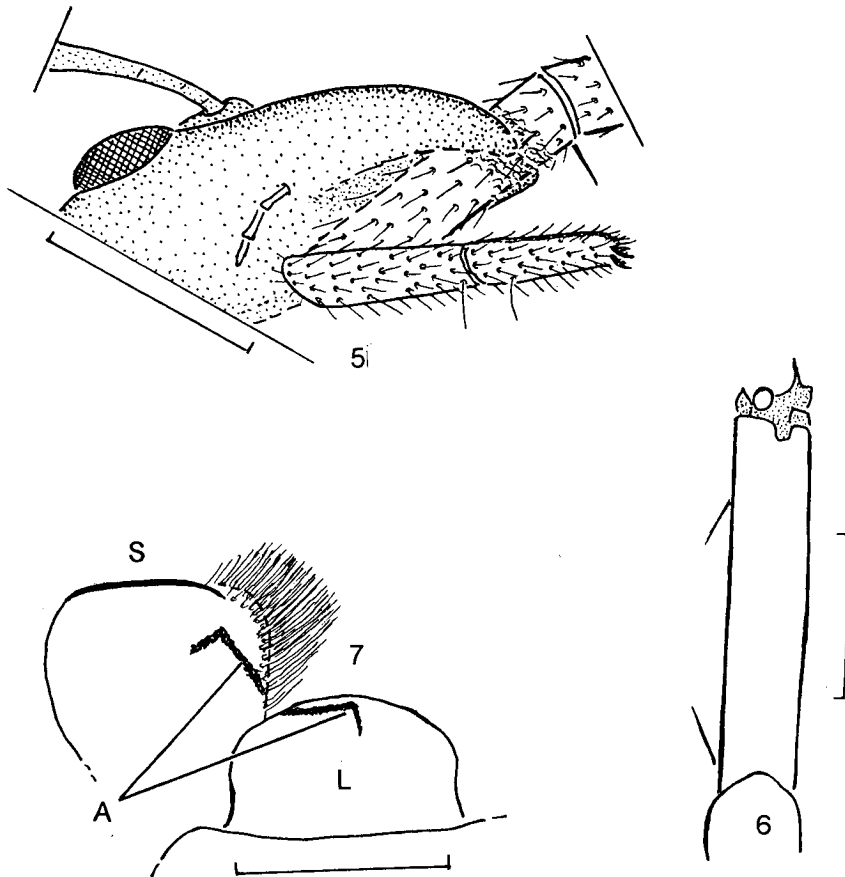
Fig. 1) Right leg II with the broken meatatarsus of a fossil spider (?Theridiidae indet.) in Baltic amber, ?ad. ♀, F154/CJW, prolateral aspect. A droplet of blood (dotted) streamed out from the body side of the metatarsus. A second - incomplete - bristle is present near the middle of the metatarsus. M = 0.5mm.

Figs. 2-5: Injuries of a male *Adorator hispidus* (KOCH & BERENDT 1854) (Zodariidae), in Baltic amber, F184/CJW, which is attacked by two ants. M = 0.2 in figs. 3-4, 0.5 in figs. 2 and 5. (Verletzungen bei einer männlichen Spinne der Familie Ameisenjäger, die im Baltischen Bernstein von zwei Ameisen attackiert wird).

2) twisted, dissected and almost amputated right leg IV with an injured patella; because of the absence of blood this wound should be not fresh.

3) Cuticula of the right coxa II which has most probably been damaged by an ant.

4) Injured and "healed" (dotted area) left patella II, dorsal aspect. Parts of the cuticula are standing out retrolaterally. The same leg has been amputated behind the patella.



5) A worker ant (Formicidae) (see the dotted head) bites in the right first tibia of the spider. Note the injured spider's tibia which is shown in the ventral aspect. Most mouth parts of the ant are hidden, the base of its right antenna is drawn. (Eine Ameisen-Arbeiterin beißt in die rechte erste Tibia der Spinne. Beachte die Verletzung der Tibia, die von unten gesehen ist).

Fig. 6) Right leg I of a member of the family Zodariidae gen. indet. 2, ?ad. ♀ in Baltic amber, F187/CJW, which has been amputated at the end of the tibia (at the top of the drawing). Apparently the wound has been healed. M = 0.4. (Offenbar geheilte Region am Ende (in der Abb. oben) der Tibia einer fossilen Ameisenjäger-Spinne).

Fig. 7) Labium (L) and right gnathocoxa with scars (A) of the cuticula of an extant ♀ of *Parazygiella* (n. gen.) *montana* (C. L. KOCH 1839), family Zygiellidae. S = weakly developed gnathocoxal serrula. M= 0.5. (Labium (L) und rechte Gnathocoxa einer heutigen Zygiellidae, mit Narben der Kutikula), (A).

ABNORMAL STRUCTURES IN FOSSIL SPIDERS (MISSBILDUNGEN BEI FOSSILEN SPINNEN)

See the chapters on autotomy and on regenerated legs.

Only very few abnormal structures have been described from fossil spiders. A male of *Sosybius* sp. indet., the "androtype" of *Adulatrix fusca* PETRUNKEVITCH 1942 sensu PETRUNKEVITCH (1958: 271-273, figs. 379-382) (Trochanteriidae) in Baltic amber has strongly malformed bulbus structures of the right pedipalpus (fig. 1); I regard the black scoop-shaped structure (sc) as an artefact. PETRUNKEVITCH did not recognize the malformed nature of this right bulbus; it is quite different from the left bulbus which possesses normal structures.

I have not focussed on abnormal structures (malformations) of fossil spiders, so I found only three of such structures - they are described below -; one concerns the development of a male pedipalpus, another one a doubled trichobothrium and a third one the number of leg bristles.

Custodela lanx n. sp. (Linyphiidae), holotype male. On patella, tibia and metatarsus of the right leg III some bristles are doubled (fig. 2): The distal ones of the patella and tibia, the basal one of the metatarsus, 3 additional bristles are present in the distal half of the metatarsus.

Ablator inevolvens n. sp. (Corinnidae), holotype male. The left pedipalpus (fig. 3) is normally developed, the right pedipalpus (fig. 4) is shortened, the femur is less bent and more robust, the small tarsus is pear-shaped as in a subadult male, hairy and slightly plaited. The length of femur/tarsus of the right pedipalpus is 0.4/0.4 in contrast to the left pedipalpus 0.6/about 0.8.

Calilinus fleissneri n. gen. n. sp. (Salticidae), holotype male. The trichobothrium on the right tarsus III possesses a doubled trichum in a common bothrium (fig. 5).

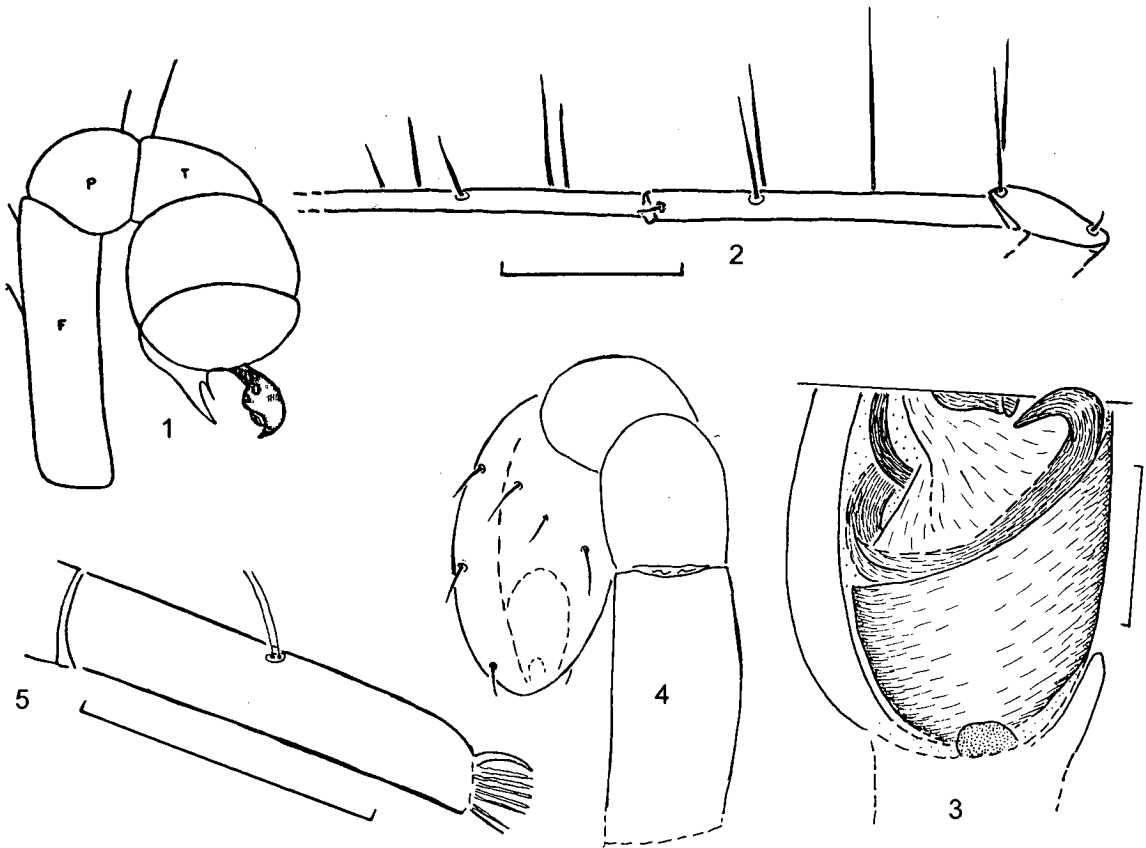


Fig. 1) Right pedipalpus of *Sositybius* sp. indet. ("androtyp" of *Adulatrix fusca* PETRUNKEVITCH 1942) (Trochanteriidae) with a strongly malformed bulb. Taken from PETRUNKEVITCH (1958: Fig. 382). (Stark mißgebildeter Bulbus des rechten Pedipalpus von *Sositybius* sp. indet. (Trochanteriidae).

Fig. 2) Patella, tibia and metatarsus of the r. leg III of the male holotype of *Custodella lynx* n. sp. (Linyphiidae) with an unnormally high number of partly doubled bristles, prolateral aspect. $M = 0.5$. (Unnormal hohe Anzahl von Bein-Borsten - teilweise sind sie verdoppelt - beim Holotypus der Baldachinspinne *Custodella lynx* n. sp.).

Figs. 3-4: *Ablator inevolvans* n. sp. (Corinnidae), ♂ holotype, which has an inevoluted and a normally evolved tarsus; $M = 0.2$. (Männchen der Ameisen-Sackspinne *Ablator inevolvans* mit einem unentwickelten und einem normalen Endglied des Pedipalpus). 3) Completely developed bulb of the left pedipalpus, ventral aspect (the distal part is hidden). (Vollständig entwickeltes Endglied des linken Pedipalpus von unten; der Endabschnitt ist verdeckt). 4) Right pedipalpus with inevoluted, pear-shaped tarsus (bulbus); femur and patella in dorsal aspect, tarsus in ventral aspect; only few tarsal hairs are drawn. (Rechter Pedipalpus mit unentwickeltem, birnenförmigem Endglied (Tarsus)).

Fig. 5) Trichobothrium of the right tarsus III of the male holotype of *Calilinus fleissneri* n. gen. n. sp. (Salticidae), retrolateral aspect, with a doubled trichum in a common bothrium. $M = 0.2$. (Verdoppelter Haar-Anteil eines Becherhaares beim Holotypus der Springspinne *Calilinus fleissneri* n. gen. n. sp.).

ON SEXUAL DIMORPHISMS AND THE REPRODUCTIVE BEHAVIOUR OF THE FOSSIL SPIDERS (ÜBER UNTERSCHIEDE DER GESCHLECHTER UND ZUM FORTPFLANZUNGSVERHALTEN DER FOSSILEN SPINNEN)

See the chapter on egg sacs.

Besides their genital organs (figs. 24, 32-34) different sexual dimorph structures have developed in male spiders in a impressive number of convergences: (a) Prosomal outgrowths/lobes (figs. 6-12), (b) stridulating organs (mainly on the chelicerae, figs. 1-3) (they may occur in females, too), (c) modifications in the first leg (figs. 13-20), (d) cheliceral outgrowth (figs. 21-23). Especially in the superfamily Araneoidea developed an impressive number of convergences of these structures. Certain of these structures allow conclusions on the spiders' reproductive behaviour; differences between the sexes indicate patterns of their courtship and mating behaviour. - By all means the courtship behaviour can be called "conservative": Already from the fossil spiders of the Early Tertiary - 50 million years ago - a highly developed reproductive behavior of is well documented, e.g., cheliceral stridulating files existed in several families similar to extant spiders (see the photos figs. 1-3); in fossil taxa of two families - Araneidae and Cyatholipidae - such organs are reported here for the first time at all. Prosomal/cheliceral outgrowths as well as modified first male legs were present in fossil spiders, too. - Reports on fossil mating couples of spiders are extremely rare, only a single couple has been described in detail; see WUNDERLICH (1982) and below.

Differences between the sexes of the same species - sexual dimorphisms. (Unterschiede zwischen den Geschlechtern derselben Art)

(1) One of the **general sexual dimorphisms** in spiders concerns the body size. Besides the larger opisthosoma - which may bear numerous eggs - the male prosoma is usually smaller than the female prosoma. This is striking in the family Araneidae. It is known to me from fossil Araneidae of the genus *Nephila* LEACH in Dominican amber and probably present in members of the Nephilinae in Baltic amber. Dwarf males occur in some Araneid taxa occur dwarf males as well as in certain Thomisidae and in the genus *Latrodectus* WALCKENAER (Theridiidae): Gigantism happens in the female sex and dwarfism in the male sex. (Cannibalism by females mainly occurs in such species in which the female is distinctly larger than the male. The reverse cannibalism - males feeding on conspecific females - may occur only accidentally). In the extant and fossil Zygellidae, certain Linyphiidae and Tetragnathidae (e.g.) the male is almost as large as the female or even larger (e.g. in some Linyphiid members of the genus *Centromerus* DAHL) as well as in *Argyroneta aquatica* LATREILLE (extant, questionable Cybaeidae) and in numerous extant Clubionidae and Corinnidae, see e.g. DEELEMAN-REINHOLD (2001). The reasons for the existence of sexual gigantism in females - which may produce a larger number of eggs (an "evolutionary strategy") - and the dwarfism in males are diverse, the reasons for the existence

of larger males are unknown - e.g. intraspecific sexual competition on the prey? The proportions of the body, body parts and legs may also be different in the sexes. Most striking are the more slender and frequently longer legs and leg bristles in the male sex (e.g. in extant and fossil Linyphiidae; in certain Linyphiidae: Erigoninae males the tibial bristles are reduced), and (e.g. in the Clubionidae) their larger chelicerae, see the fossil genus *Eodoter* PETRUNKEVITCH. In the extant male Clubionidae (*Clubiona* LATREILLE) the anterior spinnerets may be longer and cylindrical but conical in the female sex. Unfortunately conspecific Clubionid specimens of both sexes from the Baltic amber forest are still unknown.

The male opisthosoma bears scuta or stronger scuta or scuta in a larger number than the female in numerous spider families; in fossil spiders such differences are known from the families Anapidae, Araneidae, Cyatholipidae, Corinnidae, Ephalmatoridae, Salticidae, Theridiidae, Trochanteriidae and Zodariidae.

The female opisthosoma bears spines and/or pointed humps e.g. in certain taxa of the families Araneidae (e.g. in *Gasteracantha* SUNDEVALL). This and the following pattern are rare cases of a female dimorphism.

In the females of (e.g.) certain Mimetidae, Linyphiidae as *Maso* SIMON and Thomisidae the ventral tibial and metatarsal macrosetae of the first (and usually the second) leg are larger than in the males. These macrosetae are used for capturing prey.

The spinning apparatus: The spinules of certain spinnerets may be quite different in the sexes, e.g. in some members of the Gnaphosidae and Liocranidae. The male cribellum and the calamistrum are reduced in numerous taxa of (e.g.) the families Dictynidae and Uloboridae, see the papers on these families in these volumes. Also the capture webs may be different in the sexes, e.g. in numerous members of the superfamily Araneoidea s. l.. The retreat is different e.g. in certain Clubionidae. Most male spiders build a special sperm web; in one case the remains of such a web are probably preserved in Baltic amber, see the paper on spiders' webs and threads.

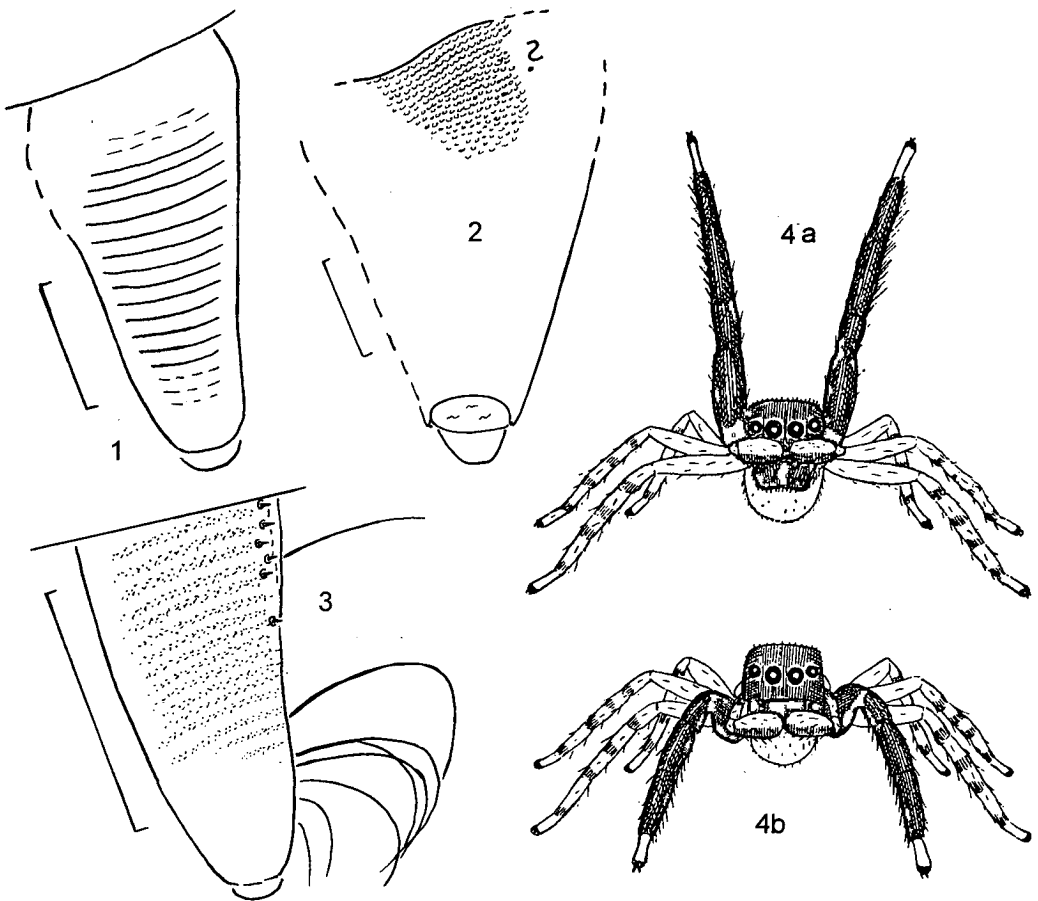
The colour of the body - as well as legs and pedipalpi - is quite different in the sexes of numerous groups of spiders; certain hairs may be dense, flattened and coloured mainly in the male sex, e.g. in extants and fossils of the families Oxyopidae and Salticidae, see the papers on these families, photos, and the chapter on the cryptic behaviour as well as the paragraph (b) below. In some Araneidae the female possesses striking colours, in certain Eresidae (e.g. *Eresus* WALCKENAER) and Salticidae (e.g. *Philaeus* THORELL) the males have conspicuous warning colours, in some Theridiidae (*Latrodectus* WALCKENAER) both sexes possess warning colours.

The prey spectrum is different in the sexes of numerous spider species, especially in those species in which a large dimorphism in size exists.

The life span is quite different in the sexes of most spiders: Especially in the plesiomorphic Mygalomorpha and Filistatidae the females may live many years but the males live only few months, and they usually die shortly after courtship. Nothing is known about the life span of fossil spiders.

(2) The courtship behaviour and sexual dimorph structures (Das Balzverhalten und nach Geschlecht unterschiedliche Strukturen)

Pheromones e. g. on the females' threads - e.g. in the Araneidae - and/or optical signals - e.g. in Lycosidae, Oxyopidae and Salticidae - may lead the males to a conspecific female. Spiders are aggressive animals, so the male has to suppress the fema-



figs. 1-3: Retrolateral cheliceral stridulatory structures of male fossil spiders in Baltic amber, seen from the right side; 1) Files of a member of the genus *Custodela* PETRUNKEVITCH 1942 sp. indet. (Linyphiidae) (CJW), $M = 0.1\text{mm}$; 2) a basal rugose field - which may be a stridulatory area - of the holotype of *Palaeonephila dilitans* n. gen. n. sp. (Araneidae), $M = 0.2$; 3) weakly developed questionable stridulatory files, short bristles and long bent hairs of *Chelicirrum stridulans* n. gen. n. sp. (Dictynidae), paratype ZMK, $M = 0.2$. See the photos 130, 261, 281.

Abb. 1-3: Seitliche, der Balz dienende Strukturen der Cheliceren bei drei fossilen männlichen Spinnen im Baltischen Bernstein; 1) Schriell-Rillen einer Baldachinspinne; 2) feinkörniges Feld einer Radnetzspinne; 3) schwach entwickelte Schriell-Rillen - ähnlich wie bei einem Waschbrett -, kurze Börstchen und lange, gebogene Haare einer Kräuselspinne. Man vergleiche die Fotos 130, 261, 281.

fig. 4a-b: Visual courtship behaviour - fascinating/mesmeric movements of the strikingly darkened and thickened first pair of legs and the pedipalpi - in an extant male Jumping Spider (*Euophrys frontalis* WALCKENAER, Salticidae). Taken from BRISTOWE 81941: Fig. 84). - Behaviour of fossil Jumping Spiders: See the text.

Abb. 4a-b: Optisch bestimmtes Balzverhalten bei einer heutigen männlichen Springspinne. Beachte die ungewöhnlichen Bewegungen insbesondere der auffällig verdunkelten und verdickten Vorderbeine, die den Beutefang-Instinkt des Weibchens unterdrücken und gleichzeitig der Balz dienen. - Verhalten bei fossilen Spinnen: Siehe den Text.

les' aggressiveness; with the help of his courtship behaviour he has to demonstrate first that he is not a prey.

An important role in the courtship behaviour of numerous spider taxa play (a) stridulatory files and bristles (mainly the files on the outer side of the chelicerae, figs. 1-3) which developed convergently in spiders probably more than 20 times; (b) structures of the modified first male leg: Special/long/dense and/or coloured hairs, bent articles and thickened articles which may bear pheromone glands (figs. 4, 13-14). In the same legs we frequently find structures as clasping spines, which are not connected with the courtship but with the mating behaviour (figs. 15-18, see below); (c) prosomal lobes which may bear pheromone glands within hairy areas or pits. Prosomal outgrowths are treated in the next paragraph, the mating behaviour.

(a) Stridulatory organs are known from different types and from numerous spider families (as well as from numerous other arthropods). The most frequent type is the "cheliceral-pedipalpal stridulatory organ": stridulatory files on the outer side of the chelicerae (fig. 1) in connection with a single stridulating bristle or tooth (or several ones) which rub along the files. These files usually occur in both sexes, are more distinct in most males and are rarely absent in the female sex. In fossil spiders of the Baltic amber forest this type is known from the following families (often hard to observe): Araneidae (one genus: *Palaeonephila* n. gen., fig. 2), Archaeidae, Cyatholipidae (one genus which is still unpublished, the description is in preparation), Dictynidae: Hahniidae (few members), most Linyphiidae (fig. 1), Pimoidae (questionable), Scytodidae (questionable) and Spatiatoridae; furthermore such files occur in the Dictynidae: Copaldictyninae in copal from Madagascar and in the Palpimanidae and Pholcidae of the Dominican amber forest; see the papers on these families in these volumes. - A different - quite special - cheliceral stridulatory organ including hairy denticles exists in the family Dictynidae, in *Chelicirrum stridulans* n. gen. n. sp. (fig. 3), see the paper on the Dictynidae in these volumes. - Posterior prosomal stridulatory files are present in several extant and fossil Theridiidae (not figured here).

Occasionally - e.g. in certain extant members of the Linyphiidae: Erigoninae - stridulatory files are present on the lung covers which are in connection with a stridulatory tooth on the posterior coxa. This type is unknown in fossil spiders.

In fossil spiders of the family Synotaxidae in Baltic amber I found two types of stridulatory organs: A field of ventral opisthosomal stridulatory denticles near stridulatory teeth of the posterior coxae in *Succinitaxus brevis* n. gen. n. sp., and a probable stridulatory organ between the sternum and an anterior ventral opisthosomal scutum; see the paper on the family Synotaxidae, figs. 78, 80a, 92.

Ventral opisthosomal stridulatory/vibratory bristles or spines are present in certain spiders of the families Liocranidae, e.g. in extant and fossil members of the genera *Apostenus* WESTRING and *Palaeospinisoma* n. gen. (see the photos) as well as in certain extant species of the family Lycosidae. These ground spiders may produce "sounds" (vibrations) by rubbing these bristles during courtship on dry leaves, and may so stimulate their female partner. Such stridulatory bristles are reported here for the first time in fossil spiders. - In *Myrmecorinna gracilis* n. gen. n. sp. long ventral opisthosomal bristles exist in front of the spinnerets, which are probably stridulatory bristles, see fig. 52 in the paper on the family Corinnidae in these volumes.

Ventral stridulatory bristles of the posterior gnathocoxae occur in some members of the Dictynidae: Hahniinae: Antisteini, see the paper on the family Dictynidae s. l. in these volumes, fig. 33, and in some members of the genus *Zora* C. L. KOCH (Zoriidae). Such bristles are unknown from fossil spiders.

(b) Structures of the first male leg (see also below) and the male pedipalpi

In spiders which orientate in an optical way - as Salticidae which are able to recognize even colours, and Lycosidae - a "visual courtship behaviour" frequently exists. Almost every species has developed its own courtship behaviour. In numerous male Salticidae the first leg pair and/or the cymbium are thickened, covered with long hairs and ornamented. Both may be moved in a striking way, see the figs. 4a-b, the pedipalpi may be moved additionally like drums.

In fossil male Salticidae of the Baltic amber forest the first leg is never strikingly hairy or thickened, but in the males of one species - *Almolinus ligua* n. sp. - the wide cymbium is densely covered with strikingly long and light hairs (photo) which indicate for the first time an visual courtship behaviour in Early Tertiary spiders.

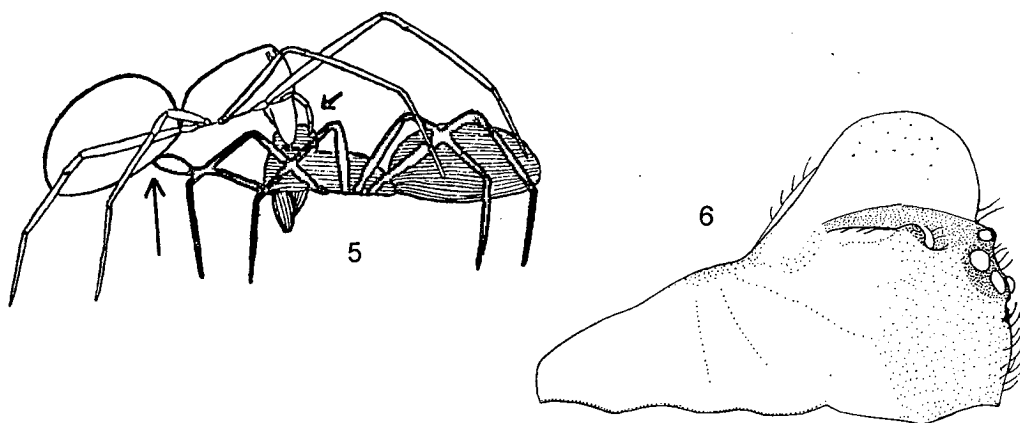
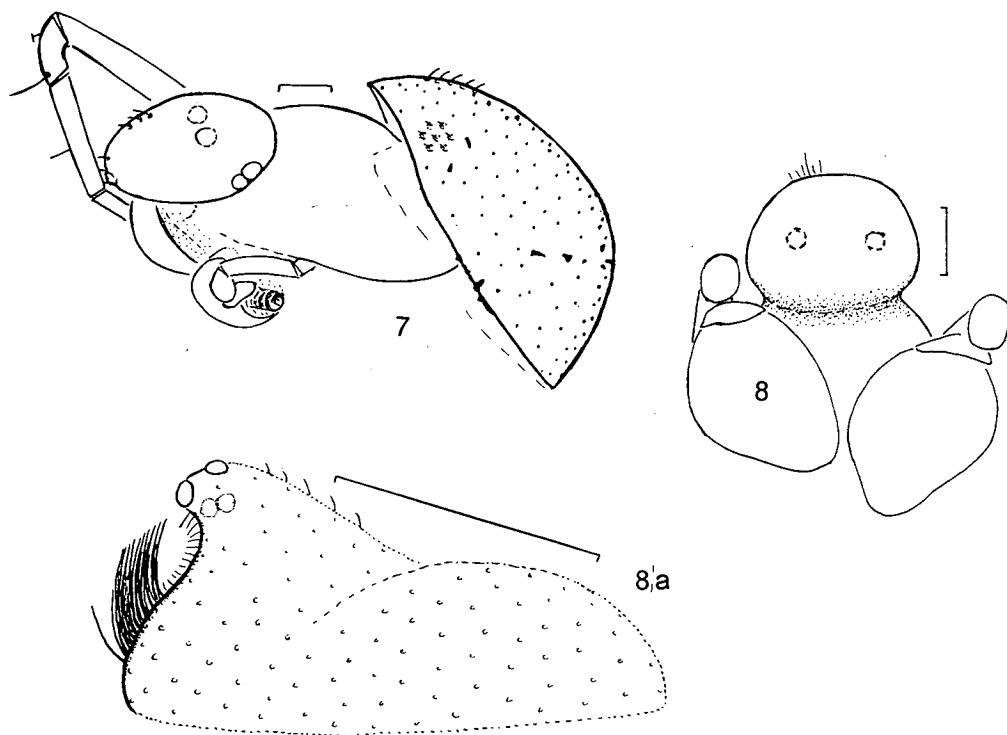


Fig. 5) Mating position in an extant species of the Dwarf Spiders (Linyphiidae: Erigoninae: *Hypomma bituberculatum* (WIDER)). The female (at the left side) grasps the divided prosomal lobe of the male with her chelicerae (short arrow), and her fangs enter the lateral grooves of the lobes. The male "feeds" his female partner with a secretion which may have the effect of a drug. One of the male pedipalpi is stretched forwards and reaches the female genital opening (long arrow). - Taken from BRISTOWE (1941: Fig. 91). Compare fig. 6).

Abb. 5) Paarungsstellung bei einer heutigen Art der Zwergspinnen. Das Weibchen (links) "beißt" in die seitlichen Gruben des Auswuchses des Vorderkörpers des Männchens (kurzer Pfeil). Das Männchen "füttert" die Partnerin mit einem Sekret, das die Wirkung einer Droge haben mag. Einer der Pedipalpen ist bis zur weiblichen Geschlechts-Öffnung vorgestreckt (langer Pfeil). Vgl. Abb. 6).

Fig. 6) Male prosoma with lobe and right groove of *Hypomma bituberculatum* (extant).
Abb. 6) Vorderkörper mit Auswuchs und rechter Grube der Zwergspinne *Hypomma bituberculatum*. Vgl. Abb. 5). - Nach WIEHLE (1960: Abb. 532).



Figs. 6-12: Variable structures (lobes, grooves, folds, furrows, hairy areas) of the male prosoma of some extant and fossil spiders. Fig. 6: See above.

Abb. 6-12: Unterschiedliche Formen (Auswüchse, Gruben, Falten, Haarzonen) des männlichen Vorderkörpers bei einigen heutigen und fossilen Spinnen. Abb. 6: Siehe oben.

Figs. 7-8: Male body of an unnamed fossil Theridiidae in Baltic amber. Note the large prosomal lobe bearing the eyes which are partly hidden; 7) dorsal-lateral aspect of the body (only one of the legs is drawn); 8) anterior aspect of the prosoma and the pedipalpi. M = 0.1.

Abb. 7-8: Männchen einer unbenannten Kugelspinne im Baltischen Bernstein. Man beachte den großen Auswuchs des Vorderkörpers, der die (teilweise verdeckten) Augen trägt; 7) Körper gesehen von oben-rechts (es ist nur eines der Beine gezeichnet); 8) Vorderkörper und Pedipalpen von vorn.

Fig. 8a) Male prosoma of a Comb-footed spider (Theridiidae), the holotype of *Eomysmena militaris* (KOCH & BERENDT 1854) in Baltic amber, lateral aspect. Note the dense hairs of the clypeus. M = 1mm.

Abb. 8a) Männlicher Vorderkörper einer Kugelspinne im Baltischen Bernstein, *Eomysmena militaris*. Man beachte die dichte Haar-Zone des Vorderkörpers.

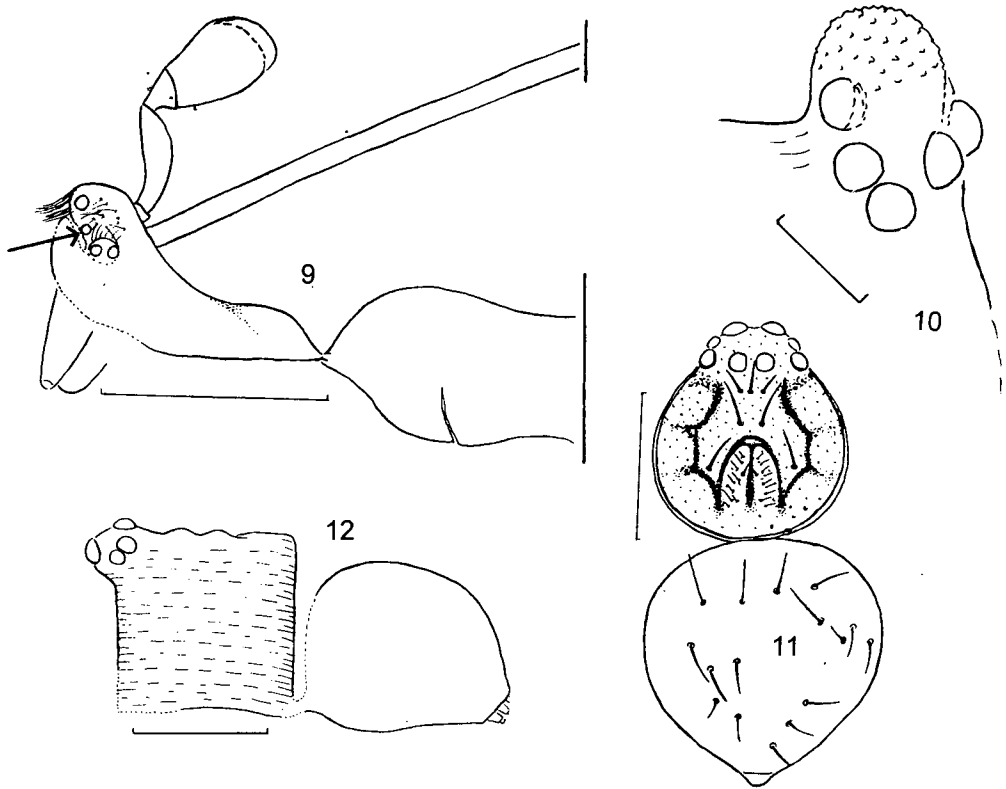


Fig. 9) Male of a fossil Comb-footed Spider (Theridiidae) - *Argyrodes crassipatellaris* WUNDERLICH 1988 - in Dominican amber, with its hairy inclination of the prosomal lobe (arrow), seen from the left side. The mating position in this extinct species was most probably similar to fig. 5. M = 1.0.

Abb. 9) Männliche Kugelspinne im Dominikanischen Bernstein. Beachte den haari- gen Einschnitt (Pfeil) im Auswuchs des Vorderkörpers. (Nur der vordere Abschnitt des Hinterkörpers und ein Teil des rechten Femurs sind dargestellt). Vermutlich war die Paarungsstellung bei dieser ausgestorbenen Art ganz ähnlich wie in Abb. 5.

Fig. 10) Denticulate prosomal lobe within and above the eye field of a fossil male in Baltic amber, *Gibbersynotaxus parvus* n. gen. n. sp. (Synotaxidae). M = 0.1.

Abb. 10) Mit winzigen Zähnchen besetzter "Scheitelhügel" im Augenfeld einer männlichen Kugelhöhlenspinne im Baltischen Bernstein, *Gibbersynotaxus parvus*.

Figs. 11-12: Body of a comb-footed fossil spider (Theridiidae), genus *Dipoena* THO- RELL (*Lasaeola*) in Dominican amber (similar species in Baltic amber), dorsal and la- teral aspect. Note the deep prosomal furrows whose function is unknown. M = 0.5mm.

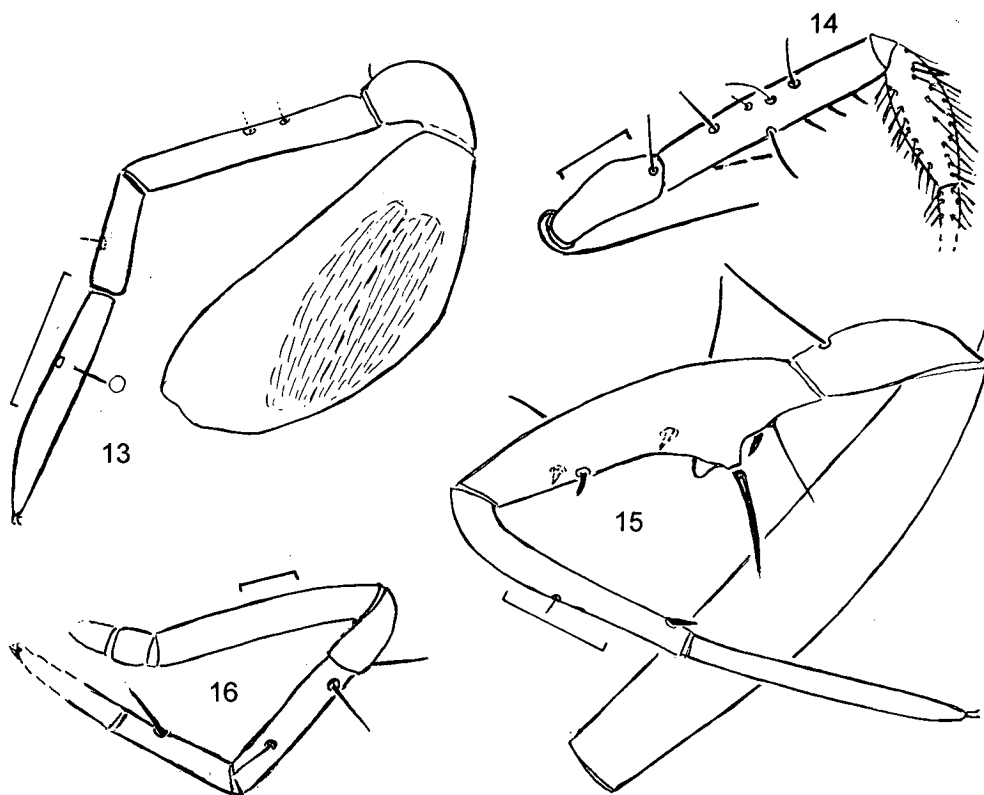
Abb. 11-12: Körper einer fossilen Kugelspinne im Dominikanischen Bernstein, Gat- tung *Dipoena* (*Lasaeola*). Ähnliche Arten existierten im Baltischen Bernstein. Man beachte die tiefen Furchen des Vorderkörpers, deren Funktion unbekannt ist.

(3) The mating behaviour and sexual dimorph structures (Das Paarungsverhalten und nach Geschlecht unterschiedliche Strukturen)

Usually the male is the sexually active partner in spiders : He searches for the female, he courts and finally frequently fixes the female during copula. (Furthermore the male pedipalpus may be fixed to the scapus of the epigyne). But there are certain exceptions: In numerous members of the Linyphiidae: Erigoninae, of the Theridiidae: Argyrodinae and probably in some Synotaxidae the female is active: It "bites" into paired grooves on an outgrowth of the male prosoma (fig. 6) which may be hairy and which spend pheromones and a secretion which is taken by the female during copulation, and which may have the effect of a drug. Her fangs enter the grooves, and this grip is maintained whilst copulation takes place (fig. 5); see BRISTOWE (1941: 494). Such prosomal outgrowths exist mainly in tiny web spiders; they are absent (superfluous) in those tiny spiders (e.g. in the Anapidae s. l., see below), in which the male fix the female during copulation (this happens with the help of their anterior legs).

Such outgrowths are unknown in fossil Linyphiidae of the Baltic amber forest because members of the Erigoninae have never been found in this kind of amber, but two males of a yet undescribed species of the family Theridiidae in the Early Tertiary Baltic amber are kept in the CJW, in which the male prosoma bears a large and blunt outgrowth (figs. 7-8). The shape and the position of this outgrowth indicate a similar mating behaviour in this species as in extant spiders which have prosomal outgrowths. From the Young Tertiary Dominican amber we know members of the family Theridiidae, too, - the genus *Argyrodes* SIMON (fig. 9) -, in which - according to extant relatives - the mating position is similar to fig. 5. So this kind of mating behaviour goes back to the Early Tertiary in the family Theridiidae. - In *Gibbersynotaxus parvus* n. gen. n. sp. (Synotaxidae) an outgrowth of the male prosoma is present, too (fig. 10, photo 228), which bears tiny denticles, and which may also play a role during the copulation. - In numerous males of the genus *Dipoena* THORELL (*Lasaeola* SIMON) - members of this extant genus occur in Baltic and Dominican amber - strong dorsal prosomal folds of an unknown function are present (figs. 11-12), which may be connected with the courtship behaviour. Such folds are absent in the female sex. - In numerous extant male members of the family Tetrablemmidae prosomal outgrowths occur, too, and in a single member of the Pholcidae - *Hedypsilus culicinus* SIMON 1893 - a "gustatorial courtship behaviour", a hairy clypeal lobe and clypeal glands exist, see HUBER (1997). Such structures and behaviour are only rarely reported in haplogyne spiders.

In numerous spider taxa the male fixes the female during copulation; in certain Crab Spiders (Thomisidae) the male even fixes the female with threads. In certain members of the superfamily Dysderoidea - e.g. in the Oonopidae and Scytodidae - the male bites into paired grooves or outgrowths in the female genital area during copulation, and both are held in this position. Such a mating couple was described by WUNDERLICH (1982) from a fossil member of the genus *Orchestina* SIMON (Oonopidae) in Baltic amber, see the paper on the Dysderoidea: Oonopidae in this volume and WUNDERLICH (1986: Fig. 294). - A couple "post copula" of *Acrometa cristata* PETRUNKEVITCH 1942 (Synotaxidae), F689/BB/CJW, is preserved in Baltic amber (photo 211). The male is situated under the female in a "venter-to-venter- position". - A questionable mating couple of the family Theridiidae - *Episinus* (= *Flegia*) *longimanus* (KOCH & BERENDT) - in Baltic amber has been shortly reported by MENGE in KOCH & BERENDT (1854: 30). On the mating positions of extant spiders see BRISTOWE (1941: 491, 494, 496) and FOELIX (1992: 199-200).



Figs. 13-20: The **modified first male legs** of selected fossil spiders.

Abb. 13-20: Die **modifizierten Vorderbeine** ausgewählter fossiler Spinnen- ♂.

Fig. 13) *Balticoroma serafinorum* n. gen. n. sp. (Anapidae: Comarominae). Note the remains of questionable muscles in the strongly thickened femur. (O = tarsal organ). M = 0.2.

Abb. 13) *Balticoroma serafinorum* (Zwerg-Kugelspinnen) im Baltischen Bernstein. Man beachte die fraglichen Reste von Muskeln im stark verdickten Femur.

Fig. 14) *Balticonopsis bitterfeldensis* n. gen. n. sp. (Anapidae: Mysmeninae). Note the thickened and hairy metatarsus (only the basal part of the tarsus is drawn). M = 0.1.

Abb. 14) *Balticonopsis bitterfeldensis* (Zwerg-Kugelspinnen) im Baltischen Bernstein. Man beachte den verdickten und haarigen Metatarsus.

Fig. 15) *Balticonopsis ceranowiczae* n. gen. n. sp. (Anapidae: Mysmeninae) in Baltic amber. Note the long and strong ventral spine of the thickened tibia which is standing out. M = 0.2.

Abb. 15) *Balticonopsis ceranowiczae* (Zwerg-Kugelspinnen) im Baltischen Bernstein. Man beachte die lange und abstehende starke Borste unter der verdickten Tibia.

Fig. 16) *Mysmena grotae* n. gen. n. sp. (Anapidae: Mysmeninae) in Baltic amber. Note the long ventral metatarsal bristle. M = 0.1

Abb. 16) *Mysmena grotae* (Zwerg-Kugelspinnen) im Baltischen Bernstein. Man beachte die lange Borste unter dem Metatarsus.

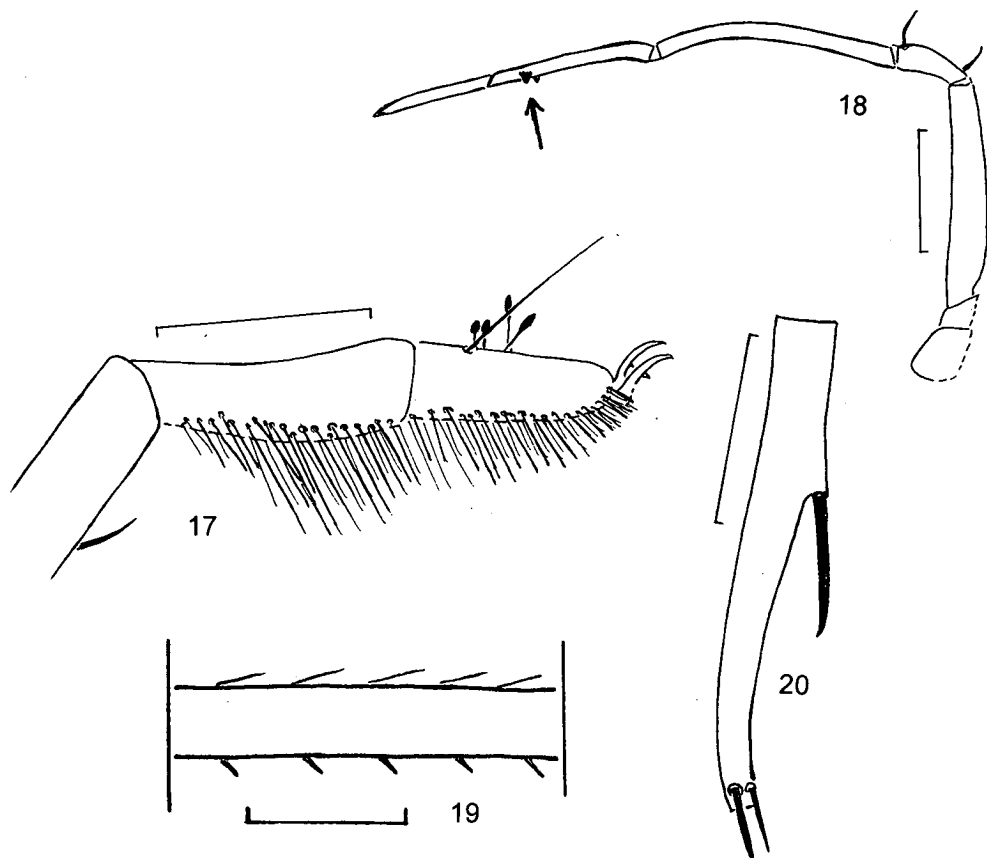


Fig. 17) *Ummidia malinowskii* WUNDERLICH 2000 (Ctenizidae). Note the ventral metatarsal bristle and the dense ventral hairs of tarsus and metatarsus. M = 1.0.

Abb. 17) *Ummidia malinowskii* (Falltürspinnen) im Baltischen Bernstein. Man beachte die Borste des Metatarsus und die dichte Behaarung unter Tarsus und Metatarsus.

Fig. 18) *Balticolipus kruemmeri* n. gen. n. sp. (Cyatholipidae) in Baltic amber, paratype b). Note the ventral metatarsal cusps (arrow). M = 0.5.

Abb. 18) *Balticolipus kruemmeri* (Becherspinnen) im Baltischen Bernstein. Man beachte die kurzen Stacheln des Metatarsus (Pfeil).

Fig. 19) ?*Coryssocnemis velteni* n. sp. (Pholcidae) in Dominican amber, middle part of the femur. Note the short ventral spines. M = 0.2.

Abb. 19) ?*Coryssocnemis velteni* n. sp. (Zitterspinnen) im Dominikanischen Bernstein, mittlerer Abschnitt des Femurs. Man beachte die kurzen unteren Stacheln.

Fig. 20) Tibia of *Plectreureys baltica* n. gen. n. sp. (Plectreuridae) in Baltic amber. Note the strong spines. M = 0.5.

Abb. 20) Tibia von *Plectreureys baltica* (Achtaugen-Fischernetzspinnen) im Baltischen Bernstein. Man beachte die starken Borsten.

The most important structures which may fix the female during copulation are the structures of the modified anterior male leg articles which most often concern the tibia and/or the metatarsus; such peculiar structures may bear "clasping spines" and exist in numerous spider families, in several fossil spider families, too. Most examples are reported from Baltic amber: Anapidae (figs. 13-16), Araneidae, Ctenizidae (fig. 17), Cyatholipidae (fig. 18), Pholcidae (?*Coryssocnemis* in Dominican amber, fig. 19), Plectreuridae (fig. 20), Segestriidae (similar to the Plectreuridae), Tetragnathidae and Theridiosomatidae (see the papers on these families in these volumes; e.g. the photos 14, 148, 150, 154, 202, 434). (In certain Theridiidae - *Phoroncidia* WESTWOOD - and extant Linyphiidae: Erigoninae - *Erigonoplus* MILLER - modified male anterior legs are present, too). What is the function of such modified legs? Some legs/spines may help to fix the female during copulation ("clasping spines"), e.g. those of the figs. 13-16, 20 (in fig. 13 apparently remains of muscles exist in the powerful femur); there is usually a single main spine. - The cusps of the bent first metatarsus in fig. 18 may be too small for such a function. The function of the short ventral femoral spines (fig. 19) are unclear to me. Does the thickened anterior femur (fig. 13) or metatarsus (fig. 14; *Erigonoplus*) bear pheromone glands? See the paper on the Anapidae: Comarominae in this volume. Do furthermore the males stimulate their mating partners with the hairs, cusps, bristles and spines of their anterior legs? Thickened and spiny first legs of fossil Salticidae in Baltic amber are unknown to me (see above), in contrast to extant Salticidae in which such modified legs - especially the tibiae - are not rare, see METZNER (1999).

The third leg is rarely modified in the male sex: It bears spines in some fossil Synotaxidae in Baltic amber, the genus *Eosynotaxus* n. gen. (photo 226), and in some members of the extant genus *Argenna* THORELL (*Altella* SIMON) (Dictynidae).

Modified male chelicerae exist in numerous spider taxa. They are most striking in extant Tetragnathidae: Tetragnathinae, in which the partners fix themselves with the help of their powerful and toothed chelicerae during copulation in a face-to-face position, see BRISTOWE (1941: Figs. 92-94). Certain extant male Salticidae (*Salticus* LATREILLE) may use their powerful chelicerae when they fight against each other, see BRISTOWE (1941: Fig. 96), fig. 2. In both families such powerful chelicerae are unknown from the Early Tertiary spiders, and probably such "modern" taxa of these families did not yet exist in the Baltic amber forest. - Also in numerous males of the families Corinnidae and Clubionidae enlarged chelicerae exist, e.g. in the questionable fossil Clubionidae *Eodoter magnificus* PETRUNKEVITCH 1958 of the Baltic amber forest, see the paper on the family Clubionidae in these volumes; photo 357b. Strongly modified - enlarged, hairy, toothed, denticulate and/or excavated - chelicerae are known (e.g.) from Young Tertiary spiders in Dominican amber, e.g. from the Dictynidae, Pholcidae and Tetrablemmidae, see WUNDERLICH (1988) and this volume. From the Early Tertiary Baltic amber forest such structures are known from the families Dictynidae (fig. 22, photo 292) and Tetrablemmidae, see the papers on these families in these volumes. In the mating position at least the male Pholcidae bring their chelicerae in contact with the females, see HUBER (2000: 18).

Further sexual dimorph structures

In certain male Araneidae and Zygellidae - see the papers on these families in these volumes - a hook exists on the male gnathocoxa and/or the first coxa.

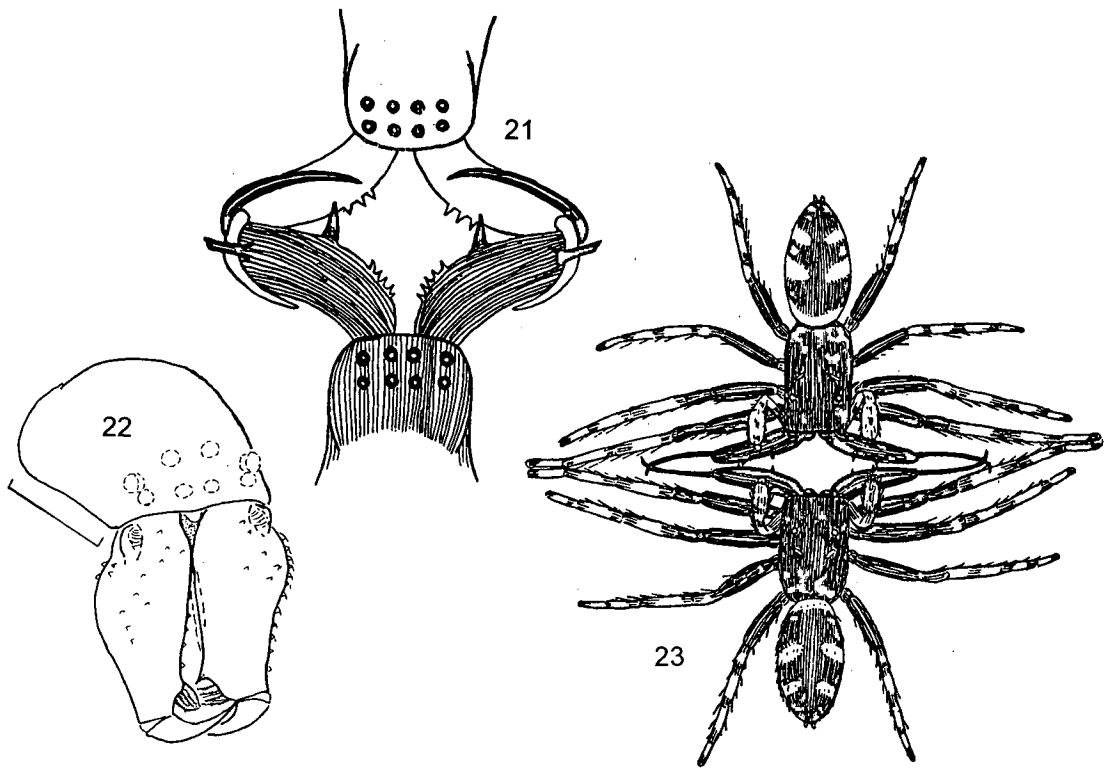


Fig. 21) The extant male *Tetragnatha* (Tetragnathidae) have a stiff spur-like process on the outer margin of their powerful and diverging chelicerae (arrow) with which the large female's chelicerae are wedged open during copula (male shaded). - Taken from BRISTOWE (1941: Fig. 94). The genus is also known from Dominican amber.

Abb. 21) Die mächtigen und auseinanderweichenden Kiefer heutiger Männchen der Gattung *Tetragnatha* (Streckerspinnen) - sie sind fossil vom Dominikanischen Bernstein bekannt - tragen an dem äußeren Rand ihrer kräftigen und divergierenden Cheliceren sporn-ähnliche Fortsätze (Pfeil), mit denen die ebenfalls sehr großen weiblichen Kiefer während der Paarung gespreizt und verhakt gehalten werden.

Fig. 22) Prosoma with the powerful chelicerae of a male Dictynidae (*Mizagalla tuberculata* n. gen. n. sp.) in Baltic amber. M = 0.5.

Abb. 22) Vorderkörper mit den mächtig entwickelten Kiefern einer männlichen Kräuselspinne im Baltischen Bernstein.

Fig. 23) Two fighting extant male Jumping Spiders (Salticidae) of the genus *Salticus* LINNAEUS - a bloodless battle. "This is the courting attitude except that when courting the fangs are not opened wide and the palps are stretched out to the side." - Taken from BRISTOWE (1941: 499, fig. 96).

Abb. 23) Zwei kämpfende heutige männliche Springspinnen der Gattung *Salticus* - ein ritualisierter, unblutiger Kampf. Ähnlich ist die Balzhaltung der Männchen, allerdings sind die Giftklauen nicht abgespreizt und die Pedipalpen sind zur Seite ausgestreckt.

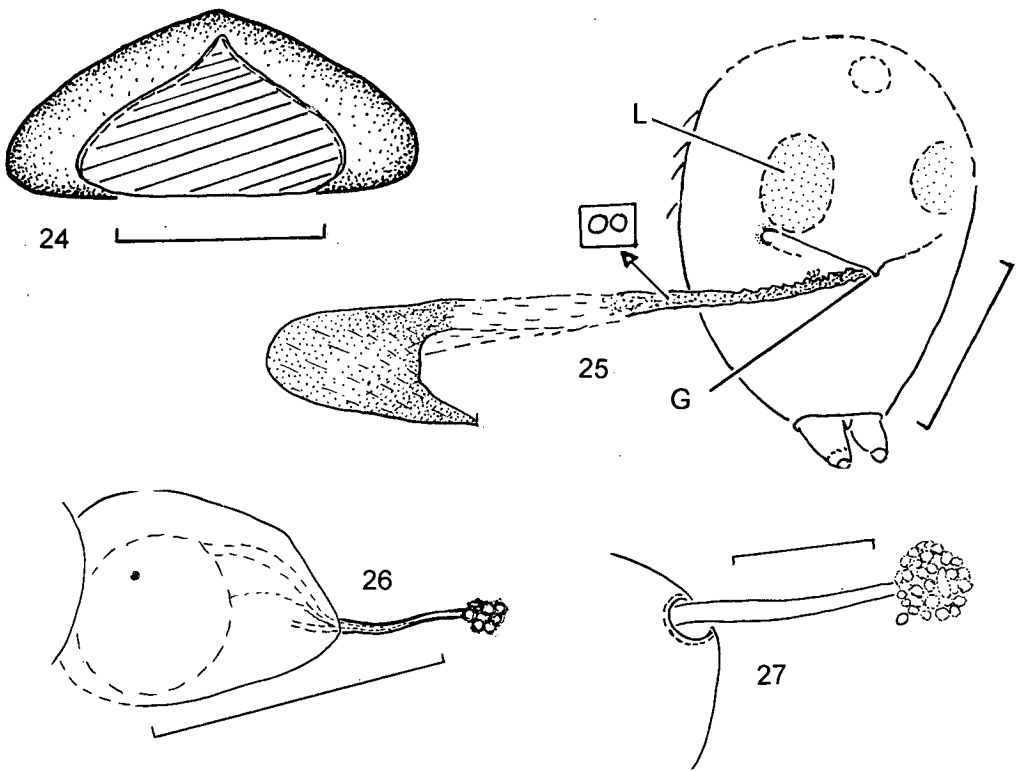


Fig. 24) A plug (hatched) closes completely the large epigynal opening of a fossil female of *Acrometa ?cristata* PETRUNKEVITCH (Synotaxidae) in Baltic amber, ventral-posterior aspect. M = 0.2.

Abb. 24) Das "Begattungs-Zeichen" einer fossilen Kugelhöhlenspinne im Baltischen Bernstein verschließt vollständig die große Öffnung der Epigyne.

Fig. 25) A droplet of secretion with enlarged questionable remains of spermatozoa (arrow) on the venter of the male holotype of *Custodela acutula* n. sp. (Linyphiidae). The droplet originates at the genital area (G), may be held together by a sperm web, and has apparently been drawn away by a flow of the resin. Bitterfeld deposit, coll. KUTSCHER. M = 0.5. L = right lung cover. Diameter of the questionable spermatozoa ca. 0.008mm.

Abb. 25) Ein Sekret-Tröpfchen, mit vergrößerten fraglichen Resten von Spermien (Pfeil) am Bauch einer männlichen Baldachinspinne. Das Sekret-Tröpfchen entspringt an der Genital-Region (G), könnte von einem Sperma-Netz zusammengehalten werden und wurde anscheinend von einem Fluß des Harzes verdriftet. Bitterfeld; Slg. KUTSCHER. L = Lungen-Deckel.

Figs. 26-31: Further remains of spermatozoa. (Weitere Reste von Spermien).

Figs. 26-27: Remains of spermatozoa at the tip of the embolus of a male paratype (coll. GRÖHN) of *Balticoblemma uniconiculum* n. gen. n. sp. (Tetrablemmidae) in Baltic amber. M = 0.2 and 0.05mm.

Abb. 26-27: Reste von Spermien an der Spitze des Embolus einer Vieraugenspinne.

(4) Male competition, fighting males (Kampfverhalten bei Spinnen-Männchen)

In several spiders which orientate visually - as Salticidae and Lycosidae - fights of conspecific males are reported, see BRISTOWE (1941: 498f), fig. 23. Such fights are unreported in fossil spiders but in the collection of a dealer I saw a couple of two large-eyed male Zodariidae - probably *Anniculus balticus* PETRUNKEVITCH - in a position close together, which have probably been embedded in the resin during their fight. - In such species in which the male prosoma is about as large as the female prosoma or even larger - see above - the male chelicerae are often enlarged/ modified; both patterns are frequently connected. Examples in Dominican and Baltic amber are members of the family Dictynidae. Probably in this family - as well as in Clubionidae, Corinnidae, Lycosidae and Salticidae - bloodless fights of males exist. In other taxa - e.g. in the Tetragnathidae: Metinae: *Meta menzei* (BLACKWALL) a male may kill his rival, see BRISTOWE (1941: 502).

(5) **Eggs and broodcare (Eier und Brutfürsorge)**: See the chapters on egg sacs and on the families Lycosidae, Pisauridae and the Dysderoidea, especially the Scytodidae and Pholcidae (the egg-carrying behaviour). An egg-laying fossil spider has never been reported. Egg-laying Diptera in amber are not too rare.

(6) Plugs ("Begattungszeichen")

Plugs are secretions of the male bulbus which close the opening(s) of the external female genital organ - the epigyne - after copulation. They may provide further transfer of sperm. Such structures are known from members of numerous families of spiders; I observed them e.g. in extant members of the Dictynidae and Theridiidae. One example is reported here for the first time from a fossil spider, from a member of the family Synotaxidae in Baltic amber, *Acrometa ?cristata* PETRUNKEVITCH 1942, coll. GRABENHORST no. 54. The wide epigynal opening is completely filled by a plug (fig. 24).

(7) Remains of sperm (Sperma-Reste) (figs. 25-31) (photos 249-250)

In spiders the testes are located within the opisthosoma. A penis is absent in spiders,

and its function is taken over by secondary copulatory organs, the pedipalpi (leg-shaped extremities in front of the legs but shorter than legs), especially by the bulbi at their tip. In almost all spiders the male build a special "sperm web" into which he deposits the sperm from his genital opening on the ventral side of the opisthosoma, and from which he sucks it up into his bulbi. During copulation the sperm is transferred to the epigyne/vulva by a free structure, the embolus, which may be needle-shaped, see figs. 26, 31, 33-34. Questionable remains of such a sperm web are preserved with the male at and near the opisthosoma of the holotype of *Custodela acutula* n. sp. (Linyphiidae) in Baltic amber (coll. KUTSCHER in Saßnitz) (fig. 25); see the chapter on spiders' webs in this volume. But in this case a sperm web is probably absent (threads are not observable), and the remains may be a mixture of sperm and a secretion. - Masses of questionable sperm (and a secretion) are also observable on the genital openings of the holotype of *Succinitaxus brevis* n. gen. n. sp. (Synotaxidae) and of a questionable Clubionidae, F246/CJW.

KOTEJA (1998) remains of sperm from Coccids (Homoptera) in Baltic amber which have been ejected into the resin; such events seem to have resulted from the shock during entrapping and entombing. Corresponding events are occasionally observable with fossil spiders, see figs. 26-31. In some cases even remains of spermatozoa cells may be preserved at the tip of the embolus, e.g. in *Balticoblemma unicorniculum* n. gen. n. sp. (Tetrablemmidae) (figs. 26-27). Apparently a bulbal secretion/spermatozoa is/are also present in further spiders which are preserved in Baltic amber: In *Ruganapis scutata* n. gen. n. sp. (Anapidae) (figs. 29-30), the holotype of *Sosybius perniciosus* n. sp. (Trochanteriidae), the holotype of *Microlinus folium* n. gen. n. sp. (Linyphiidae) (both are not figured here) as well as in a specimen of *Pensacolatus coxalis* WUNDERLICH 1988 (Salticidae) in Dominican amber, see WUNDERLICH (1988: Fig. 679).

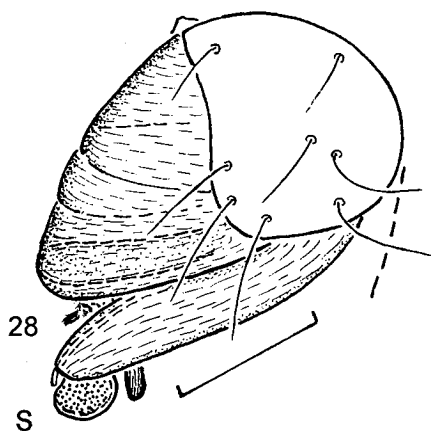
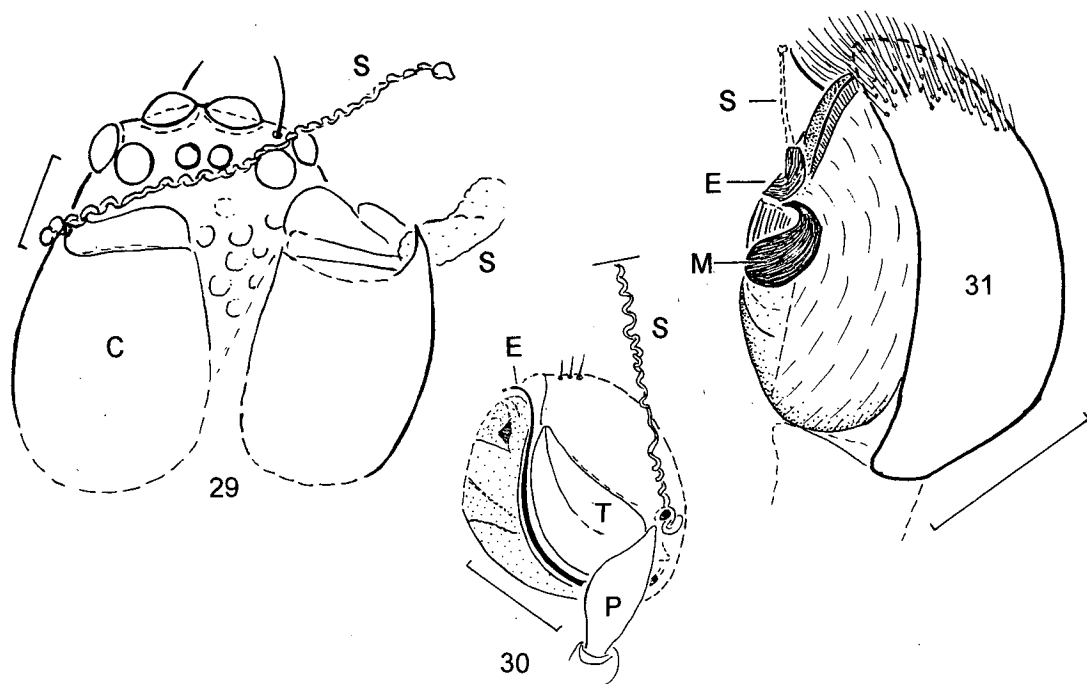


Fig. 28) A droplet of secretion (S) with questionable spermatozoa at the tip of the embolus of the male holotype *Eonephila excellens* n. gen. n. sp. (Araneidae) in Baltic amber. M = 0.1.

Abb. 28) Sekret-Tropfchen (S) mit fraglichen Spermien an der Spitze des Embolus eines Männchens der Radnetzspinne *Eonephila excellens* im Baltischen Bernstein.



Figs. 29-30: Remains of secretion (S) at the pedipalpi of the male holotype of *Ruganapis scutata* n. gen. n. sp. (Anapidae) in Baltic amber, M = 0.1; 29) frontal aspect of prosoma and pedipalpi; 30) prodorsal aspect of the r. pedipalpus. The tape-shaped structure seems to originate at the basal-dorsal part of the cymbium (C). E = embolus, P = patella, T = Tibia.

Abb. 29-30: Sekret-Reste (S) an den Pedipalpen der Zwerg-Kugelspinne *Ruganapis scutata* im Baltischen Bernstein; 29) Vorderkörper und Pedipalpen von vorn gesehen; 30) rechter Pedipalpus mit bandförmiger Struktur (S), die nahe der Basis des Cymbiums (C) zu entspringen scheint. E = Embolus, P = patella, T = Tibia.

Fig. 31) A "stalk" of secretion (S) at the tip of the embolus of the male holotype of *Sosybius lateralis* n. sp. (Trochanteriidae) in Baltic amber. M = 0.5. E = embolus, M = median apophysis.

Abb. 31) Ein "Stiel" von Sekret (S) an der Spitze des Embolus des männlichen Holotyps von *Sosybius lateralis* (Schenkelring-Spinnen) im Baltischen Bernstein.

Figs. 32-34: Examples of external female (epigyne) and male (pedipalpi) genital organs of fossil spiders in Baltic amber. M = 0.2. (Beispiele äußerer weiblicher Geschlechtsorgane (Epigyne) oder männlicher Geschlechtsorgane (Pedipalpen) bei fossilen Spinnen).

Fig. 32) A complicated epigyne of a Linyphiid spider (*Custodeia*), with a pair of grooves and a long outgrowth (scapus) which almost reaches the spinnerets. Numerous "higher" spiders possess epigynal scapes or grooves; a large groove is present e.g. in the extinct genus *Acrometa* (Synotaxidae) (fig. 24). In archaic spiders as Mygalomorpha - as well as in the Dysderoidea and most Eresoidea - a sclerotized epigyne or outgrowths in this area are absent.

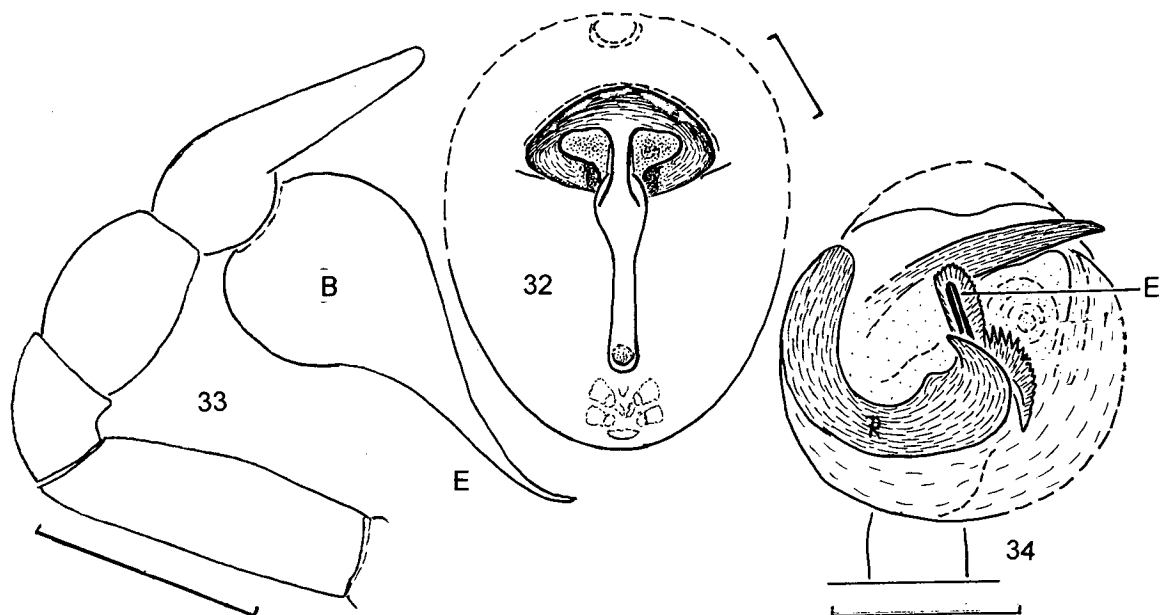


Abb. 32) Komplizierte Epigyne einer Baldachinspinne der Gattung *Custodela*, mit einem Paar von Gruben und einem langen Auswuchs, der nahezu die Spinnwarzen erreicht. Zahlreiche "höhere" Spinnen besitzen Auswüchse oder Gruben der Epigyne; eine große Grube existiert bei der ausgestorbenen Gattung *Acrometa* (Abb. 24). Bei ursprünglichen Spinnen wie den Längskieferspinnen - wie auch den Sechsaugenspinnen-Verwandten und den meisten Röhrenspinnen-Verwandten - fehlen eine sklerotisierte Epigyne oder Auswüchse in dieser Region.

33. Complicated bulbi and slender male pedipalpal articles are present in most of the "higher" spider taxa and are connected with the complicated external female genitalia.

Abb. 34) Männlicher Pedipalpus mit einer fossilen Baldachinspinne der Gattung *Custodela* mit kompliziertem Bulbus, der mehrere Apophysen trägt, vgl. fig. 33. Komplizierte Bulbi und schlanke Glieder des ♂-Pedipalpus existieren bei den meisten "höheren" Spinnen und stehen in Verbindung mit den komplizierten äußeren weiblichen Geschlechtsorganen.

Fig. 33) Male pedipalpus with simple bulbus (B) of a fossil Segestriidae, the genus *Vetsegestria* n. gen., in which the pear-shaped bulbus bears the sperm transferring embolus (E) but no other apophyses, compare fig. 34. Simple bulbi without or with only few apophyses are frequent in archaic spiders as the Mygalomorpha, Dysderoidea and Eresoidea, in which most often one or several pedipalpal articles are thickened as in this figure.

Abb. 33) Männlicher Pedipalpus einer fossilen Fischernetzspinne, Gattung *Vetsegestria*, mit einfachem Bulbus (B), bei der der birnenförmige Bulbus den spermaübertragenden Embolus (E) trägt, aber keine weitere Apophyse; vgl. Abb. 34. Einfache Bulbi ohne oder solche mit nur wenigen Apophysen sind häufig bei ursprünglichen Spinnen wie den Längskieferspinnen, Sechsaugenspinnen-Verwandten und Röhrenspinnen-Verwandten, bei denen meist ein oder mehrere Glieder des Pedipalpus verdickt sind wie in dieser Abbildung.

Fig. 34) Male pedipalpus with a complicated bulbus of a fossil Linyphiidae, the genus *Custodela* PETRUNKEVITCH, which bears several apophyses/sclerites, comp. fig.

QUESTIONABLE PARTHENOGENESIS IN FOSSIL SPIDERS (FRAGLICHE JUNGFERNZEUGUNG BEI FOSSILEN SPINNEN)

Photos 65-67.

Parthenogenesis is a monosexual kind of reproduction from a female gamete without fertilization by a male gamete. Males are rare or may even be absent. Parthenogenesis is well-known from numerous taxa of insects, e.g. from plant-louses (Aphids), Walking sticks (Phasmida) and male honey bees (development of drones), but rarely reported from spiders, e.g. from the extant European *Dysdera hungarica* KULCZYNSKI 1897 (Dysderidae), see GRUBER (1990). In the laboratory of GRUBER a female bred for three generations without a male.

Naturally we cannot breed fossils (members of extinct species), so we can only conclude on the probable parthenogenesis in fossil spiders from comparisons of fossil with extant spiders and from observations in the fossils. Concerning extant spiders in traps - resin is a kind of trap - males of almost all species are to be found much more frequently than females at least in the season of mating. The explanation is that the males - at least during the season of mating - run around looking for females that are ready to mate and so get into traps. If females are caught in traps to a greater extent or even exclusively, parthenogenesis can be suspected. From Europe I know one single species to which these conditions apply (the male is still unknown): *Hahnia microphthalma* SNAZELL & DUFFEY (Dictynidae s. l.: Hahniinae), see the paper on these taxa in these volumes.

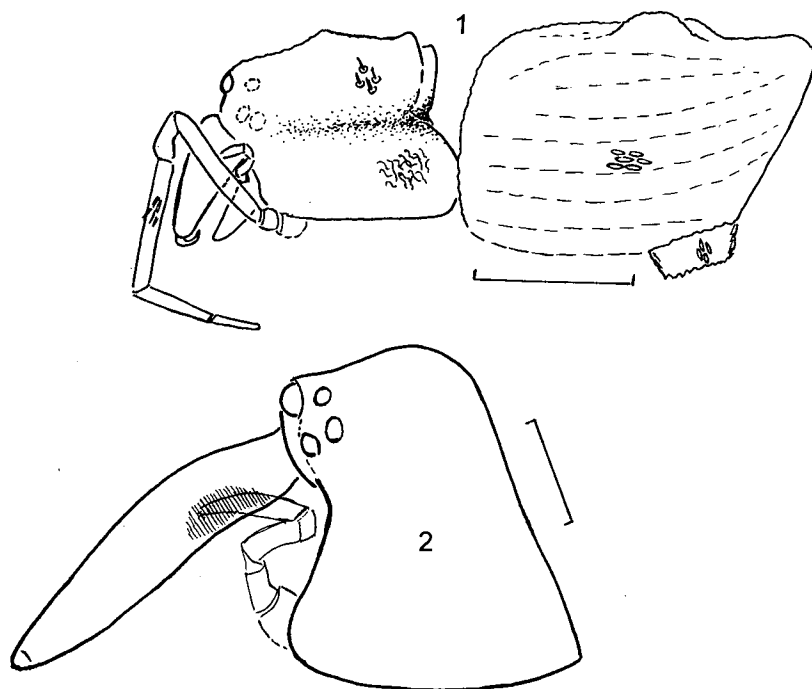
In German: Jungfernzeugung (Parthenogenese) ist eine eingeschlechtliche Art der Fortpflanzung durch weibliche Keimzellen (Eizellen) ohne Befruchtung durch männliche Keimzellen (Spermien). Männchen sind selten oder fehlen sogar vollständig. Parthenogenese ist von zahlreichen Insekten-Gruppen bekannt, z. B. von Blattläusen, Stabheuschrecken und männlichen Honigbienen (die Entwicklung von Drohenen); von Spinnen ist sie aber nur selten beschrieben worden, z. B. von der heutigen Europäischen Sechsaugenspinne *Dysdera hungarica* KULCZYNSKI 1897, siehe GRUBER (1990). Im Labor von GRUBER wurden Weibchen über drei Generationen ohne Männchen gezüchtet.

Natürlich lassen sich Fossilien (Vertreter ausgestorbener Arten) nicht züchten; so können wir auf mögliche Parthenogenese bei fossilen Spinnen lediglich aufgrund bestimmter Beobachtungen rückschließen. Bei heutigen Spinnen finden sich in Fallen - sie sind vergleichbar mit den fossilen Harzfallen - Männchen nahezu aller Arten deutlich häufiger als Weibchen. Die Erklärung liegt darin, daß die Männchen - wenigstens während der Paarungszeit - nach paarungsbereiten Weibchen suchend umherlaufen und in Fallen geraten. Sofern in Fallen ganz überwiegend oder ausschließlich Weibchen gefangen werden, liegt der Verdacht nahe, daß Jungfernzeugung vorliegt. Aus Europa kenne ich lediglich eine einzige Art, auf die diese Verhältnisse zutreffen (das Männchen ist noch unbekannt): *Hahnia microphthalma* SNAZELL & DUFFEY (Dictynidae s. l.: Hahniinae), siehe den Beitrag über die Familien Dictynidae s. l. (Hahniidae).

Observations in fossil spiders: Among several hundred species of fossil spiders I

have seen the males - usually distinctly - more frequent than the females; only in *Archaea paradoxa* KOCH & BERENDT 1854 (Archaeidae) the males are probably slightly rarer than the females. - Among the five genera of Archaeidae in Baltic amber there are two genera - *Baltarchaea* ESKOV 1992 (fig. 1) and *Eoarchaea* FORSTER & PLATNICK 1984 (fig. 2): I did not find a single male but more than 30 adult and several juvenile females in *Eoarchaea*, and 2 females and a juvenile female in *Baltarchaea*. In the remaining genera males are not rare. Concerning these finding it is likely that parthenogenesis existed in these two extinct genera. In the Early Tertiary species of the family Archaeidae the "tendency" to parthenogenesis probably existed.

Remark: ESKOV (1992) regards the members of the genus *Eoarchaea* as juveniles of the genus *Archaea* KOCH & BERENDT 1854. According to the proportions of prosoma, opisthosoma and the legs (see the photos), the complete absence of a "neck" - which is present in juvenile *Archaea* - and the absence of intermediate classes of size I regard the larger specimens of *Eoarchaea* as adult females but not as juveniles.



Figs. 1-2: Fossil females of two fossil species of the family Archaeidae in Baltic amber in which parthenogenesis probably occurred, seen from the left side; 1) body and first left leg of *Baltarchaea conica* KOCH and BERENDT 1854). M = 1mm; 2) prosoma of *Eoarchaea vidua* n. sp., holotype. M = 0.2mm.

Abb. 1-2: Fossile Weibchen zweier Arten der Familie Urspinnen im Baltischen Bernstein, bei denen möglicherweise Jungfernzeugung (Parthenogenese) vorkam, gesehen von links; 1) Körper und linkes Vorderbein von *Baltarchaea conica*. M = 1mm; 2) Vorderkörper von *Eoarchaea vidua* n. sp. M = 0.2mm.

FOSSIL SPIDERS AS TRANSPORTERS AND DISTRIBUTERS OF MICROORGANISMS (FOSSILE SPINNEN ALS VERBREITER VON MIKROORGANISMEN)

According to my studies vagrant fossil spiders as Salticidae may transport and distribute Bacteria (questionable), spores of fungi and pollen grains - and also parasitic or phoretic animals as Acari and Nematoda - on their body and legs by walking and most probably by ballooning, too, see the chapters on parasites, phoresy and spiders' threads (aeronautic behaviour). Questionable Bacteria and fungal spores may be attached to the leg scopulae and claw tufts, but are easily overlooked.

Well observable are spores of Fungi (indet.) and numerous pollen grains - larger air bag pollen grains and tiny grains of questionable Fagaceae - on the cuticula of the dissected holotype of *Gerdiopsis infrigens* n. gen. n. sp. (Hersiliidae), F50/CJW; see the paper on the Oecobioidea in these volumes. Photo 89; see the chapter on decomposition.

Questionable tiny spores of a Fungus - or Bacteria? - are preserved (e.g.) within the claw tufts of the posterior legs of a male of *Gorgopsina frenata* (KOCH & BERENDT 1854) (Salticidae), F268/BB/AR/SALT/CJW. The diameter of such a particle is about 0.005 mm. A closer study of these "particles" is wanting. Photos 427-428.

PHORESY IN FOSSIL SPIDERS (PHORESIE BEI FOSSILEN SPINNEN)

Phoresy is the transport of non-parasitic organisms by specimens of a different species. (In German: Phoresie ist der Transport nicht-parasitischer Lebewesen (der "Phoresiegäste") durch Vertreter anderer Arten (der "Phoresiewirte")). In arachnids it mainly is known from mites and pseudoscorpions, see WEITSCHAT & WICHARD (2002: Figs. 11a-c, 14a-b). Members of both orders may use Opiliones as transporters. Extant phoretic spiders are unknown to me; reports are absent e.g. in the books of BRISTOWE and FOELIX. A questionable phoretic fossil spider is reported below (a). Extant spiders as transporters of phoretic organisms are rarely found and have never been reported from fossils up to now, see below, the transport of mites (b), an insects' larva (c) and roundworms (Nematoda) (d).

(a) A questionable phoretic fossil spider carried by a beetle

Photos 587-588.

A questionable phoretic fossil spider - *Balticoroma* sp. indet. (Anapidae), body length 1.5mm, is biting in the apical structures of a beetle (Coleoptera: Staphylinidae), body length 6.3mm, see the photo. The enfolded hind wings of the beetle indicate that this animal has come flying to the sticky resin, carrying the spider at the end of its body. The spider does not cling to the beetle; so this case may be an accidental transport of a spider by a beetle. Baltic amber, F87/BB/AR/ANA/CJW. An extant hitchhiking spider is unknown to me.

(b) Fossil spiders as transporters of mite's larvae

Photo 584

A phoretic mite's larva of the family Histiostomatidae (A. WOHLTMANN det.), body length 0.2mm, is attached with its posterior body part to the promargin of the cymbium of the left pedipalpus of the Jumping Spider (Salticidae) *Eolinus* sp. indet. (fig. 1) in Baltic amber, F314/BB/AR/SAL/CJW.

A flat phoretic mite's larva - Astigmata: *Lyopus* sp. indet., M. JUDSON det. -, body length 0.15mm, is attached with its ventral side to the dorsal surface of the male holotype of *Dasumiana emicans* n. gen. n. sp. (Dysderidae) in Baltic amber (fig. 2). There are several hair-shaped - attaching? - structures around the mite, see the paper on the family Dysderidae (Dysderoidea) in this volume. F540/BB/AR/DYS/CJW.

An indet. mite larva in Baltic amber is attached at the base of the right femur II of *Eolinus ?tystschenkoi* (Salticidae), F316/CJW.

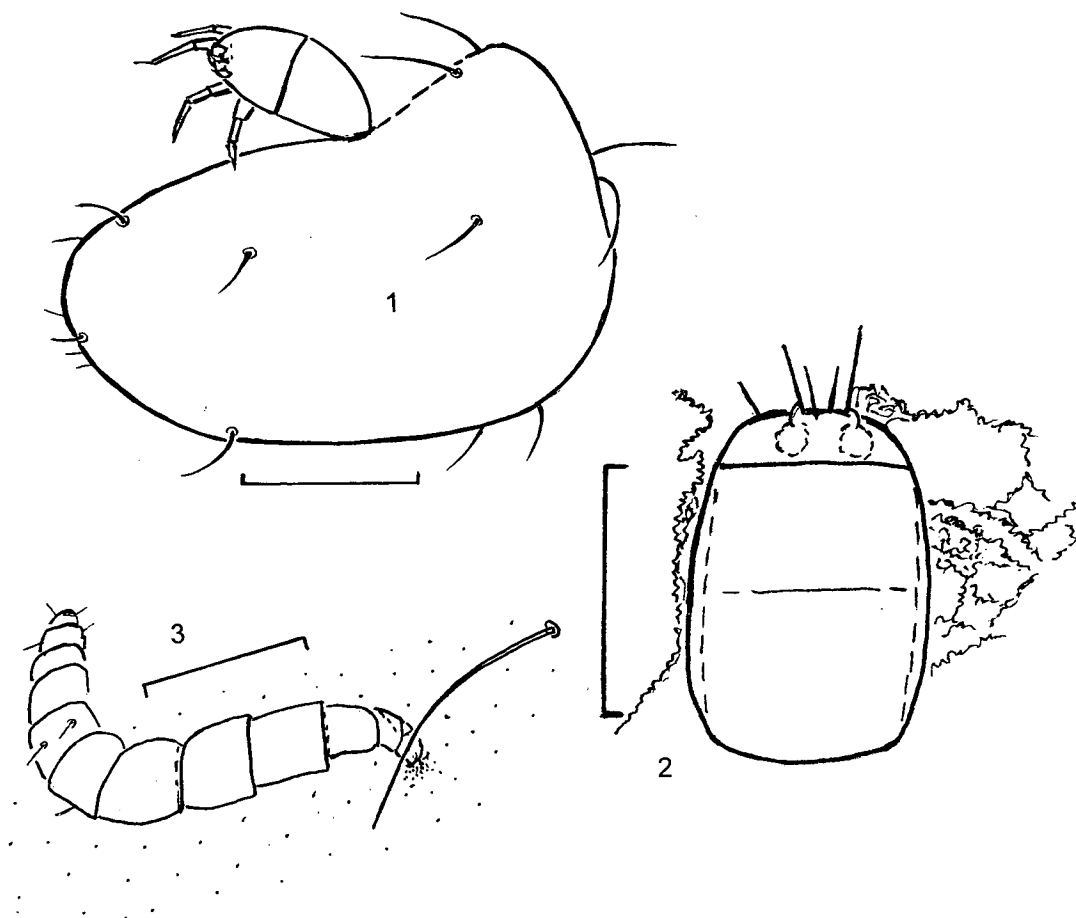


Fig. 1) A fossil phoretic mite larva (Acari: Astigmata: Histiostomatidae), body length 0.2mm, is attached with its posterior body part on the promargin of the cymbium of the left pedipalpus of the Jumping Spider (Salticidae), *Eolinus* sp. indet. in Baltic amber. Only few cymbial hairs are drawn. F314/CJW. M = 0.2mm. (Eine fossile phoretische Milben-Larve, die mit ihrem hinteren Körperteil am Cymbium des linken Pedipalpus einer Springspinne angeheftet ist).

Fig. 2) A flattened fossil phoretic mite larva (Astigmata: *Lyopus* sp. indet.) attached to the central part of the prosoma of the male holotype of *Dasumiana emicans* n. gen. n. sp. (Dysderidae) in Baltic amber. M = 0.1. (Eine abgeflachte fossile phoretische Milben-Larve, die am mittleren Teil des Vorderkörpers einer Sechsaugenspinne angeheftet ist).

Fig. 3) A probably phoretic fossil insect larva which head - on the right side - is in contact with (and probably attached to) the prosoma of a male of *Myrmecorinna gracilis* n. gen. n. sp. (Corinnidae) in Baltic amber, F662/CJW. M = 0.1. (Eine möglicherweise phoretische Insekten-Larve in Kontakt - und möglicherweise angeheftet - mit dem Vorderkörper einer Ameisen-Sackspinne).

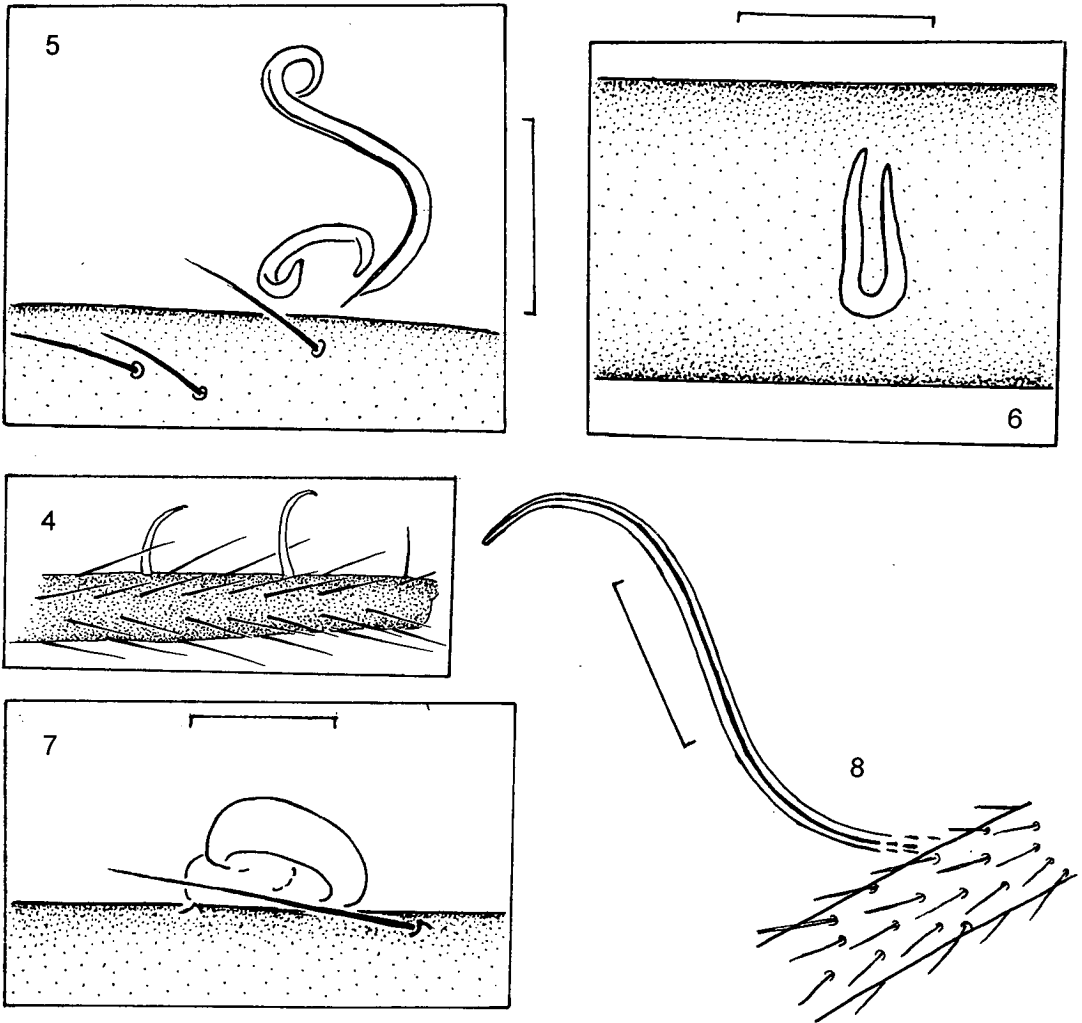


Fig. 4) Two permanent larvae of an extant phoretic Nematoda: Rhabditida attached to a metatarsus of the Linyphiid spider *Centromerus sylvaticus* (BLACKWALL). (Zwei Dauerlarven eines heutigen Fadenwurms angeheftet am Bein einer Baldachinspinne).

Figs. 5-7: Fossil phoretic Nematoda: Rhabditida near or attached to the surface of the opisthosoma (fig. 5) and the right femur I (figs. 6-7) of the male holotype of *Eotrechalea annulata* n. gen. n. sp. (?Trechaleidae). Note the right Nematoda in fig. 5 which is attached to the opisthosoma by a tiny stalk. M = 0.05mm in fig. 7, 0.2mm in figs. 5-6. (Fossiler phoretischer Fadenwurm nahe oder angeheftet am Hinterkörper (Abb. 5) und dem rechten Femur bei einer Spinne (möglicherweise Familie Trechaleidae). Beachte das Stielchen in Abb. 5, mit dem der rechte Fadenwurm an den Hinterkörper der Spinne angeheftet ist).

Fig. 8) Questionable phoretic fossil Nematoda (or a fungus?) on a loose metatarsus of the male holotype of *Mizalia spirembolus* n. sp. (Oecobiidae). M = 0.2mm. (Fraglicher phoretischer fossiler Fadenwurm (oder ein Pilz?) an einer Scheibennetzspinne).

(c) A fossil spider as a probable transporter of an insect larva Photos 585 and 605.

A strongly sclerotized, legg-less and 0.33mm long probably phoretic larva of an insect (Coleoptera?) (fig. 3, photos) which possess about a dozen articles of the body, is in contact with/and is apparently attached to the prosoma of a male of *Myrmecorinna gracilis* n. gen. n. sp. (Corinnidae), F662/CJW.

(d) Fossil spiders as transporters of larvae of Nematoda: Rhabditida Photos 335-337.

NOORDAM et al. (1998) report a large number of phoretic Nematoda: Rhabditida (fig. 4) attached on the extant spider species *Centromerus sylvaticus* (BLACKWALL 1841) (Linyphiidae). Fossil phoretic Rhabditida on a Diptera (Limoniinae) are reported by WEITSCHAT & WICHARD (1998: Figs. 7a-b). - With fossil spiders in Baltic amber I occasionally found members of the Rhabditida, e.g. on and around the male holotype of *Eotrechalea annulata* n. gen. n. sp. (?Trechaleidae), figs. 5-7. In fig. 5 a Rhabditida is shown which is attached by a stalk to the opisthosoma of the spider.

A probably phoretic "object", a questionable phoretic Nematoda - or a fungus? -, F54/BB/AR/CJW, 0.33mm long, is preserved on a loose metatarsus of *Mizalia spirembolus* n. sp. (Oecobiidae), fig. 8. A similar "object" 0.8mm long, is preserved in the piece F216/BB/CJW.

CRYPTIC BEHAVIOUR, CAMOUFLAGE, MASKING AND RESTING POSITIONS IN FOSSIL SPIDERS (SCHUTZANPASSUNG, TARNUNG UND RUHEPOSITIO- NEN BEI FOSSILEN SPINNEN)

Certain animals which look for their prey in a mainly optical way - as numerous birds and lizards - feed on spiders or their eggs. Thus it may be advantageous for spiders to hide themselves (see the chapters on masked chambers and egg sacs) or to look different from a spider: (a) In their colour and/or shape of their body, (b) in their behaviour. In the following I will discuss some examples:

(1) Playing death (Thanatosis) (in German: Sichtotstellen) with contracted legs: It is known from numerous extant spiders, e.g. from many Araneidae. Apparently there is no difference of the thanatosis and the leg position of numerous dead spiders in amber as shown in certain photos.

(2) A "fixed" resting position (in German: Ruhehaltung) may be of advantage in spiders which are easily recognized when moving. There is a special position of the legs in those spiders, and such spiders may imitate dead leaves, see the male Araneidae which is shown above on p. 120 in the book of PRESTON-MAFHAM (1991). I found few fossil spider in Baltic amber, which may show such a position: *Sosybius* sp. indet. (Trochanteriidae), juv. ♀, F242/BB/CJW, some Segestriidae as the paratype F688/BB/CJW of *Vetsegestria quinquespinosa* n. sp., see the photos 390-391.

(3) Mimicry (imitation of dangerous animals as ants and wasps; see the next chapter on the relationships between fossil spiders and ants).

(4) Mimesis (in German: Mimese; imitation of quite different objects as excrement, leaves or the bark of trees; in German: Schutzanpassungen). See also above (2): Certain tropical members of the families Araneidae and Thomisidae imitate excrement. Others, e.g. members of the families Hersiliidae and Trochanteriidae which are dwellers on the bark of trees, may possess a flattened body and legs which are stretched out sideways; they imitate the surface of the bark or plants as lichens which grow on it. Unfortunately the original colour of fossil Hersiliidae in amber is unknown; see the figs. 299 and 300 in the book of WUNDERLICH (1986). Leaf-dwelling members of several families as certain Sac Spiders (Clubionidae) and Jumping Spiders (Salticidae) imitate leaves with the help of the green pigments of their body. The green colour disappears in resin and usually in alcohol, too. - See also the chapter on egg sacs and a retreat.

Extant slender and long-legged members of the family Tetragnathidae stretch their legs I-II forwards and their legs III-IV backwards; thus sitting, e.g. on a blade of grass such spiders are hard to discover. The very long legs in some fossil spiders indicate the presence of this kind of behaviour already in the Early Tertiary, see the photo 121. Change of colour of the body is known, e.g. from certain advanced extant members of the Crab Spiders (family Thomisidae) which wait on flowers for their prey (such behaviour and such taxa are unknown in fossil spiders).

(5) Seemingly disappearing spiders:

(a) Extant members, e.g. of the Daddy long-legged Spiders (Pholcidae, German name: Zitterspinnen) shake their capture web when alarmed so rapidly that they seem

to disappear. Pholcidae are reported from Baltic and Dominican amber but nothing is known of their behaviour on this matter.

(b) Certain extant spider taxa - striking e.g. in the families Oxyopidae and Salticidae (see the photos) - bear patches or stripes of coloured or white hair on their body as well as annulated legs (figs. 1-2). Due to such markings the outline of the body may disappear best in an unmoving animal, e.g. in a zebra (Mammalia) or in a Zebra spider (the genus *Salticus* LATREILLE 1804, family Salticidae, Jumping Spiders, German name: Springspinnen) (fig. 1). Also in the extant Jumping Spiders of *Pseudicius encarpatus* (WALCKENAER 1802) the outline of the opisthosoma does not appear homogeneous due to two longitudinal white bands (fig. 2). Quite similar bands exist on the opisthosoma of *Eolinus* (Salticidae) in Baltic amber, a male of the coll. of the author (F1243) and a male just after moulting (coll. C. GRÖHN no. 3947), see the photos. See also the photo of a female Salticidae indet. (coll. EICHMANN) and of a juvenile questionable *Esuritor* sp. indet. (Pisauridae) (probably coll. LUDWIG), in which two light prosomal bands and three opisthosomal bands are present. Thus this kind of camouflage already existed in spiders of the Early Tertiary Baltic amber forest. Photos 325-326, 335, 338, 417-420, 430, 471.

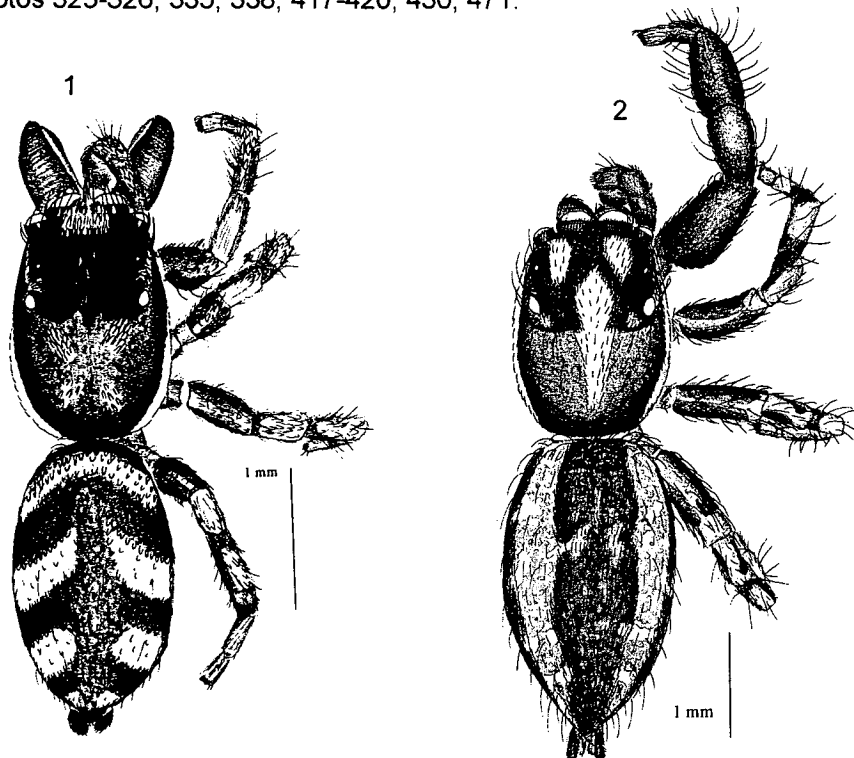


Fig. 1) *Salticus zebraneus* (C. L. KOCH 1837), family Salticidae, extant, Europe, body length 3mm, habitus of the male (the left legs are not drawn; taken from METZNER (1999: T. 82, fig. a), with distinct opisthosomal markings (camouflage);

fig. 2) *Pseudicius encarpatus* (WALCKENAER 1802), family Salticidae, extant, Europe, body length 3mm, habitus of the male (the left legs are not drawn); taken from METZNER (1999: T.57, fig.a), with distinct paired longitudinal white bands, a camouflage which is similar to fossil males of the genus *Eolinus* (Salticidae) in Baltic amber.

THE RELATIONSHIPS BETWEEN FOSSIL SPIDERS AND ANTS, MYRMECOMORPHY (DIE BEZIEHUNGEN ZWISCHEN FOSSILEN SPINNEN UND AMEISEN, AMEISEN-ÄHNLICHKEIT)

Introduction

Terms: Mimicry is the close resemblance of a species (the mimic) to a non-related species (the model) in order to deceive a third (the operator). - Hymenopteromorphs are arthropods that have evolved a morphological and/or ethological resemblance to Hymenoptera. The most frequent hymenopteromorphs are myrmecomorphs: Arthropods which look like (imitate) ants. "Myrmecomorphy is generally considered a type of Batesian mimicry in which spiders are gaining protection from predators through their resemblance to aggressive or unpalatable ants. Selection pressure from spider predators and eggsac parasites may trigger greater integration into ant colonies among myrmecophilic spiders." (Taken from CUSHING (1997: 165)). - "Myrmecophiles" live near ant nests or even - as synoecs (in German: "Mitbewohner") (commensals, parasites or symbionts) - in ant nests.

On the coevolution of spiders and ant: See the paper on the phylogenetics in this volume. The diversification of ants probably did not happen before the beginning of the Tertiary, and the same may be true for the origin of distinct myrmecomorphy and myrmecophagy.

About 50 species of extant spiders in Central Europe (= about 4%) possess closer relationships to ants, see WUNDERLICH (1995). In spiders one can find the following 5 groups of spider-ant relationships at least:

- (1) Batesian mimicry; myrmecomorphy and myrmecoid behaviour, e.g., various Corinnidae and some Salticidae (not known from Baltic amber!);
- (1a) Batesian mimicry combined with a second - aggressive - relationship, the predator-prey relationship (myrmecophagy), model and prey are identical, e.g. numerous Zodariidae, *Callilepis* (extant, Gnaphosidae), *Aphantochilus* (extant, Thomisidae);
- (2) Predator-prey relationship (myrmecophagy), e.g., numerous Theridiidae, Oecobiini, see (1a);
- (3) Prey-predator relationship (ants as enemies), frequent, see (1a);
- (4) Competition, e.g., plant-louses (aphids) may be protected by ants but eaten by spiders (not treated in this volume);
- (5) "Myrmecophily", synoecy (at least the extant members of *Mastigusa*, Dictynidae), symbiosis (e.g. with aphids).

Hymenopteromorphy - Batesian mimicry - of fossil spiders in Baltic and Dominican amber:

kind of amber	myrmecomorphy	possible mutillomorphy	possible ichneumomorphy
Baltic amber	Zodariidae, e.g. <i>Adorator</i> , Corinnidae, e.g. <i>Ablator</i> ad part.?, <i>Eomazax</i> and <i>Crypto-</i> <i>planus</i> , " <i>Phrurolithus</i> " sensu PETRUNKEVITCH, <i>Harpac-</i> <i>tea</i> (Dysderidae), <i>Vetseges-</i> <i>tria</i> (Segestriidae), <i>Spatiator</i> (Spatiatoridae), probably <i>Myr-</i> <i>mecarchaea</i> (Archaeidae)	<i>Ablator</i> ad part. (Corinnidae)	<i>Myrmecarchaea</i> (Archaeidae)
Dominican amber	<i>Descangeles</i> and ? <i>Descanso</i> (Salticidae), <i>Castianeira</i> (Co- rinnidae), probably <i>Veterator</i> (Trochanteriidae or Corinnidae)	--	--

(1) Batesian mimicry

Note: Taxa in Dominican amber: See WUNDERLICH (1988).

General remarks:

Various ants are dangerous to most arthropods and vertebrates, they possess painful stings and the soldiers powerful jaws; they may use formic acid, too. Most birds be-ware of ants. If a spider looks like an ant it may be protected in a special way.

The resemblance of some spiders to ants (Formicidae) is well-known and is present in various families of extant spiders, see the figs. 4-12; it is most striking in the fami-lies Salticidae, Gnaphosidae and Corinnidae, which are hunters, but it is also present in web-building spiders as Cyatholipidae, Linyphiidae and Therididae (see below, the

figs. 7-9). - Much less known is the mimicry of spiders to other Hymenoptera, e.g., to members of the family Mutillidae (fig. 3), the mutillimorphy. Members of the family Mutillidae - in which the females are wingless - have exceedingly painful stings.

Numerous spiders evolved similar structures and/or behaviour to "imitate" ants, which are their "models". Most striking are the following morphological differences of spiders and ants:

- (a) Spiders possess 2 body parts (fig. 1), ants - and other Hymenoptera (fig. 3) - have 3, as well as a segmented abdomen;
- (b) spiders possess 4 pairs of legs, insects 3 pairs;
- (c) the petiolus of spiders is basically inconspicuous but striking in ants;
- (d) antennae are absent in spiders; pedipalpi are present which are shorter/stouter than antennae and are basically not raised in the way of antennae.

Previously I distinguished roughly 3 grades of spider-ant resemblance, see WUNDERLICH (1995: 452), compare the figs. below:

- (a) A low resemblance: Slender legs and usually a slender body, frequently iridescent hairs and/or white spots on the body, occasionally a raised tip of the opisthosoma;
- (b) a medium to distinct resemblance: In addition frequently a seemingly three-partite body mainly through a weak saddle-shaped constriction of the opisthosoma or/and a constriction of the prosoma, and/or spots/bands of white hairs of prosoma and/or opisthosoma; locomotion by jerks;
- (c) a striking resemblance: Distinct white hairs and constriction(s) of the opisthosoma or/and prosoma - the result may even be a four-partite body! (A "superoptimal character"?), in addition frequently a very long petiolus, striking slender body, pedipalpi and legs, most often reduced eye lenses (except in numerous Zodariidae and the anterior median eyes in the Salticidae), as well as frequently adaptations of the behaviour: (1) raised legs I or II which may be moved during the locomotion like insects' antennae ("antennae illusion") and (2) a distinctly raised tip of the opisthosoma ("opisthosomal warning").

A. Probable mutillimorphy (figs. 1-3)

With a note on probable Ichneumomorphy.

Mutillidae are wingless wasps in the female sex (figs.) which possess a painful sting; so they are suitable subjects for Batesian mimicry, see BRISTOWE (1941: 456).

No fossil mutillimorph spider has been recognized up to now, and only few facts are known about extant mutillomorphic spiders, which are members of the families Co-

rinnidae and Salticidae, see BRISTOWE (1941: 456-458), PRESTON-MAFHAM (1991: 124).

Mutillimorphic spiders possess white spots of the opisthosoma similar to certain Mutillidae and myrmecomorphic spiders; their prosoma may bear a constriction (figs. 1-2), but they have a stouter body as well as more robust legs and pedipalpi than myrmecomorphs, the prosoma may bear long fine hairs, and a long petiolus is never present. Compare the body shape of a model (fig. 3). On the other hand stouter ants existed in Baltic amber: Members of the subfamily Ponerinae; thus the mutillimorphy of the fossil spiders in Baltic amber is questionable.

Certain extant European spider species of the family Gnaphosidae resemble Mutillidae, especially members of the genus *Callilepis* WESTRING 1874, which has been regarded as myrmecomorphic. Similar - and probably also mutillimorphic- are members of the genera *Aphantaulax* SIMON 1878 and *Poecilochroa* WESTRING 1874, see SAUER & WUNDERLICH (1997: 56-57, photos).

Among the fossil spiders I regard members of the genus *Ablator* PETRUNKEVITCH 1942 (Corinnidae) as probably mutillimorphic: Body, legs and male pedipalpi are stout, the prosoma is hairy, the opisthosoma usually bears three spots of white hairs, see the paper on the family Corinnidae in these volumes and the photos. Fossil mutillid wasps of the genus *Protomutilla* BISHOFF 1916 in Baltic amber may have been the models of the possibly mutillimorphic fossil spiders. - Already KOCH & BERENDT 1854 described a fossil spider in Baltic amber - and accurately figured its opisthosomal markings - which I consider as a possible mutillimorphic spider, *Ablator triguttatus* (KOCH & BERENDT 1854) (fig. 4), see the paper on the family Corinnidae in these volumes. Similar opisthosomal markings and relatively large bulbi are known from extant mutillimorphic spiders. Photos 367-368, 386.

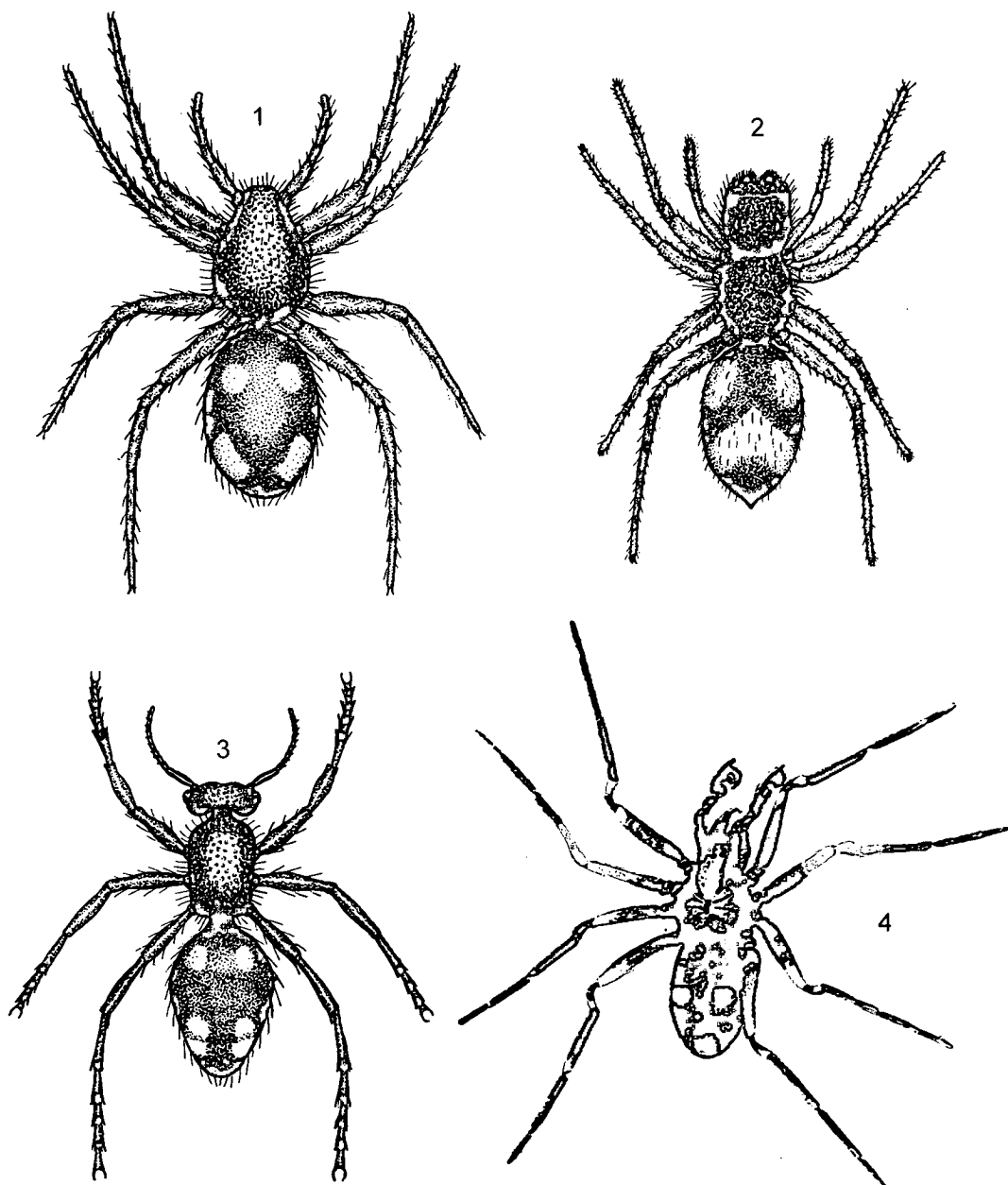
Note: Members of the genus *Myrmecarchaea* n. gen. - Archaeidae; the paper on the superfamily Eresoidea in these volumes -, which possess an extremely long petiolus, probably imitated members of another family of the Hymenoptera: Ichneumonidae, which may be wingless. This is a questionable case of Ichneumonomorphy, but in my opinion members of this genus are more likely myrmecomorphic, see below. So the most sophisticated type of - questionable - myrmecomorphy in the Early Tertiary evolved in the "archaic" family Archaeidae, in the genus *Myrmecarchaea*. Photos 75-79.

B. Myrmecomorphy

Key to the genera of myrmecomorphic spiders in Baltic amber:

Remark: See also the mutillimorphic (wasp-shaped) genus *Ablator* (Corinnidae), the paper on the family Cyatholipidae in these volumes and GRISWOLD (1997: 269).

1 Leg bristles completely absent. 2



Figs. 1-4: Mutillimorph extant spiders (figs. 1-2), a mutillid wasp (fig. 3) and a probably mutillimorph fossil spider of the Baltic amber forest (fig. 4). Figs. 1-3 are taken from BRISTOWE (1942: Figs. 70-72), fig. 4 is taken from KOCH & BERENDT (1854: Fig. 141). - Abb. 1-4: Wespenähnliche heutige Spinnen (Abb. 1-2), eine Wespe der Familie Mutillidae, die im Baltischen Bernsteinwald existierten (Abb. 3) und eine vermutlich wespenähnliche fossile Spinne des Baltischen Bernsteinwaldes (Abb. 4):

1) *Graptartia* sp. indet. (Araneae: Corinnidae), female, which mimics *Glossotilla liopyga* in Uganda; comp. fig. 3. - Unbestimmtes Weibchen der Gattung *Graptartia*, Familie Ameisen-Sackspinnen, die die Wespe *Glossotilla liopyga* in Uganda nachahmt; vgl. Abb. 3.

2) Female of the family Salticidae (Araneae), which mimics the wasp *Glossotilla liopyga* in Uganda; comp. fig. 3. - Weibchen der Familie Springspinnen, das die Wespe *Glossotilla liopyga* in Uganda nachahmt; vgl. Abb. 3.

3) A mutillid wasp, *Glossotilla liopyga* BISCH. from Uganda, female, which has two spider mimics; comp. the figs. 1-2. - Eine Wespe der Familie Mutillidae (*Glossotilla liopyga*) aus Uganda, die das Vorbild für zwei Spinnenarten ist; vgl. Abb. 1-2.

4) Male of *Ablator triguttatus* (KOCH & BERENDT 1854), (Araneae: Corinnidae), body length probably ca. 4mm, from the Baltic amber forest. Note the light opisthosomal spots and the annulated legs. - Männchen der Ameisen-Sackspinne *Ablator triguttatus*, Körper-Länge etwa 4mm, aus dem Baltischen Bernsteinwald. Beachte die hellen Flecken auf dem Hinterkörper und die geringelten Beine.

- Leg bristles present. 3

2(1) Petiolus and legs extremely long (photo). Archaeidae. Photo 76. Myrmecarchaea

- Petiolus short, legs of medium length. Spatiatoridae. Photos. 84-85. Spatiator

3(1) 6 eyes. 4

- 8 eyes. 5

4(3) eyes in a nearly circular position. Photos. 23ff. Harpactea

- eyes in two rows of 4 and 2. Photo 20. Vetsegestria

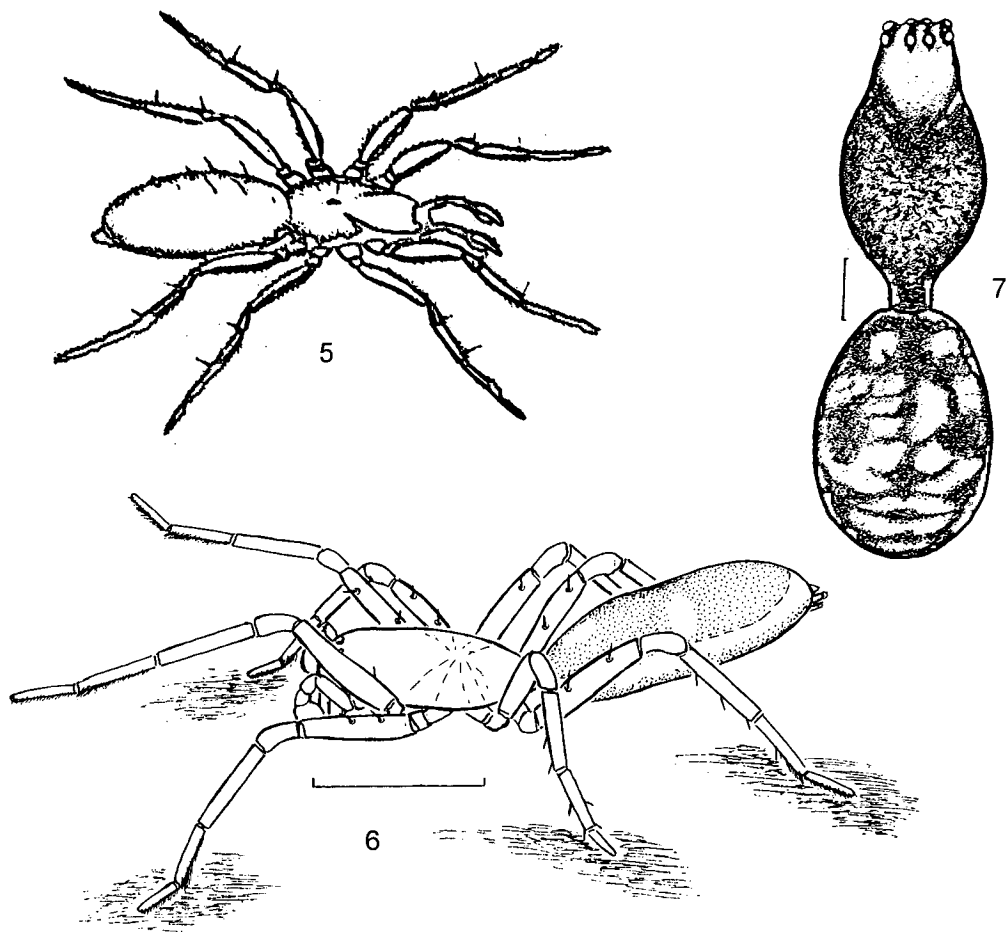
5(3) 3 tarsal claws, caput raised. Zodariidae. Photos. 346-347 e.g. Adorator

- 2 tarsal claws, caput low. Corinnidae...e.g. fig. 6: Eomazax and "Phrurolithus" sensu
Photo 376. PETRUNKEVITCH 1958

KOCH & BERENDT (1954) already described the very first known fossil myrmecomorphic spider - *Eomazax procera* in Baltic amber (family Corinnidae, sub *Macaria*), figs. 5-6, photos, see below. At that time *Macaria* stood for *Micaria* WESTRING 1854 and similar spiders, family Gnaphosidae (at that time Drassidae). These authors compared the body shape of *procera* with the myrmecomorphic extant spider species *Micaria fulgens* (= *Macaria fastuosa*), and probably recognized the myrmecomorphy of their specimens although they did not express that explicitly. The resemblance of this species to its ant model may be placed between grades 2 and 3 (see above).

According to the extremely long petiolus the spiders of the genus *Myrmecarchaea* (*Archaeidae*) are more ant-shaped than spider-shaped, their body is not bipartite but tripartite, the opisthosoma is long and slender and may bear a saddle-shaped inclination and a band of white hairs, see the photos and the paper on the family *Archaeidae* (superfamily *Eresoidea*) in this volume. The grade of myrmecomorphy may be three. (Probably these spiders imitated wasps of the family *Ichneumonidae*, see above). - Members of other genera of these spider-eating spiders are not myrmecomorphic, but the long body, the long and slender legs as well as the large chelicerae are predispositions to myrmecomorphy. Probably worker ants of the subfamily *Dolichoderinae* were the model of these myrmecomorphic *Archaeidae* in the Baltic amber forest; spiders of *Myrmecarchaea* are apparently more similar to ants of this subfamily than to members of other subfamilies. Photos 75-78.

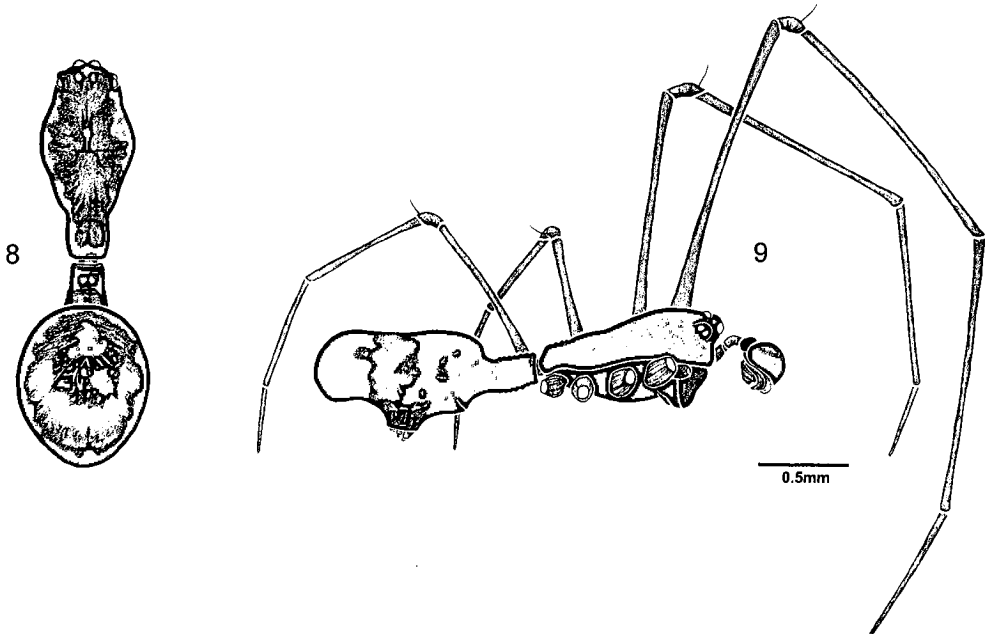
According to their narrow body the fossil members of the genera *Harpactea* BRISTOWE 1939 (*Dysderidae*) and *Vetsegestria* n. gen. (*Segestriidae*) are myrmecomorphs of the grade one. Spiders of both families are known to feed on ants. The myrmecomorphic extant species *Harpactea hombergi* (SCOPOLI) mainly lives under the bark of trees.

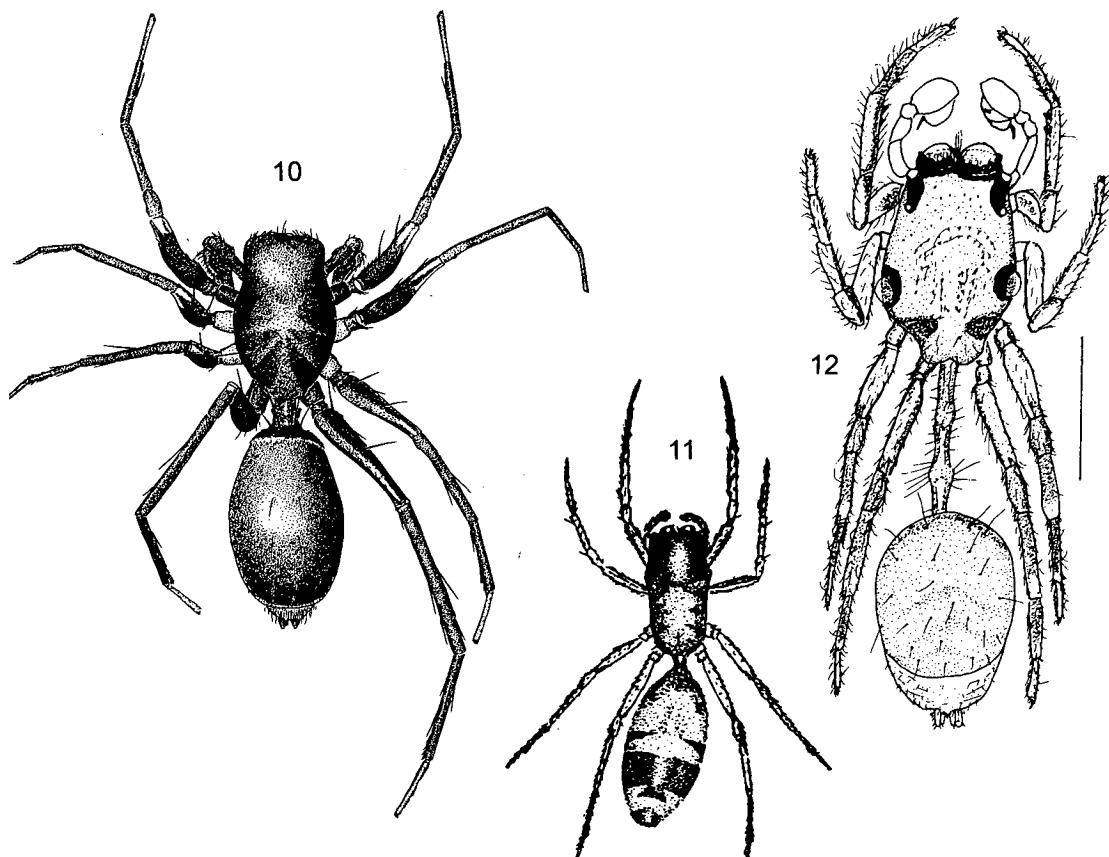


Figs. 5-12: Myrmecomorphic (ant-shaped) fossil (figs. 5-6) and extant (figs. 7-12) spiders of various families - Fig. 5 is taken from KOCH & BERENDT (1854: Fig. 55), figs. 8-9 from GRISWOLD (2001: Figs. 104 E, A), fig. 10 from DEELEMEN-REINHOLD (2001: Fig. 514), fig. 11 from LOCKET & MILLIDGE (1951: Fig. 116 A) and fig. 12 from DEELEMEN-REINHOLD & FLOREN. - Abb. 5-12: Ameisen-ähnliche fossile (Abb. 5-6) und heutige (Abb. 7-12) Spinnen verschiedener Familien.

5-6) Males of *Eomazax procera* (KOCH & BERENDT 1854) (Corinnidae), body length 4.5-5mm, preserved in Baltic amber. The specimen which is shown in fig. 5 was the the first described ant-shaped fossil spider, although it apparently was not recognized as myrmecomorphic at that time, the middle of the 19th century. In fig. 6 a reconstructed male is shown which lifts the anterior legs and the opisthosoma. A similar behaviour is known from extant spiders which frequently have also a saddle-shaped constriction of the opisthosoma with a band of light hairs (arrow). - Abb. 5-6) Männchen der Ameisen-Sackspinne *Eomazax procera*, Körper-Länge 4.5-5mm, erhalten im Baltischen Bernstein. Die in Abb. 5 dargestellte Spinne war die erste beschriebene ameisen-ähnliche fossile Spinne, obwohl sie damals - in der Mitte des 19. Jahrhunderts - offenbar nicht als solche erkannt wurde. Abb. 6 zeigt die Rekonstruktion eines Männchens, das die vorderen Beine und den Hinterkörper anhebt. Ein entsprechendes Verhalten ist von heutigen Spinnen bekannt, die ebenfalls eine sattelförmige Einschnürung des Hinterkörpers und ein Band heller Haare (Pfeil) besitzen.
Photo 376.

Figs. 7) *Cresmatoneta mutinensis* (CANESTRINI 1868) (Linyphiidae, S-Europe), body in the dorsal aspect. Note the elongated prosoma. M = 0.2mm. - Abb. 7) Körper der süd-europäischen Baldachinspinne *Cresmatoneta mutinensis* von oben. Beachte den verlängerten Vorderkörper und die hellen Flecken auf dem Hinterkörper. M = 0.2.



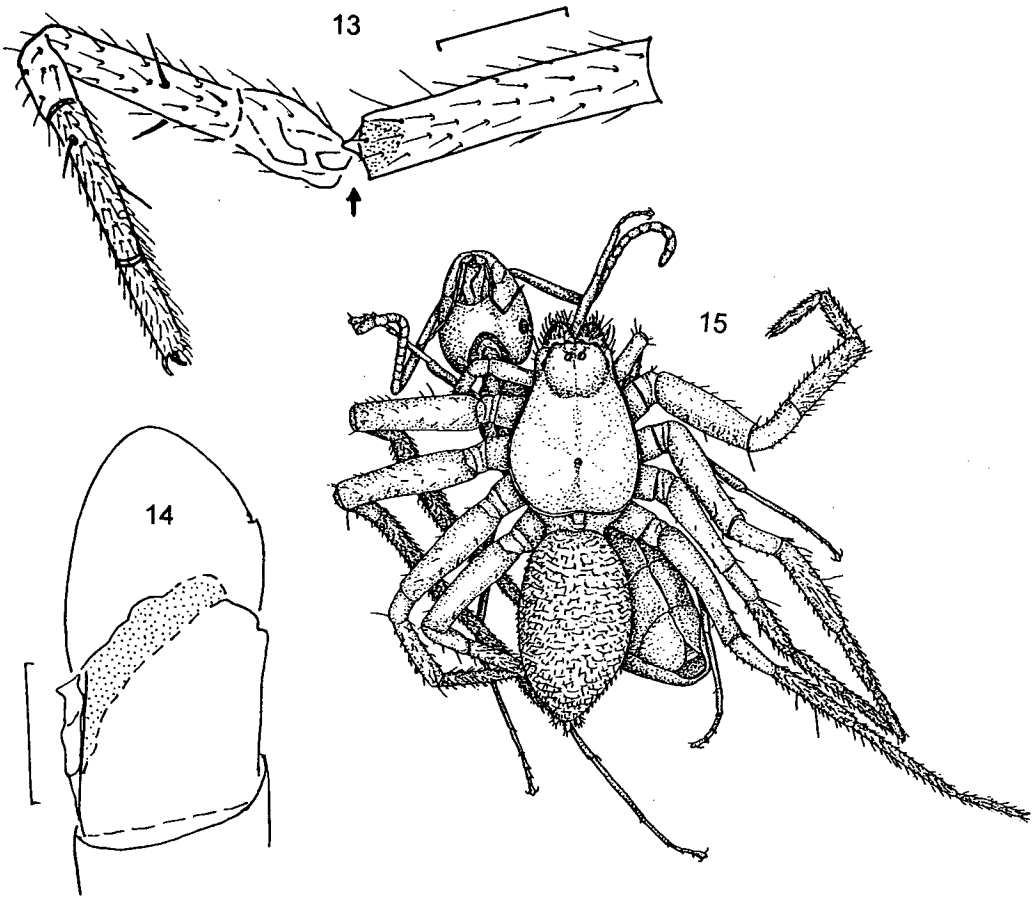


Figs. 8-9) Body of the african Cyatholipidae *Scharffia holmi* GRISWOLD 2001 (fig. 8) and *S. chinja* GRISWOLD 2001 (fig. 9) in the dorsal and lateral aspect: Note the elongated prosoma and the modified opisthosoma. M = 0.5mm. - Abb. 8-9) Körper der afrikanischen Becherspinnen *Scharffia holmi* und *chinja* von oben und seitlich. Beachte den verlängerten Vorderkörper und den abgewandelten Hinterkörper.

Fig. 10) Dorsal aspect of a male of *Serendib suthepica* DEELEMEN-REINHOLD 2001 (Corinnidae), from Thailand body length 5.2mm. Note the slender body and legs and the light prosomal stripes. - Abb. 10) Männchen der Ameisen-Sackspinne *Serendib suthepica* aus Thailand von oben, Körper-Länge 5.2mm. Beachte den schlanken Körper, die dünnen Beine und die hellen Streifen des Vorderkörpers.

Fig. 11) Female of the ant-shaped Salticidae *Myrmarachne formicaria* MAC LEAY 1839 in the dorsal aspect. Note the light opisthosomal bands. - Abb. 11) Weibchen der ameisen-ähnlichen Springspinne *Myrmarachne formicaria* von oben. Beachte die hellen Bänder des Hinterkörpers.

Fig. 12) Male of the ant-shaped Salticidae *Depreissia decipiens* DEELEMEN-REINHOLD & FLOREN in the dorsal aspect. Note the extremely elongated petiolus. - Abb. 12) Männchen der ameisen-ähnlichen Springspinne *Depreissia decipiens* von oben. Beachte den extrem verlängerten Petiolus. - See photo 440.



Figs. 13-14: Injured leg articles of a male of *Adorator hispidus* (KOCH & BERENDT 1854) (Zodariidae), F184/CJW, which is preserved in Baltic amber, fighting against two ants; comp. the photos. 13) Strongly injured - and nearly amputated - right leg IV with bite marks between femur and patella and on the patella. 14) Distinctly injured and apparently healed patella of the left leg II which is amputated behind the article. M = 0.5 and 0.2. - Abb. 13-14: Verletzte Beinlieder des Männchens von *Adorator hispidus*, Familie Ameisenjäger, F184/CJW, das im Baltischen Bernstein im Kampf mit zwei Ameisen konserviert ist, vgl. die Fotos. 13) Stark verletztes - und beinahe amputiertes - rechtes Bein IV mit Beißspuren zwischen Femur und Patella und auf der Patella. 14) Deutlich verletzte und offenbar verheilte Patella des linken Beins II, das nach der Patella amputiert ist. M = 0.5 und 0.2mm. Photos 608-609.

Fig. 15) A juvenile specimen of the genus *Sosybius* KOCH & BERENDT 1854 (in-det.), Trochanteriidae, coll. LIEDTKE no. 418, body length 3.7mm, holds ventrally an ant (Formicidae) as its prey, which is a bit longer than the spider. - Drawing by G. LIEDTKE; taken from WEITSCHAT & WICHARD (2002: Fig. 36), erroneously sub Dysderidae; I add the outlines of the lenses of the posterior median eyes. Abb. 15) Eine Jungspinne der Gattung *Sosybius*, Familie Schenkelringspinnen, Slg. LIEDTKE, Körper-Länge 3.7mm, hält unter sich eine Ameise als Beute, die etwas länger als die Spinne ist. Zeichnung G. LIEDTKE. Photo 630.

According to their slender body *Spatiator praeceps* PETRUNKEVITCH 1942 (*Spatiatoridae*; see the photos and the paper on the superfamily Eresoidea in this volume) was an ant-shaped spider of grade one of myrmecomorphy.

Most fossil members of the family *Zodariidae* - see the paper on this family in these volumes and below (1a) - are less myrmecomorphic. Species of the genus *Adorator* PETRUNKEVITCH, e.g., may only have been "prae-myrmecomorphic".

Besides the Archaeidae I found the most striking ant-shaped spiders within the family *Corinnidae*, 4 of 7 genera, grades 2 to 3 of myrmecomorphy, see the photos, fig. 6 (*Eomazax*), and the paper on this family in these volumes.

Surprisingly not a single myrmecomorphic member of the family *Salticidae* (figs. 11-12) has ever been found in Baltic amber (but in the Young Tertiary Dominican amber, see Wunderlich (1988)). Probably the myrmecomorphy in the *Salticidae* had not yet developed in the Early Tertiary - at least not in spiders of the Baltic amber forest.

C. A short report on Batesian mimicry in extant spider species of the family Theridiidae

In S-France - Provence, near Cuers, May 2002, on a bush in a light forest - I observed two males of the family Theridiidae: *Steatoda* (*Asagena*) *meridionalis* (KULCZYNSKI 1894), body length 5 mm, and *Neottiura herbigrada* (SIMON 1873), body length 2.2 mm (CJW). Both genera are not mentioned in the list of myrmecomorphic spiders in the paper of CUSHING (1997: 178), photo 241.

Most species of the genus *Steatoda* possess yellow to white dorsal opisthosomal spots similar to numerous ant-mimicking spiders. The male of *S. meridionalis* looked ant-like when moving.

The case of *Neottiura herbigrada* is more exciting: The males of this genus possess unusual large pedipalpi. The male in question stretched his pedipalpi forwards close together, so that the large bulbi looked like the head of an ant, and the animal seemed to possess a tripartite body! The spider showed a "head illusion" by its voluminous and seemingly attached pedipalpi. - The opisthosoma of this spider has two pairs of small dorsal yellow spots. While walking it moved the long and slender legs of the first pair alternating up and down similar to the antennae of an ant ("antennae illusion"). - Body shape and behaviour of the spider indicate grade two or three of myrmecomorphy. The model of the species is unknown. Because of its small pedipalpi the female of this species is not myrmecomorphic, thus this is a case of "sexually dimorphic Batesian mimicry" (a "multiple myrmecomorphy", too).

Males of both spider species could well be ant-mimicking, but I do not want to exclude that the more stout male of *Steatoda meridionalis* is mutillimorphic. According to its body also *Crustulina sticta* (O. PICKARD-CAMBRIDGE 1861) may be myrmeco-

morphic. Unfortunately most Theridiid spiders are only known as dead from collections in alcohol, so their behaviour - e.g. their locomotion - is unknown.

1a) Batesian mimicry combined with a predator-prey relationship

In this case two different kinds of relationships are combined: Extant and fossil species of the families Dysderidae, Segestriidae (see above) as well as of the Zodariidae may resemble ants and feed on ants - model and prey are identical. As far as I know these spiders do not deceive the ants by their behaviour as "the wolf in sheep's clothing".

In the following I will report two cases of "frozen behaviour" of members of the family Zodariidae. Two pieces of Baltic amber contain ants and spiders of the family Zodariidae which indicate that Early Tertiary members of this family were already aggressive ant mimics. Furthermore these pieces also give hints at the "ant models" of the spiders: Together with the male of *Adorator hispidus* (F184) two worker ants of *Liometopum goepperti* (MAYR) (Formicidae: Dolichoderinae) are preserved which are of the same size as the spider; this species may well have been the model of the spider species. - Together with the male of the second species - Zodariidae gen. indet. 4, F102 - two worker ants are preserved. The larger ant - *Lasius* sp. indet. (Formicinae) - is slightly larger than the spider; it is in contact with its potential hunter and may have been the model of this spider species. Photo 606.

"Frozen behaviour" (1): (figs. 13-14, Photos 608-610)

Material: A male of a fossil spider (Zodariidae) in Baltic amber, *Adorator hispidus* (KOCH & BERENDT 1854) and two ants, workers of *Liometopum goepperti* (MAYR) (Formicidae: Dolichoderinae; det. BARONI-URBANI) in the same piece of amber, F184/BB/AR/ZOD/CJW.

This is the fight of a Zodariid spider with two ants of the same size, about 3.5mm. Spider and ants are well preserved, some parts are covered with a white emulsion, they are lying in a close position and partly in contact, see the photo. One of the ants bites into the right tibia I (fig. 13), their left legs I-III are laying on the mouth parts of the spider. An injured leg article is shown in fig. 14. A double dragline - which is running from the anterior spinnerets to the right side of the spider - indicates that the spider came into resin alive. The presence of stellate hairs and air-bag pollen grains in the same amber layers as the animals makes it likely that the trio was blown up to the place of their grave by the wind.

Ant-hunters as Zodariidae are usually "single fighters", most feed on ants only. During a fast attack they bite an ant, retreat and wait for the poison to work until the ant

is paralyzed. Undoubtedly ants are dangerous to spiders, especially because of their great number. In the case which is treated here the socially living ants apparently were too many and thus successful; they captured and injured the spider before the trio was fixed in the resin. The spider was not a "beginner" in ant-hunting but an "old warrior": The left leg I is amputated before the end of the femur, the left leg II is amputated behind the patella (fig. below), the patella itself is injured (split in the cross direction, fig. below and photo) and "healed" - no fresh blood (haemolymph) is coming out from the injured articles. Furthermore the right leg IV is squeezed at the end of the femur, and is nearly loose, and surely this leg did not function any more. The end of this leg shows no blood, either, therefore the violations happened some time before the trio was captured in the resin, and thus the living spider was attacked by the ants, not transported as a dead body.

"Frozen behaviour" (2). Photo 606.

Material: A male of a fossil spider (Zodariidae) in Baltic amber, Zodariidae gen. indet. 4 and two ants (Formicidae), workers of *Lasius* sp. and *Liometopum ?oligocenicum* WHEELER (det. BARONI URBANI) in the same piece of amber, F102/BB/AR/ZOD/CJW.

Again a fight of an ant-hunting Zodariid spider - body length 4mm - with an ant, a worker of *Lasius* sp. indet. - body length 4.6mm -, see the photo. The right legs of the spider are partly in contact with the left legs and the left body side of the ant. The heavy emulsion of the bodies of both animals indicates that they were captured in the resin alive. Both arthropods are apparently not injured. The presence of stellate hairs and pollen grains in the same amber layer as the animals indicates that probably the wind blew them into the resin during their fight. The numerous iridescent hairs of body and legs as well as the long opisthosoma show that the spider is myrmecomorphic. The ant is not much larger than the spider; this *Lasius* species may have been the (evolutionary) model of the Zodariid spider species.

The relationships (3) (see 1a) and (4) are not treated in this paper.

(2) Predator-prey relationship (myrmecophagy) Photos 355, 438, 606ff and 630ff.

See the chapter on the prey of fossil spiders in this volume.

Workers of ants (Formicidae) are the most frequent prey of spiders which are preserved in Baltic amber: More than 90% of the remains of the spiders' prey which are captured by webs are ants, numerous specimens are kept in the private collection of the author, e.g. F657/BB/CJW (a female of the family Theridiidae, ?*Dipoena* sp. indet., body length about 1mm, holds an ant in its anterior legs), and F1146/BB/CJW (Formicidae indet. which is spun in). Fig. 28 in the book of WUNDERLICH (1986) shows an indet. member of the genus *Lasius* which is dissected and hanging in a capture web.

Members of various families of spiders feed on ants, see KIRCHNER (1990). Theridiidae belong to the most frequent predators of ants which are preserved in Baltic amber (see above), and in Dominican amber, too, see the fig. 29 in the book of WUNDERLICH (1986), which shows a fossil female of the Theridiid genus *Dipoena* THORELL, 1869 holding a member of the Myrmicinae which is spun in in spider's thraeds. In the collection of H. EHLEN in Hamburg, no. 356, a further female of the family Theridiidae is preserved, which holds two dissected ants in its anterior legs; the ants are partly spun in. A small part of a spider web including droplets is preserved in the same piece of amber. - Extant spiders of the genus *Dipoena* are also successful catchers of ants. Ants as the prey of Zodariidae are only rarely preserved, see above (1a). They are not spun in in spider's threads. Few questionable pieces are kept in the CJW.

A juvenile specimen of the genus *Sosybius* KOCH & BERENDT 1854 (Trochanteridae) holds an ant beneath its body, see above and fig. 15, photo 630.

Numerous extant Oecobiinae feed on ants, but nothing is known about the prey of fossil Oecobiidae: Mizaliinae (the genus *Mizalia*) of the Baltic amber forest.

BACHOFEN-ECHT (1949: 53, fig. 51) published a female of *Archaea paradoxa* KOCH & BERENDT 1854 (Archaeidae) which seemingly holds an ant in its fangs. I saw the specimen in the Zool. Staatssammlung München: The ant is not in direct contact to the spider; in my opinion the animals got together through an accident. Extant Archaeidae usually feed on spiders.

A male of the genus *Apyretina* STRAND 1932 (Thomisidae) which was feeding on an ant worker, is preserved in young copal from N-Madagascar, F809/CJW, photo.

(5) "Myrmecophily", synoecy

A symbiosis - like aphids and ants - of a fossil spider species and an ants' species is unknown to me. Synoecy with ants is known from various arthropods, e.g., beetles (Paussidae, certain Pselaphidae) and spiders, see CUSHING (1997), WUNDERLICH (1995).

A symbiosis between ants and plant-louses (aphids) existed already in the Early Tertiary. Some ants feed on the secretions of aphids which is let out by their siphons on the abdomen. Two aphids and two ants are preserved in the same layer of the piece of amber, F1334/CJW; on the left siphon of one of these aphids a secretion is preserved. BACHOFEN-ECHT (1949: 125) reports of a colony of aphids which is preserved together with 15 ants in the same piece of amber.

Extant spiders of the European genus *Mastigusa* MENGE 1854 (Dictynidae s. l.: Cryphoecinae, two or three species) live in nests of ants, e.g., of *Formica* sp. and

Lasius sp.; they are also found at tree trunks and under stones. Their close relationships to ants and their prey are unknown. Specimens of *M. arietina* (THORELL 1871) possess a light colour of the body and most often reduced eye lenses; embolus and conductor are unusually long in this genus. From Baltic amber I know 8 species, see the paper on the family Dictynidae s. l. in these volumes and the photos. The original colour of the fossil spiders is unknown; apparently they are not depigmented. The eye lenses of these spiders are small but not reduced, thus at the Early Tertiary members of *Mastigusa* probably did not yet live in ant's nests or they just started this life style. Photos 276-277.

Mastigusa is one of about 15% of those genera of the Baltic amber forest which are not extinct. The adaptations as synoecids of ants and the constant conditions in ant's nests may be the reasons for the "longevity" of this genus.

PALAEOFAUNISTIC and PALAEODIVERSITY of the spider faunas in Baltic and Dominican amber (Die Vielfalt der Spinnenfaunen im Baltischen und Dominikanischen Bernstein)

Frequently the term biodiversity is used in the narrow sense of 'species diversity' but it also may mean the diversity of higher taxa as well as the ecological, genetical and ethological diversity, see HOBOM (2000), NIEKISCH (2002). Biodiversity describes the diversity of life on Earth on various levels: (1) the diversity of taxa, e.g. of species and orders (the 'faunal diversity s. str. '), (2) the intraspecific diversity, e.g. of genes and behaviour, (3) the interspecific diversity, e.g. mimicry and parasitism and (4) the diversity of ecosystems. A second 'dimension' of diversity are changes in time and the evolution, e.g. of different mechanisms of speciation or changes of physiological mechanisms within ecosystems, transformations of ecosystems.

The knowledge of the palaeobiodiversity is still low; I can add facts mainly on the 'faunal diversity s. str. '.

According to RAUP, New Scientist, 1786: 48, taken from "DIE ZEIT", 41 (1991), altogether about 5 to 50 billion species of organisms (creatures) lived/lives on Earth - that means about 99.9% of all species are extinct - (probably about 20 million species live today), and only 250 000 fossil species are described - that means 0.01% (= 1 of 10 000).

Most fossil species are not fossilized or preserved only as fragments. The existence of excellently preserved animals in fossil resins opens the chance to know a quite higher percentage of fossils: We know now about 500 extinct species of Araneae from the Baltic amber forest (see below) (less than 700 fossil spider species are known altogether); if about 2000-2500 species lived in the Baltic amber forest we would know about 20-25% of these spider fauna! (Remark: The extant spider fauna may contain about 100 000 species worldwide (described are more than 40 000 species) - that means that nearly every 200th species of organisms is a spider). Members of the superfamily Araneoidea (s.l.) are of special interest in the study of Tertiary spiders: All the 13 extant as well as two extinct families are present in the Baltic amber, most members occur in higher strata of the vegetation and appear in the fossil resin.

The study of the palaeobiodiversity of spiders stands at its beginning. It is of great interest to compare several fossil faunas with each other and with the extant faunas. The work of PENNEY & PEREZ-GELABERT (2002) on the extant and Miocene faunas of the Dominican Republic (Hispaniola) was an important step although today's fauna is most probably more weakly known than the fossil fauna. I suppose that probably only 1/5 of the taxa has been reported, and the resin could capture only a small part - about 1/5, too? - of the complete fossil spider fauna of a region.

Amber is certainly the best medium to preserve the taxonomical important structures of fossils in all details, the genital structures of male spiders are freely observable, and both offer the best requirements for a qualified study to find out not only

the "higher taxonomic diversity", but also the diversity on the genus and species level. The diverse order Araneae may be a good indicator for the diversity of a fauna; spiders occur in nearly all terrestrial biotopes.

A "Global Biodiversity Project" would be incomplete without a comparable project of fossil faunas, a "Global Palaeobiodiversity Project", and finally a "Project of Chronobiodiversity", because we would like to know the changes of the faunas and ecosystems in quality and quantity according to time, changes of climate and ecology, etc. We may better understand today's biodiversity - as well as (e.g.) evolutionary trends and co-evolutions, invasions and extinctions of taxa ("dynamic biogeography"), faunal gaps, speciation, origin and development of parasitism and mimicry - if we know more about ancient/lost faunas and their diversities. To my knowledge DIVERSITAS - the "International Programme of Biodiversity Science" - regards only today's faunas.

The faunas and their diversity: What can be said about the number of spider taxa in the Eocene Baltic amber forest, the Miocene Dominican amber forest as well as in the regions of these forests? I start with a comparison on the species level and focus on the Baltic amber fauna.

Remarks: (1) Only a part of the fossil faunas is known up to now - see the number of species whose description is based on a single specimen in the list of Baltic amber spiders below; a larger number of still undescribed species is kept in my private collection and in museums' collections. (2) The diverse family Theridiidae in Baltic amber has not yet been revised. (3) Large spiders of various families, ground spiders as Gnaphosidae and most Thomisidae, species from special biotopes - as caves, microcaves, ant nests, rocks, dunes, meadows, non-resin producing plants, wet localities (here occur(ed) some of the Anapidae and Theridiosomatidae) - are very much underrepresented in most fossil resins. Thus we will only know a small part of the real diversity. (4) As aeronauts - mainly juveniles - spiders can fly hundreds of kilometers; so we may find in the fossil resins some spiders from outside the forests - even from meadows, sandy/sunny biotopes or from mountain areas far away - which are not taxa from the amber forest but from other regions/localities, biotopes; thus the "amber fauna" is not quite identical with the "fauna of the amber forest". Examples may be (a) the single male of the Plectreuridae *Palaeoplectreurys baltica* n. gen. n. sp. which may have come from a sunny locality outside - or within - the area of the Baltic amber forest, (b) the rare members of the genus *Pimoa* CHAMBERLIN & IVIE 1943 (Pimoidae) which probably lived in mountain areas outside or at the margin of the Baltic amber forest, (c) the origin of the three-clawed spiders which are similar to the Toxopidae and Crab Spiders, and only found as - aeronautic? - juveniles which is a mystery.

In the following I compare the families and species of the Baltic amber, Dominican amber, the extant Central European and the extant Hispaniolan faunas.

(a) The number of the known spider species (at the end of the year 2003) in/on:

- Central Europe.....1300-1350,
- Baltic amber.....ca. 500,
 (the complete number may be 1000-1500)
 (the complete number of the region may have been >3000),
- Dominican amber..... 152,
 (the complete number may be about 500)
 (the complete number of the region may have been 1000-1500),
- Hispaniola.....296,
 (the complete number may be 1000-2000)

(b) The number of known fossil spider species of 10 selected spider families in Europe and on Hispaniola:

Family	Central Europe	Baltic amber	Dominican amber	Hispaniola
Oonopidae	5	12	5	3
Linyphiinae	200 (!)	36	5	3
L': Erigoninae	275 (!)	-- (!)	--	4
Theridiidae	85	ca. 50?(!)	37	33
Araneidae s. str.	50	14	7	56
Anapidae s. l.	3	27 (!)	3	--
Dictyninae	27	5	16	1 (!)
Lycosidae	100 (!)	-- (!)	1?	7
Gnaphosidae	110 (!)	3? (!)	1	3
Thomisidae	58 (!)	2 (!)	2	6
Salticidae	96	34	10	51

Remarks: (1) Only the fauna of Central Europe is well known! (2) E.g. "Ground spiders" as Gnaphosidae and Thomisidae and large spiders as most Araneidae are underrepresented in the fossil resins. (3) Linyphiidae: Erigoninae, Lycosidae as well as the numerous advanced taxa of the Thomisidae and Salticidae were probably still absent in the Early Tertiary Baltic amber forest. (4) Tiny spiders as Ana-

pidae have most probably been overlooked on Hispaniola. (5) Already 50 million years ago Theridiidae was the dominant family in higher strata of the vegetation in the Baltic amber forest similar to tropical and several subtropical forests as well as in Dominican amber and copal from Columbia, Hispaniola and Madagascar (pers. obs.). (6) The family Linyphiidae is most diverse today in Central Europe as in all moderate climates of the Northern Hemisphere; numerous taxa are adapted in moderate or cold climates.

Juvenile spiders usually cannot be determined as to the species or genus level. So I suppose that only 1/4-1/5 (1/7?) of the species of the Baltic amber forest is known up to now. That means we probably have to expect 2000-2500 (3500?) species of spiders in the Baltic amber forest. Today's fauna of Europe contains more than 3000 species. On the level of families and subfamilies the Early Tertiary European spider fauna was clearly more diverse than the Central Europe spider fauna of today (see the list below) and was probably more diverse than the extant spider fauna of Europe. If we consider the diverse fauna of (e.g.) Anapidae, Theridiidae and Synotaxidae, the Early Tertiary European amber forests were probably somewhat like "fossil hotspots" of the evolution and of biodiversity when we compare these faunas with the fauna of the Dominican amber forest.

Qualitative changes of the European fauna during the Tertiary and extinctions/gaps (see also below): The extant spider fauna of Central Europe and even the whole Europe is quite different from the Early Tertiary Baltic amber fauna: (1) Five families (and several subfamilies and tribus, see the lists below) are totally extinct but were still - mostly rare - present in the Baltic amber forest: Baltsuccinidae, Ephalatoridae, Insecutoridae (a questionable family of its own), Protheridiidae and Spatiatoridae. (2) Absent today in Europe - extinct in this area - are Archaeidae, Borboropactidae, Cyatholipidae, Deinopidae, Plectreuridae, Tetrablemmidae, Synotaxidae, Trechaleidae and Trochanteriidae as well as the subfamilies Stephanopinae of the Thomisidae and the Cocalodinae of the Salticidae; most are tropical taxa. (3) Most striking is the absence of the Lycosidae and Linyphiidae: Erigoninae - and probably Philodromidae and Sparassidae - in the Early Tertiary European amber forests, see the discussion below.

Survey of the taxa in Baltic and Dominican amber and comparison with related extant faunas (Übersicht über die Gruppen im Baltischen und Dominikanischen Bernstein und Vergleich mit benachbarten heutigen Faunen). See also below

(1) Hispaniola (Dominican Republic). See PENNEY & PEREZ-GELABERT (2002: 217), WUNDERLICH (1986, 1988):

	families	genera	species
Miocene	36	82	152
extant (Hispan.)	41	166	296
shared taxa	29	>30	0
extinct taxa	0	27(=33%)	
totals	47	>220	448

(2) Europe. See WUNDERLICH:

	families	genera	species
Eocene	51	>200	>500
extant (Central Europe)	46	ca 330	>1300
shared taxa	39	ca 13	0
extinct taxa	5	>175(ca.88%)	
totals	58	>500	>1800

Discussion:

(1) In families, subfamilies, genera and species the preserved and known Eocene subtropical European spider fauna is up to about 2 1/2 times more diverse than the Miocene tropical spider fauna of Hispaniola; the diversity of the well-known extant Central European spider fauna is (in the known species) more than four times as high as the fauna of Hispaniola (the Hispaniolan fauna is less well known!). The number of subfamilies is 70 in the Baltic amber fauna, but only 52 in the Dominican amber fauna, see below. In contrast to Europe the fauna of Hispaniola is restricted on an Island. The Baltic amber fauna is furthermore more diverse because there are elements of the tropic and moderate climates as well. The fauna of the Mygalomorpha - which distinctly prefer tropical climates - is quite more diverse in the Dominican amber, see below. In contrast to the Dominican amber fauna the older Baltic amber fauna includes families - as the Archaeidae, Cyatholipidae and Synotaxidae - which are (nearly) extinct today in the Northern Hemisphere as well as 5 families and several subfamilies which are completely extinct (extant and fossil Archaeidae and Cyatholipidae are unknown from both Americas).

(2) Most striking are the differences in the extinct higher taxa in the Baltic/ Dominican amber faunas: 5/0 families and >175 (= 88%)/27(= 33%) genera. Most probably the extinctions of families of the Baltic amber fauna - e.g. Ctenizidae, Dipluridae, Tetrablemmidae, Archaeidae, Deinopidae, most Anapidae s. l., Cyatholipidae, Synotaxidae, Zoropsidae, Trochanteriidae - were caused by the climatic change during the Oligocene. Most Ctenizidae, Dipluridae, Anapidae and Zoropsidae had to migrate to southern parts of Europe.

(3) The ratio of genera to species is 1.85 in the Dominican amber fauna and 2.5 in the Baltic amber fauna.

(4) Within the families in question the families Oonopidae, Tetragnathidae, Theridiidae and Dictynidae are more diverse in the number of genera in the Dominican amber fauna than today; for example only a single genus of the Dictynidae is known from the extant spider fauna of Hispaniola but there are four fossil extinct genera in Dominican amber; all are members of the subfamily Dictyninae.

(5) The following families are (partly distinctly) more diverse in genera in the Baltic amber fauna than extant in Central Europe and in the fauna in Dominican amber: Uloboridae, Anapidae, Theridiosomatidae, Cyatholipidae (extinct in Europe), Synotaxidae (extinct in Europe), Mimetidae, Zoropsidae, Zodariidae, Corinnidae and Trochanteriidae.

(6) The following families are distinctly more diverse today in genera in the extant fauna of Central Europe - or of Europe: In parenthesis - than in Baltic amber: (Dysderidae), (Oonopidae), (Pholcidae), Araneidae, Linyphiidae, Lycosidae (unknown in Baltic amber), Clubionidae, (Liocranidae), Gnaphosidae, Philodromidae (unknown in Baltic amber), (Sparassidae; unknown in Baltic amber), Thomisidae and Salticidae. In several families - as Linyphiidae, Thomisidae and Salticidae - members of the derived subfamilies are still absent in the older Baltic amber fauna, but except the Linyphiidae: Erigoninae - they are already present in the Dominican amber fauna.

Comparable list of the families and subfamilies

In the following list the extinct suprageneric taxa are underlined. Extant families and subfamilies of the area are only listed if they are known from fossils. * = taxa which are only reported from juveniles. - Compare the list given by WUNDERLICH (1986: 19-20).

Discussion: Not reported from fossils in Baltic amber (as well as in Dominican amber besides the questionable Lycosidae) are the following 9 families and one subfamily which are known today from Europe: Atypidae, Nemesiidae, Filistatidae, Eresidae, Linyphiidae: Erigoninae, Cybaeidae, Titanoecidae, Lycosidae, Cithaeroididae and Zoridae. - Remarkable is the absence of the Lycosidae, probably the Philodromidae, the Sparassidae and Tetragnathidae: Tetragnathinae in Baltic amber. Not reported from Dominican amber are 12 or 13 families which are known today from the Island of Hispaniola: Filistatidae, Sicariidae, Drymusidae, Deinopidae, Lycosidae, Pisauridae, Agelenidae, Desidae, Amaurobiidae, Zodariidae, Zoridae and probably the families Miturgidae, Liocranidae and Philodromidae. - Striking is the

absence of extant and fossil members of the cosmopolitically distributed families Agelenidae (which usually are large spiders and therefore difficult to keep in the fossil resin) and Zodariidae on Hispaniola. - Only reported from fossils (but not from extant spiders) are the following families from Hispaniola: Anapidae s.l. (Anapinae, Mysmeninae), Ctenizidae: Cyrtaucheniinae, Ochyroceratidae, Tetrablemmidae, Palpimanidae, Hersiliidae and probably Trochanteriidae (*Veterator*).

Today we know about 46 families of spiders from Europe and 41 from Hispaniola.

	extant,	Baltic	Dominican	extant,
	Europe	amber	amber	Hispaniola

Infraorder **Mygalomorpha** (= Orthognatha):

Barychelidae: Trichopelmatinae.	—	—	+	+
Ctenizidae s. l.: Pachylomerinae.	+	+	—	—
— : ?Ctenizinae.	+	+	—	—
? — : ? Cyrtaucheniinae.	—	—	+	+
Dipluridae s. l.: Macrothelinae.	+	+	—	—
— : Ischnothelinae.	—	—	+	+
Microstigmatidae: <u>Parvomygalinae</u> n.sf.	—	—	+	—
Theraphosidae: ?Ischnocolinae.	+	—	+	+

Infraorder **Araneomorpha** (= Labidognatha):

Segestriidae: Ariadninae n. subfam.	+	+	+	+
— : Segestriinae.	+	+	—	—
Plectreuridae: Plectreurinae.	—	+	—	—
Dysderidae: Harpacteinae.	+	+	—	—
Oonopidae: Gamasomorphinae.	+	?+	+	+
— : Oonopinae.	+	+	+	+
Caponiidae: Nopinae.	—	—	+	+
Scytodidae.	+	+	+	+
Loxoscelidae.	+	—	+	+
Leptonetidae: Leptonetinae.	+	+	—	—
Telemidae.	+	+	—	—
Tetrablemmidae: Tetrablemminae.	—	+	+	—
Ochyroceratidae: Ochyroceratinae.	—	—	+	—
Pholcidae: Pholcinae.	+	+	+	+
Archaeidae s. l.: Archaeinae.	—	+	—	—
<u>Spatiatoridae</u>	—	+	—	—
Palpimanidae: Otiothopini.	—	—	+	—
Oecobiidae: Oecobiinae: Oecobiini.	+	—	+	+
— : <u>Mizaliinae</u>	—	+	—	—

Hersiliidae	+	+	+	--
Uloboridae	+	+	+	+
Deinopidae	--	+	--	+
Zygiellidae n. stat. : Zygiellinae	+	+	--	--
-- : Chrysometinae	--	?+	--	+
Araneidae: Araneinae	+	+	+	+
-- : Argiopinae	+	--	--	+
-- : <u>Miraraneinae</u> n. subfam.	--	+	--	--
-- : Nephilinae	--	+	+	+
Tetragnathidae: Aziliinae	--	--	+	+
-- : Diphyinae (Metinae?)	--	+	--	--
-- : Leucauginae	--	--	?+*	+
-- : Tetragnathinae	+	--	+	+
Theridiosomatidae	+	+	+	+
Anapidae s. l.: Anapinae	+	+	+	--
-- : Comarominae n. subfam.	+	+	--	--
-- : Mysmeninae	+	+	+	--
-- : Synaphrinae	+	+	--	--
<u>Baltsuccinidae</u> n. fam.	--	+	--	--
<u>Protheridiidae</u> n. fam.	--	+	--	--
Cyatholipidae	--	+	--	--
Synotaxidae	--	+	--	--
Nesticidae	+	+	+	+
Theridiidae: Aneloseminae	+	?-	+	+
-- : Argyrodinae	+	--	+	+
-- : Hadrotarsinae	+	+	+	+
-- : Latrodectinae	+	+	+	+
-- : Pholcommatinae	+	+	+	+
-- : Spintharinae	+	+	+	+
-- : Theridiinae	+	+	+	+
Mimetidae: Mimetinae: Mimetini	+	+	+	+
-- : Mimetinae: Oarcini n. stat.	--	+	--	--
Pimoidae	+	+	--	--
Linyphiidae: Linyphiinae	+	+	+	+
-- : Micronetinae	+	?+	+	+
Amaurobiidae: Amaurobiinae	+	+	--	--
Dictynidae s. l.: Cryphoecinae	+	+	--	--
-- : Dictyninae	+	+	+	+
-- : Hahniinae n. stat. & comb.	+	+	--	--
-- : Mizagallinae n. subfam.	+	+	--	--
Agelenidae: Ageleninae	+	+	--	--
<u>Insecutoridae</u>	--	+	--	--
Zoropsidae: <u>Eomatachiini</u> n. trib.	--	+	--	--
-- : <u>Eoprychiini</u> n. trib.	--	+	--	--
Pisauridae	+	?+	?+	+
Lycosidae	+	-	?+	+
Trechaleidae: Eotrechaleinae n. subfam.	--	+	--	--

Oxyopidae	+	+	+	+
Ephalmatoridae	--	+	--	--
Zodariidae: Storenomorphinae	--	?+	--	--
- : Zodariinae	+	+	--	--
Anyphaenidae	+	+	+	+
Clubionidae: Clubioninae	+	?+	+	+
- : Systariinae	--	+	--	--
Liocranidae: Liocraninae	+	+	?+	?+
Corinnidae: Castianeirinae	--	--	+	--
- : Corinninae	--	?+	+	+
- : Phrurolithinae	+	+	?+	+
- : Trachelinae	+	--	+	+
Miturgidae	--	--	?+	?+
Gnaphosidae (= Drassidae): Drassodinae	+	?+	+	+
Trochanteriidae: Trochanteriinae	--	+	?+	--
- : ?-- : <u>Sosybiini</u> n. trib.	--	+	--	--
Ctenidae: Calocteninae	--	--	?+	--
Philodromidae	+	?+*	?+*	+
Sparassidae: Sparianthinae	--	--	+	+
Selenopidae	--	--	+	+
Borboropactidae n.fam. : Borboropactinae	--	?+	--	--
-- : <u>Succiniraptorinae</u> n. subfam.	--	+	--	--
Thomisidae: Stephanopinae	--	+	--	?-
- : Thomisinae s. l.	+	?-	+	+
Salticidae: Cocalodinae n. stat. subfam.	--	+	+	?-
- : Lyssomaninae	--	--	+	+
- : Euophryinae s. l.	+	--	+	+
- : Salticinae s. l.	+	--	+	+

sum families/subfamilies: 62/91 39/58 51/70(!) 39/52 36/50

List of the fossil taxa in Baltic amber which are treated in this volume, excl. most genera and species of the Theridiidae, synonyms and dubious species. 408 species of 170 genera are listed, 310 species and 83 genera are described for the first time. (Liste der fossilen Spinnen im Baltischen Bernstein, die in diesem Band behandelt werden, ausschließlich der meisten Gattungen und Arten der Kugelspinnen, der Synonyme und der zweifelhaften Arten. 408 Arten aus 170 Gattungen werden aufgeführt, 310 Arten und 83 Gattungen werden erstmals beschrieben).

See the "complete list of all described Oligocene Amber Spiders", PETRUNKEVITCH (1958: 368-385) and, the "list of Tertiary spiders other than found in Baltic amber", PETRUNKEVITCH (1958: 385-393). - See also the remarks below.

Underlined = extinct families/subfamilies/tribus, heavily printed - besides the order and the infraorders - are the **extant genera**. In parenthesis: (Sub)family names in the German language. "?" means an unsure taxonomical position of the taxon.

Order **ARANEAE** - Spiders (Spinnen)

(1) Infraorder **MYGALOMORPHA** - Mygalomorphs (Längskieferspinnen)

CTENIZIDAE - Trapdoor Spiders (Falltürspinnen)

PACHYLOMERINAE - Pachylomerines

Ummidia THORELL 1875

U. damzeni WUNDERLICH 2000, *malinowskii* WUNDERLICH 2000

?CTENIZINAE - True Trapdoor Spiders (Eigentliche Falltürspinnen)

Baltocteniza ESKOV & ZONSTEIN 2000

B. kulickae ESKOV & ZONSTEIN 2000

Electrocteniza ESKOV & ZONSTEIN 2000

E. sadilenkoi ESKOV & ZONSTEIN 2000

DIPLURIDAE - Funnelweb Mygalomorphs (Trichternetz-Längskieferspinnen)

?MACROTHELINAE - Macrothelines (Großspinnwarzen-Spinnen)

Clostes MENGE 1869

C. priscus MENGE 1869

(2) Infraorder **ARANEOMORPHA** - Araneomorphs (Querkieferspinnen)

SEGESTRIIDAE - Segestriids (Fischernetzspinnen)

ARIADNINAE **n. subfam.** - Ariadnines (Ariadnes Spinnen)

Ariadna SAVIGNY & AUDOUIN 1827

Ariadna defuncta **n. sp.**

SEGESTRIINAE - Segestriines (Eigentliche Fischernetzspinnen)

Segestria LATREILLE 1804

S. flexio **n. sp.**, *mortalis* **n. sp.**, *tomentosa* KOCH & BERENDT 1854

Vetsegestria **n. gen.**

V. quinquespinosa **n. sp.**

PLECTREURIDAE - Plectreurids (Achtaugen-Fischernetzspinnen)

PLECTREURINAE - Plectreurines (Eigentliche Achtaugen-Fischernetzspinnen)

Paraplectreurys **n. gen.**

P. baltica **n. sp.**

DYSDERIDAE - Dysderids (Sechsaugenspinnen)

HARPACTEINAE - Harpacteines (Haken-Sechsaugenspinnen)

Dasumiana n. gen.

D. emicans n. sp., ?*D. subita* (PETRUNKEVITCH 1958) (= *Dasumia* s.),
valga n. sp.

Harpactea BRISTOWE 1939

H. communis n. sp., *emicans* n. sp., *extincta* PETRUNKEVITCH 1950

OONOPIDAE - Oonopids (Zwerg-Sechsaugenspinnen)

GAMASOMORPHINAE - Gamasomorphines (Gepanzerte Zwerg-Sechsaugensp.)

?**Stenoonops** SIMON 1891

?*S. rugosus* n. sp.

OONOPINAE - Oonopines (Eigentliche Zwerg-Sechsaugenspinnen)

Orchestina SIMON 1882

O. baltica PETRUNKEVITCH 1942, *breviembolus* WUNDERLICH 1981,
cochlembolus WUNDERLICH 1981, *crassimbolus* WUNDERLICH 1981,
crassipatellaris WUNDERLICH 1981, *crassitibialis* WUNDERLICH 1981,
forceps WUNDERLICH 1981, *furca* WUNDERLICH 1981, *gracilitibialis*
n. sp., *imperialis* PETRUNKEVITCH 1963, *tuberosa* WUNDERLICH 1981

SCYTODIDAE - Spitting Spiders (Speispinnen)

Scytodes LATREILLE 1804

S. weitschati WUNDERLICH 1993

LEPTONETIDAE - Leptonetids (Schlankbeinspinnen)

LEPTONETINAE - Leptonetines (Eigentliche Schlankbeinspinnen)

Eoleptoneta WUNDERLICH 1991

E. curvata n. sp., *duocalcar* n. sp., *kutscheri* WUNDERLICH 1991

Oligoleptoneta n. gen.

O. altoculus n. sp.

TELEMIDAE - Telemids (Höhlen-Sechsaugenspinnen)

Telema SIMON 1882

?*T. moritzi* n. sp.

TETRABLEMMIDAE - Tetrablemmids (Vieraugenspinnen)

TETRABLEMMINAE - Tetrablemmines (Eigentliche Vieraugenspinnen)

Balticoblemma n. gen.

B. unicorniculum n. sp.

PHOLCIDAE - Daddy-long-legs Spiders (Zitterspinnen)

PHOLCINAE - True Daddy-long-legs Spiders (Eigentliche Zitterspinnen)

Paraspermophora n. gen.

P. bitterfeldensis n. sp., *perplexa* n. sp.

ARCHAEIDAE - Archaeids (Urspinnen)

ARCHAEINAE - Archaeines (Eigentliche Urspinnen)

Archaea KOCH & BERENDT 1854

A. bitterfeldensis **n. sp.**, *compacta* **n. sp.**, *paradoxa* KOCH & BERENDT 1854, *pougneti* SIMON 1884
Baltarchaea ESKOV 1992
B. conica (KOCH & BERENDT 1854)
Eoarchaea FORSTER & PLATNICK 1984
E. hyperoptica (MENGE in KOCH & BERENDT 1854), *vidua* **n. sp.**
Myrmecarchaea **n. gen.**
M. pediculus **n. sp.**, *petiolus* **n. sp.**
Saxonarchaea **n. gen.**
S. dentata **n. sp.**, *diabolica* **n. sp.**

SPATIATORIDAE - Spatiatorids (Dickkopfspinnen)

Spatiator PETRUNKEVITCH 1942
S. praeceps PETRUNKEVITCH 1942

OECOBIIDAE - Oecobiids (Scheibennetzspinnen)

MIZALIINAE - Mizaliines (Bernstein-Scheibennetzspinnen)

Mizalia KOCH & BERENDT 1854
M. blauventi (PETRUNKEVITCH 1942), *gemini* **n. sp.**,
rostrata KOCH & BERENDT 1854, *spirembolus* **n. sp.**

HERSILIIDAE - Hersiliids (Kreiselspinnen)

?*Hersilia* AUDOUIN 1826
? *H. miranda* KOCH & BERENDT 1856
Gerdia MENGE 1869
G. myura MENGE 1869
Gerdiosis **n. gen.**
G. infrigens **n. sp.**
Gerdiorum **n. gen.**
G. inflexum **n. sp.**

ULOBORIDAE - Uloborids (Kräusel-Radnetzspinnen)

Eomiagrammopes **n. gen.**
E. maior **n. sp.**, *minor* **n. sp.**, *singularis* **n. sp.**, *spinipes* **n. sp.**
Hyptiomopes **n. gen.**
H. bitterfeldensis **n. sp.**
Hyptiotes WALCKENAER 1837
H. convexus **n. sp.**, *glaber* **n. sp.**, *saetosus* **n. sp.**, *stellatus* **n. sp.**
triqueter (KOCH & BERENDT 1854)
Opellianus **n. gen.**
O. excellens **n. sp.**, *kazimierasi* **n. sp.**, *ludwigi* **n. sp.**
Ulobomopes **n. gen.**
U. unicus **n. sp.**

DEINOPIIDAE - Ogre-faced Spiders (Käscherspinnen)

?*Menneus* SIMON 1876
? *M. pietrzeniukae* **n. sp.**

ZYGIELLIDAE SIMON 1929 (n. stat.) - Missing Sektor Orbweavers (Sektor-Spinnen)

ZYGIELLINAE - True Missing Sektor Orbweavers (Eigentliche Sektor-Spinnen)
Eozygiella n. gen.

E. calceata (PETRUNKEVITCH 1950), *compacta* n. sp.

Graea THORELL 1869 (= *Eustaloides* PETRUNKEVITCH 1942)

?*G. aberrans* n. sp., *bitterfeldensis* n. sp., *brevimbolus* n.sp., *brevis* n.sp.,
epeiroides (K. & B.), *impudica* n. sp., *lingula* n. sp., *setosa* n. sp.

CHRYSOMETINAE - Chrysometines

Chrysometata n. gen.

C. palaeoarctica n. sp.

ARANEIDAE - Orb-weavers (Radnetzspinnen)

?ARANEINAE - True Orb-weavers (Eigentliche Radnetzspinnen)

Anepeira n. gen.

A. complicata n. sp.

Bararaneus n. gen.

?*B. annulatus* n. sp., *evolvens* n. sp.

Eoaraneus n. gen.

E. complexus n. sp.

MIRARANEINAE - Miraraneines (Bernstein-Radnetzspinnen)

Miraraneus n. gen.

M. peregrinus n. sp.

NEPHILINAE - Golden Silk Orb Weavers (Seidenspinnen)

Eonephila n. gen.

E. bitterfeldensis n. sp., *excellens* n. sp., *longembolus* n. sp.

Luxurioneophia n. gen.

L. spinifera n. sp.

Palaeonephila n. gen.

P. brevis n. sp., *curvata* n. sp., *dilitans* n. sp., *fibula* n. sp.,
longipes n. sp.

TETRAGNATHIDAE - Tetragnathids (Strecker-spinnen)

DIPHYINAE - Diphyines

Corneometa n. gen.

C. baltica n. sp., *pilosipes* n. sp.

Eometa PETRUNKEVITCH 1958

E. calefacta n. sp., *longipes* PETRUNKEVITCH 1958, *occulta* n. sp.,
perfecta n. sp., *samlandica* PETRUNKEVITCH 1958

Praetermeta n. gen. - METINAE?

P. velans n. sp.

Priscometa PETRUNKEVITCH 1958

P. capta n. sp., *minor* n. sp., *tenuipes* PETRUNKEVITCH 1958

THERIDIOSOMATIDAE - Ray Spiders (Zwerg-Radnetzspinnen)

Eoepeirotypus n. gen.

E. retrobulbus n. sp.

Eotheridiosoma n. gen.

E. tuber n. sp., *volutum* n. sp.

Spinitheridiosoma n. gen.

S. balticum n. sp., *bispinosum* n. sp., *rima* n. sp.

Umerosoma n. gen.

U. multispina n. sp.

ANAPIDAE s. l. - Anapids (Zwerg-Kugelspinnen im weiteren Sinne)

ANAPINAE s. str. - Anapines (Gepanzerte Zwerg-Kugelspinnen)

Balticonopsis n. gen.

B. bispina n. sp., *bitterfeldensis* n. sp., *bulbosa* n. sp., *ceranowiczae* n. sp., *holti* n. sp., *perkovskyi* n. sp. (Rovno amber), *thomasi* n. sp.

Dubianapis n. gen.

D. obscura n. sp.

Flagellapis n. gen.

F. voigti n. sp.

Fossilapis n. gen.

F. anderseni n. sp., *baetcheri* n. sp., *eichmanni* n. sp., *flexiotarsus* n. sp., *saltans* n. sp., *unispinum* n. sp.

Rugapis n. gen.

R. scutata n. sp.

Saxonapis n. gen.

S. grabenhorsti n. sp.

Tuberapis n. gen.

T. parvibulbus n. sp.

COMAROMINAE n. subfam. - Comaromines (Sandbeerenspinnen)

Balticoroma n. gen.

B. ernstorum n. sp., *gracilis* n. sp., *reschi* n. sp., *serafinorum* n. sp., *tibialis* n. sp.

MYSMENINAE - Mysmenines (Stachelbein-Zwergkugelspinnen)

Eomysmenopsis n. gen.

E. spinipes n. sp.

?*Mysmena* SIMON 1894 s. l.

M. groehni n. sp., *M. grotae* n. sp.

Palaeomysmena n. gen.

P. hoffeinsorum n. sp.

SYNAPHRINAE - Synaphrines (Einzahn-Zwergkugelspinnen)

Iardinidis n. gen.

I. spinipes n. sp.

BALTSUCCINIDAE n. fam. - Baltsuccinids (Bernstein-Baldachinspinnen)

Baltsuccinus n. gen.

B. flagellaceus n. sp., *similis* n. sp.

PROTHERIDIIDAE n. fam. (Ur-Kugelspinnen)

Praetheridiini n. trib.

Praetheridion n. gen.

P. fleissneri n. sp.

Protheridiini n. trib.

Protheridion **n. gen.**

P. bitterfeldensis **n. sp.**, *detritus* **n. sp.**, *obscurum* **n. sp.**,
punctatum **n. sp.**, *tibialis* **n. sp.**

CYATHOLIPIDAE - Cyatholipids (Becherspinnen)

Balticolipus **n. gen.**

B. kruemmeri **n. sp.**

Cyathosuccinus **n. gen.**

C. elongatus **n. sp.**

Erigolipus **n. gen.**

E. griswoldi **n. sp.**

Spinilipus WUNDERLICH 1993

S. bispinosus **n. sp.**, *curvatus* **n.sp.**, *glinki* **n.sp.**, *longembolus* **n. sp.**

Succinilipus WUNDERLICH 1993

S. abditus **n. sp.**, *aspinosus* **n. sp.**, *saxoniensis* **n. sp.**, *similis* **n. sp.**

SYNOTAXIDAE - Synotaxids (Kugelhöhlenspinnen) (the subfamilies are not listed)

Acrometa PETRUNKEVITCH 1942

A. clava **n. sp.**, *cristata* PETRUNKEVITCH 1942, *eichmanni* **n. sp.**, *incidens*
n. sp., *pala* **n. sp.**

Anandrus MENGE 1856 (= *Elucus* PETRUNKEVITCH 1942)

A. inermis PETRUNKEVITCH 1942 and probably three more species

Cornuanandrus WUNDERLICH 1986

C. bifurcatus **n.sp.**, *corniculans* **n.sp.**, *maior* WUNDERLICH 1986, *minor* **n.sp.**

Dubiosynotaxus **n. gen.**

D. perfectus **n. sp.**

Eosynotaxus **n. gen.**

E. custodens **n. sp.**, *bispinosus* **n. sp.**, *bitterfeldensis* **n. sp.**, *fastigatus* **n.**
sp., *paucispina* **n. sp.**, *spinipes* **n. sp.**, *wegneri* **n. sp.**

Gibbersynotaxus **n. gen.**

G. parvus **n. sp.**

Protophysoglenes **n. gen.**

P. impressum **n. sp.**

Pseudacrometa WUNDERLICH 1986

P. gracilipes WUNDERLICH 1986, *wittmanni* **n. sp.**

Succinitaxus **n. gen.**

S. brevis **n. sp.**, ?*S. minutus* **n. sp.**

Sulcosynotaxus **n. gen.**

S. cavatus **n. sp.**

NESTICIDAE - Nesticids (Höhlenspinnen)

Balticonesticus WUNDERLICH 1986

B. flexuosus WUNDERLICH 1986

Heteronesticus WUNDERLICH 1986

H. magnoparacymbialis WUNDERLICH 1986

Eopopino PETRUNKEVITCH 1942

E. budrysi ESKOV & MARUSIK 1992, *inopinatus inopinatus* WUNDERLICH
1986, *inopinatus affinis* WUNDERLICH 1986, *longipes* PETRUNKEVITCH
1942, *palanga* ESKOV & MARUSIK 1992, *rarus rarus* WUNDERLICH 1986,

rarus solitarius WUNDERLICH 1986, *rudloffii* n. sp.

THERIDIIDAE - Combfooted Spiders (Kugelspinnen)

See the paper on this family in this volume; a revision of the fossil members of this family is in preparation. Members of the Argyrodinae and probably of the Anelosiminae are absent in Baltic amber.

HADROTARSINAE - Hadrotarsines (Dickfuß-Kugelspinnen)

Dipoena 1869 (probable synonyms: *Lasaeola* SIMON 1881 and *Dipoenata* WUNDERLICH 1988)

LATRODECTINAE - Latrodectines (Witwen-Verwandte)

Steatoda SUNDEVALL 1833

PHOLCOMMATINAE - Pholcommatines (Gepanzerte Kugelspinnen)

Phoroncidia WESTWOOD 1835

SPINTHARINAE - Spintharines (Höcker-Kugelspinnen)

Episinus WALCKENAER 1809

?THERIDIINAE - True Combfooted Spiders (Eigentliche Kugelspinnen)

questionable genera, e.g. *Clya* KOCH & BERENDT 1854 (= *Nanomysmena* PETRUNKEVITCH 1958)

MIMETIDAE - Pirate Spiders (Spinnenfresser-Spinnen)

MIMETINAE - True Pirate Spiders (Eigentliche Spinnenfresser-Spinnen)

MIMETINI

Mimetus HENTZ 1832

?*M. brevipes* n. sp., ?*M. gintaras* (ESKOV 1992), ?*M. longipes* n. sp.

Palaeoero n. gen.

P. longitarsus n. sp.

Succinero n. gen.

S. aberrans (PETRUNKEVITCH 1958), *carboneana* (PETRUNKEVITCH 1942), *permunda* (PETRUNKEVITCH 1942), *rovnoensis* n. sp. (Rovno amber), *setulosa* (KOCH & BERENDT 1854)

OARCINI n. stat.

Praeoarces n. gen.

P. exitus n. sp.

PIMOIDAE - Pimoids (Ur-Baldachinspinnen)

Pimoa CHAMBERLIN & IVIE 1943 (?= *Memoratrix* PETRUNKEVITCH 1942)

P. expandens n.sp., *hormigai* n.sp., *inopinata* n.sp., *liedtkei* n.sp., *lingula* n.sp., *multicusculi* n. sp., ?*P. rydei* (PETRUNKEVITCH 1942) (= *Memoratrix* r.)

LINYPHIIDAE - Sheet-web Weavers (Baldachinspinnen)

LINYPHIINAE - True Sheet-web Weavers (Eigentliche Baldachinspinnen)

***Agynetiophantes* n. gen.**

A. gibbiferus n. sp.

***Custodelela* n. gen.**

C. hamata n. sp.

Custodela PETRUNKEVITCH 1942

C. acuta n. sp., *acutula* n. sp., *bispinosa* n. sp., *cheiracantha* KOCH & BERENDT 1854), *clava* n. sp., *curva* n. sp., *curvata* n. sp., *divergens* n. sp., *expandens* n. sp., *falcata* n. sp., *femurspinosa* n. sp., *henningseni* n. sp.,

kochi n. sp., *laminata* (WUNDERLICH 1988) (n. comb.), *lanx* n. sp., *oblonga* (KOCH & BERENDT 1854), *obtusa* n. sp., *parva* n. sp., *pseudokochi* n. sp., *stridulans* n. sp., *tibialis* n. sp., ?*C. tenuipes* (PETRUNKEVITCH 1942) (sub *Obrnisius* t., n. comb.)

Eolabulla n. gen.

falcata n. sp., *gladiformis* n. sp., *perforata* n. sp., *sagitta* n. sp., *similis* n. sp.

Eophantes n. gen.

E. complicatus n. sp.

Paralabulla n. gen.

P. bitterfeldensis n. sp., *dubia* n. sp., *succinifera* n. sp.

Succiphantes n. gen.

S. tanasevitchi n. sp., *velteni* n. sp.

-- : ?MICRONETINAE - Dwarf Weavers (Zwergweber)

Succineta n. gen.

S. brevispina n. sp.

AMAUROBIIDAE - Amaurobiids (Finsterspinnen)

Remark: No member of this family has been described from Baltic amber to the species level; see the papers on the families Amaurobiidae and Zoropsidae with the genus *Eomatachia* PETRUNKEVITCH in this volume. A juvenile member of the subfamily Amaurobiinae is kept in the private collection of the author, F827/BB/AR/AMA/CJW.

DICTYNIDAE s. l. - Dictynids (Kräuselspinnen)

CRYPHOECINAE - Cryphoecins (Versteckspinnen)

Balticocryphoea n. gen.

B. curvitarsi n. sp.

Cryphoezaga n. gen.

C. dubia n. sp.

Eocryphoea PETRUNKEVITCH 1946 (Probably a member of the Agelenidae)

E. bitterfeldensis n. sp., *electrina* n. sp., *falcata* n. sp., *gibbifera* n. sp., *gracilipes* (KOCH & BERENDT 1854), *ligula* n. sp., *mammilla* n. sp., *splendens* n. sp.

Gibbermastigusa n. gen.

G. lateralis n. sp.

***Mastigusa* MENGE** in KOCH & BERENDT 1854

M. acuminata MENGE in KOCH & BERENDT 1854, *arcuata* n. sp., *bitterfeldensis* n. sp., *laticymbium* n. sp., *magnibulbus* n. sp., *media* WUNDERLICH 1986, *modesta* WUNDERLICH 1986, *scutata* n. sp.

Protomastigusa n. gen.

P. complicata n. sp.

DICTYNINAE - Dictynines (Eigentliche Kräuselspinnen)

Brommellina n. gen.

B. longungulae n. sp.

Chelirirrum n. gen.

C. stridulans n. sp.

Eobrommella n. gen.

E. scutata n. sp.

Eodictyna n. gen.

E. communis n. sp.
(*Eolathys* PETRUNKEVITCH 1950)
(*E. debilis* PETRUNKEVITCH 1950)
(*E. succini* PETRUNKEVITCH 1950)
Scopulyna n. gen.

S. cursor n. sp.
HAHNIIINAE (rev. stat. & rel.) - Hahniines (Bodenspinnen)

Cymbiohahnia n. gen.

C. parens n. sp.

Eohahnia PETRUNKEVITCH 1958

E. succini PETRUNKEVITCH 1958

Protohania n. gen.

P. antiqua n. sp., *tripartita* n. sp.

MIZAGALLINAE n. subfam. - Mizagallines

Mizagalla n. gen.

M. quattuor n. sp., *tuberulata* n. sp.

AGELENIDAE - Funnel Weavers (Trichterspinnen)

AGELENINAE - True Funnel Weavers (Eigentliche Trichterspinnen)

?*Agelena* WALCKENAER 1805

?*A. tabida* KOCH & BERENDT 1854

?*Tegenaria* LATREILLE 1804

?*T. fragmentum* n. sp., ?*T. obtusa* n. sp.

INSECUTORIDAE - Insectorids

Insecutor PETRUNKEVITCH 1942

I. aculeatus PETRUNKEVITCH 1942, ?*I. mandibulatus* PETRUNKEVITCH
1942, *pecten* n. sp., *spinifer* n. sp., ?*I. rufus* PETRUNKEVITCH 1942

ZOROPSIDAE - Zoropsids (Wolfspinnenähnliche Kammspinnen)

EOMATACHIINI n. trib.

Eomatachia PETRUNKEVITCH 1942

E. barbarus n. sp., *bipartita* n. sp., *divergens* n. sp., *duplex* n. sp., *latifrons*
PETRUNKEVITCH 1942, *recedens* n. sp., *wegneri* n. sp., *xanthippe* n. sp.

Succiniropsis n. gen.

S. kutscheri n. sp., *samlantica* n. sp.

EOPRYCHIINI n. trib.

Eoprychia PETRUNKEVITCH 1958

E. succini PETRUNKEVITCH 1958, *succinopsis* n. sp., *vicina* n. sp.

PISAURIDAE - Nursery Web Spiders (Jagdspinnen)

There are three questionable genera (see the Trechaleidae):

Episaurella PETRUNKEVITCH 1958, *Esuritor* PETRUNKEVITCH 1942 and
Linoptes MENGE in KOCH & BERENDT 1854

TRECHALEIDAE - Trechaleids (Wolfspinnenähnliche Jagdspinnen)

?SUBFAMILY (see the Pisauridae)

Questionable genera: *Esuritor* PETRUNKEVITCH 1942 and *Linoptes* MEN-
GE in KOCH & BERENDT 1854

EOTRECHALEINAE n. subfam.

Eotrechalea n. gen.

E. annulata n. sp.

OXYOPIDAE - Lynx Spiders (Scharfaugenspinnen)

?***Oxyopes* LATREILLE 1804**

?*O. succini* PETRUNKEVITCH 1958

EPHALMATORIDAE - Ephalmatorids

Ephalmator PETRUNKEVITCH 1950

E. bitterfeldensis n. sp., *calidus n. sp.*, *debilis n. sp.*, *distinctus n. sp.*, *ellwangeri n. sp.*, ?*E. eximius* PETRUNKEVITCH 1958, *fossilis* PETRUNKEVITCH 1950, *kerneggeri n. sp.*, *petrunkevitchi n. sp.*, *ruthildae n. sp.*, *trudis n. sp.*, *turpiculus n. sp.*

ZODARIIDAE - Zodariids (Ameisenjäger)

?**STORENOMORPHINAE - Storenomorphines**

Zodariodamus n. gen.

Z. recurvatus n. sp.

ZODARIINAE - True Zodariines (Eigentliche Ameisenjäger)

Adorator PETRUNKEVITCH 1942

A. brevipes PETRUNKEVITCH 1942, *hispidus* (KOCH & BERENDT 1854)

Angusdarion n. gen.

A. humilis n. sp.

Anniculus PETRUNKEVITCH 1942

A. balticus PETRUNKEVITCH 1942

Eocydrele PETRUNKEVITCH 1958

E. mortua PETRUNKEVITCH 1958

Spinizodarion n. gen.

S. ananulum n. sp.

ANYPHAENIDAE - Anyphaenids (Zartspinnen)

"*Anyphaena*" *fuscata* sensu PETRUNKEVITCH 1946

CLUBIONIDAE - Sac Spiders (Sackspinnen)

CLUBIONINAE - True Sac Spiders (Eigentliche Sackspinnen)

Eodoter PETRUNKEVITCH 1958

E. magnificus PETRUNKEVITCH 1958

E. eopala n. sp.

SYSTARIINAE DEELEMEN 2001 - Systariines

Systariella n. gen.

S. magniocoli n. sp.

LIOCRANIDAE - Liocranids (Feldspinnen)

***Apostenus* WESTRING 1851**

A. arnoldorum n. sp., *bigibber n. sp.*, *spinimanus* (KOCH & BERENDT 1854)

Palaeospinisoma n. gen.

P. femoralis n. sp.

CORINNIDAE (= Myrmeciidae) - Corinnids (Ameisen-Sackspinnen)

?CORINNINAE - Corinnines (Eigentliche Ameisen-Sackspinnen)

Cornucymbium n. gen.

C. insolens n. sp.

PHRUROLITHINAE - Phrurolithines (Steinwächter)

Ablator PETRUNKEVITCH 1942

A. biguttatus n. sp., *curvatus* n. sp., *deminuens* n. sp., *depressus* n. sp.,
duomammillae n. sp., *inevolvens* n. sp., *longus* n. sp., *nonguttatus* n. sp.,
parvus n. sp., *robustus* n. sp., *scutatus* n. sp., *splendens* n. sp., *trigutta-*
tus (KOCH & BERENDT 1854)

Alterphrurolithus n. gen.

A. longipes n. sp.

Cryptoplanus PETRUNKEVITCH 1958

C. bulbosus n. sp., *complicatus* n. sp., *incidens* n. sp., *lanatus* (PETRUN-
KEVITCH 1958), *paradoxus* PETRUNKEVITCH 1958, *sericatus* (KOCH &
BERENDT 1854), *sinuosus* n. sp.

Eomazax PETRUNKEVITCH 1958

E. pulcher PETRUNKEVITCH 1958

Myrmecorinna n. gen.

M. gracilis n. sp.

Protoorthobula n. gen.

P. bifida n. sp., *deelemani* n. sp.

GNAPHOSIDAE (= Drassodidae) - Gnaphosids (Plattbauchspinnen)

?DRASSODINAE - Drassodines (Greifspinnen)

Questionable genera: *Captrix* PETRUNKEVITCH 1942 and *Eomactator*
PETRUNKEVITCH 1958

TROCHANTERIIDAE - Trochanteriids (Schenkelring-Spinnen)

TROCHANTERIINAE - Trochanteriines (Eigentliche Schenkelringspinnen)

SOSYBIINI n. trib. (Bernstein-Schenkelringspinnen)

Sosybius KOCH & BERENDT 1854

S. berendti n. sp., *decumana* (KOCH & BERENDT 1854), *falcatus* n.
sp., *kochi* n. sp., *major* (KOCH & BERENDT 1854), *lateralis* n. sp., *lon-*
gipes n. sp., *mizgirisi* n. sp., *perniciosus* n. sp., *tibialis* n. sp., *unispino-*
sus n. sp.

QUESTIONABLE TRIBUS

Trochanteridromulus n. gen.

T. glabripes n. sp.

Trochanteridromus n. gen.,

T. scutatus n. sp.

PHILODROMIDAE - Philodromids (Laufspinnen)

Only questionable taxa are known; fossils of this family in Baltic amber have
probably never been found.

BORBOROPACTIDAE n. fam. - Borboropactids (Ur-Krabbenspinnen)

?BORBOROPACTINAE - Borboropactines (Eigentliche Ur-Krabbenspinnen)

?*Borboropactus* SIMON 1884

?*B. radiatus* (KOCH & BERENDT 1854) (**n. comb.**, from *Syphax*)

SUCCINIRAPTORINAE n. subfam. - Succiniraptorines

Succiniraptor **n. gen.**

S. paradoxus **n. sp.**

THOMISIDAE - Crab Spiders (Krabbenspinnen)

STEPHANOPINAE - Stephanopins (Kronen-Krabbenspinnen)

Succinaenigma **n. gen.**

S. raptor **n. sp.**

Syphax KOCH & BERENDT 1854

S. megacephalus KOCH & BERENDT 1854

Thomisiraptor **n. gen.**

T. liedtkei **n. sp.**

SALTICIDAE - Jumping Spiders (Springspinnen)

COCALODINAE n. stat. - Cocalodines (Urspringspinnen) (comp. the subfamily Spartaeninae)

Almolinus PETRUNKEVITCH 1958

A. bitterfeldensis **n. sp.**, *clarus* PETRUNKEVITCH 1958, *ligula* **n. sp.**

Cenattus PETRUNKEVITCH 1942

C. exophthalmicus PETRUNKEVITCH 1942

Distanilinus **n. gen.**

D. filum **n. sp.**, *nutus* **n. sp.**, *paranutus* **n. sp.**, *pernutus* **n. sp.**

Eolinus PETRUNKEVITCH 1942

E. bitterfeldensis **n. sp.**, ?*E. fasciatus* (KOCH & BERENDT 1854), *fungus* **n. sp.**, *insuriens* **n. sp.**, *prominens* **n. sp.**, *samlandica* **n. sp.**, *succineus* PETRUNKEVITCH 1942, *theryi* PETRUNKEVITCH 1942, *tystschenkoi* PROSZYNSKI & ZABKA 1980, *tystschenkoides* **n. sp.**, *vates* **n. sp.**

Gorgopsidis **n. gen.**

G. bechlyi **n. sp.**

Gorgopsina PETRUNKEVITCH 1955

G. amabilis **n. sp.**, *constricta* **n. sp.**, *expandens* **n. sp.**, *frenata* (KOCH & BERENDT 1854), *formosa* (KOCH & BERENDT 1854), *fractura* **n. sp.** (Rovno amber), *inclusa* **n. sp.**, *jucunda* (PETRUNKEVITCH 1942), *melanocephala* (KOCH & BERENDT 1854), ?*G. naumanni* (GIEBEL 1856), *speciosa* **n. sp.**

Microlinus **n. gen.**

M. calidus **n. sp.**, *folium* **n. sp.**

Paralinus PETRUNKEVITCH 1942

P. crosbyi PETRUNKEVITCH 1942

Prolinus PETRUNKEVITCH 1958

P. fossilis PETRUNKEVITCH 1958

Steneattus BRONN 1856 (a dubious genus)

S. promissa (KOCH & BERENDT 1854) (sub *Leda promissa*)

General remarks:

During the 19th and partly the 20th century, too, several families - as Thomisidae and Philodromidae - were united/regarded as lower taxa (tribus or subfamily), e.g. the Cyatholipidae and the Synotaxidae, other families were still unknown or undescribed, e.g. the Pimoidae.

The limitation of several families and the relationships of some subfamilies and genera are not definitive. Cyrtaucheniidae is included in this volume with some hesitation in the Ctenizidae, Hahniidae in the Dictynidae s. l., Mysmeninae and Synsphyrinae in the Anapidae s. l., the extinct Acrometidae in the Synotaxidae, the Zygellidae is regarded as a family of its own (not a subfamily of the Araneidae or Tetragnathidae), the Loxoscelidae is again regarded as a family of its own (not a subfamily of the Sicariidae).

Remarks on selected higher taxa in Baltic amber:

Amaurobiidae: See the papers on the Amaurobiidae and the Zoropsidae.
Arthrodictynidae PETRUNKEVITCH 1942 is not a family of its own, see WUNDERLICH (1986: 24) and the paper on the family Dictynidae in this volume.

Ctenidae (questionable *Eoprychia*: See WUNDERLICH (1986: 24) and the paper on the Zoropsidae in this volume.

Drassidae sensu KOCH & BERENDT 1854 = Gnaphosidae.

Enyoidae sensu KOCH & BERENDT 1854 = Zodariidae.

Epeiridae sensu KOCH & BERENDT 1854 = Araneidae (= Argiopidae).

Eresidae sensu KOCH & BERENDT 1854: See Zodariidae.

Eriodontidae sensu KOCH & BERENDT 1854: See the paper on the family Trochanteriidae in this volume. PETRUNKEVITCH (1958: 374) lists the strange genus *Sosybius* KOCH & BERENDT 1854 (sub *Sosibius*) in the family Clubionidae, WUNDERLICH (1986: 29) in the family Sparassidae (sub Heteropodidae). (The type genus - *Eriodon* - is a synonym of *Missulena* which is a member of the mygalomorph family Actinopodidae whose representatives were formerly placed in the Ctenizidae!).

Erigonidae - now a subfamily of the Linyphiidae - was regarded as a family of its own e.g. by PETRUNKEVITCH (1958: 375).

Heteropodidae and Eusparassidae = Sparassidae; JÄGER (1993).

Inceptoridae PETRUNKEVITCH 1942: A dubious taxon, see WUNDERLICH (1986: 25).

Lycosidae are not known from Baltic amber; see the paper on the family Zoropsidae in this volume.

Mimetarchaeinae ESKOV 1992: A synonym of the Mimetidae: Mimetini.

Mithraeidae KOCH & BERENDT 1854 = Uloboridae.

Mizaliidae THORELL 1870 = Oecobiidae: Mizaliinae.

Myrmeciidae = Corinnidae.

*Philodromidae was regarded as a subfamily of the Thomisidae in former times.

Psechridae sensu PETRUNKEVITCH: See Zoropsidae.

(Scolytidae sensu WEITSCHAT & WICHARD (1998: 74) - probably a misspelling

of Scytodidae - was erroneously reported as a spider family in Baltic amber, but is in fact a family of the beetles).
 Segestriidae was regarded as a subfamily of the Dysderidae in former times.
 Uroceidae - now part of the Oecobiidae - was regarded as a family of its own in former times. See the Mizaliinae of the Oecobiidae.
 Zoridae: See WUNDERLICH (1986: 24) (not known from Baltic amber).
 Zoropsidae sensu PETRUNKEVITCH (1942, 1958) (*Adamator* PETRUNKEVITCH) = *Sosybius* KOCH & BERENDT 1854, see the family Trochanteriidae.
Zygiella, *Graea* and its relatives are placed here in the family Zygiellidae (n. stat.) but not in the Araneidae or Tetragnathidae.

POINAR (1992: 260) in his citation of WUNDERLICH (1986) erroneously reported the spider families Caponiidae (sub Coponiidae) and Pycnothelidae from Baltic amber, but I reported both families correctly from Dominican amber only, see WUNDERLICH (1986: e.g. p. 19), (1988). The same author (1992: 260) erroneously reported the families Archaeidae and Oecobiidae: Urocteinae from Dominican amber, but members of the Archaeidae are only known from Baltic amber and members of the Urocteinae are unknown from fossils, see WUNDERLICH (1986: 19) and this volume.

Abundance, frequency and rarity (Häufigkeit und Seltenheit)

See WUNDERLICH (1986: 48-51)

Resin functions as a kind of trap. Traps have been used by ecologists for more than half of a century, and they frequently use terms similar to those noted below. (The abundance is the percentage of the sum of all taxa of a taxon of this group in the same traps or resin or a defined area).

It is generally accepted that about 5% within the Arthropoda specimens in Baltic amber are spiders.

The number of specimens which are preserved in amber is firstly an indicator of the activity/mobility (the abundance of activity) of these animals and only secondly an indicator of the frequency in a special biotope: Larger spiders as adult members of the Ageleninae or less mobile web building spiders as members of the family Linyphiidae are underrepresented compared with mobile members of the genus *Orchestina* (Oonopidae) which are overrepresented. Especially in web building spiders and during the time of reproduction the number of mobile male spiders - which are searching for females and are trapped - is much higher than the number of females. This is true for spiders - and certain for other animals - in the field as well as in the fossil resins.

Remarks: (1) The examination of larger collections of unsorted material is needed for scientifically exact results, but such collections are rare - usually dealers select larger inclusions and overlook or ignore tiny ones. (2) Usually adult specimens are used/needed for a sure determination; exceptions are e.g., members of *Orchestina* - which have strongly thickened femora IV - or *Archaea* - which have strongly enlarged chelicerae - cannot be mistaken even as juveniles. (3) One has to be careful and not compare "apples with pears", e.g. the abundance of a family with the abundance of a species or genus.

What is meant with a "frequent fossil species"? There seems to be no agreement between different authors or even objectively defined definitions exist. I propose a standardization and terms of the abundance/frequency of animal amber inclusions, with examples of Arachnida taxa - usually Araneae - in Baltic amber:

>80%....extremely frequent (= superdominant): E.g. specimens and species of *Orchestina* within the Oonopidae, specimens of *Archaea paradoxa* within the genus *Archaea*, specimens of *Acrometa cristata* within the genus *Acrometa*, specimens and species of the order Acari within specimens of all orders of the class Arachnida;

30-80%....very frequent (= eudominant): E.g. specimens of *Balticoroma serafinorum* within the subfamily Comarominae of the Anapidae, specimens of *Archaea paradoxa* within the family Archaeidae and specimens of *Custodella* within the family Linyphiidae;

10-30%....frequent (= dominant): Specimens of the genera *Orchestina* (Oonopidae), *Acrometa* (Synotaxidae) as well as *Clya* (= *Nanomysmena*) and *Dipoena/Lasaeola* (Theridiidae) within the order Araneae; specimens of *Orchestina brevipalpus* and *O. furca* (Oonopidae) within the genus *Orchestina*;

5-10%.... fairly frequent (= subdominant): Probably - compare the "frequent taxa" - specimens of *Custodella* (Linyphiidae), *Acrometa* (Synotaxidae), *Clya* and *Dipoena/Lasaeola* (Theridiidae) as well as juveniles (!) of *Sosybius* (Trochanteridae);

1-5%....not rare (= recedent): Probably e.g. specimens of the genera *Mizalia* (Oecobiidae), *Balticoroma* (Anapidae), *Anandrus* (= *Elucus*) (Synotaxidae) and *Eomatachia* (Zoropsidae) (in some collections Archaeidae) as well as members as of the families Zygellidae (e.g. *Graea*) and Nesticiidae (e.g. *Eopopino*), which reach about 5%) within the order Araneae;

0.1-1%....rare (= subrecedent): E.g. specimens of the genera *Archaea* (Archaeidae), *Eomysmena* (Theridiidae), *Mastigusa* (Dictynidae) and *Gorgopsina* (Salticidae) as well as of the families Segestriidae, Theridiosomatidae and probably Archaeidae within the order Araneae;

0.01-0.1%....very rare (eurecedent): E.g. most probably specimens of the families Scytodidae, Hersiliidae, Protheridiidae and Ephalmatoridae (*Ephalmator*), of

the questionable Micronetinae (Linyphiidae), and of the genus *Eomiagrammopes* (Uloboridae) and adult males (!) of the genus *Archaea* (Archaeidae) within the order Araneae;

<0.01%....extremely rare (= superrecedent) (in higher taxa): E.g. adults of the families Ctenizidae (no female is known), Dipluridae (no female is known), Plectreuridae (only a single male is known), Scytodidae, Telemidae, Tetrablemmidae, Oonopidae: Gamasomorphinae (only a single male), Deinopidae (no male is known but several juveniles), Anapidae: Synaphrinae (a single male is known), Mimetinae: Oarcini (only a single juvenile), Baltsuccinidae (only two males), Amaurobiinae (only a single juvenile specimen), Dictynidae: Mizagallinae (only two males), Agelenidae (probably only three specimens), Pisauridae (no sure male is known), Oxyopidae (only two specimens), questionable members of the Stenomorphinae (Zodariidae), questionable Corinninae (Corinnidae), Eotrechaleinae (Trechaleidae), Systariinae (Clubioninae), Anyphaenidae (only a single juvenile), questionable Gnaphosidae and Philodromidae, Borboropactidae (two specimens) and Thomisidae within specimens of the order Araneae.

Most diverse in genera and species is the family Theridiidae, most diverse in species are, e.g., the genera *Orchestina* (Oonopidae), *Custodella* (Linyphiidae), *Clya* (= *Nanomysmena*) (Theridiidae) and *Dipoena/Lasaeola* (Theridiidae). (As in today's spiders most often one or two species within a genus is/are most frequent). The tiny members of *Orchestina* are known to live in higher strata of the vegetation including the bark of trees. The remaining families are members of the superfamily Araneoidea which most often build capture webs in higher strata of the vegetation. - Some of the most rare families (as adults) are the Ctenizidae, Dipluridae, Deinopidae, Oxyopidae, Anyphaenidae as well as the questionable Pisauridae - which in most cases are large(r) spiders - and the Plectreuridae which mainly live in sunny and dry biotopes similar to the Solifugae, which are also extremely rare in amber (a single specimen in Baltic amber).

On average probably about 70-80% of the fossil spiders in Baltic amber are juveniles, but in *Orchestina* the percentage may be less than 30%, and in *Archaea*, *Sosybius* (Trochanteriidae), Thomisidae and the questionable Pisauridae probably even more than 90%. Some of these spiders may have come as aeronauts to the fossil resin or only juveniles are small enough to be trapped. - Most rich in adult specimens are the families Oonopidae (*Orchestina*), Theridiidae (mainly *Clya*, *Dipoena/Lasaeola*, *Episinus*), Synotaxidae (mainly *Acrometa* and *Anandrus* (= *Elucus*)), Linyphiidae (mainly *Custodella*) and Salticidae (mainly *Eolinus* and *Gorgopsina*).

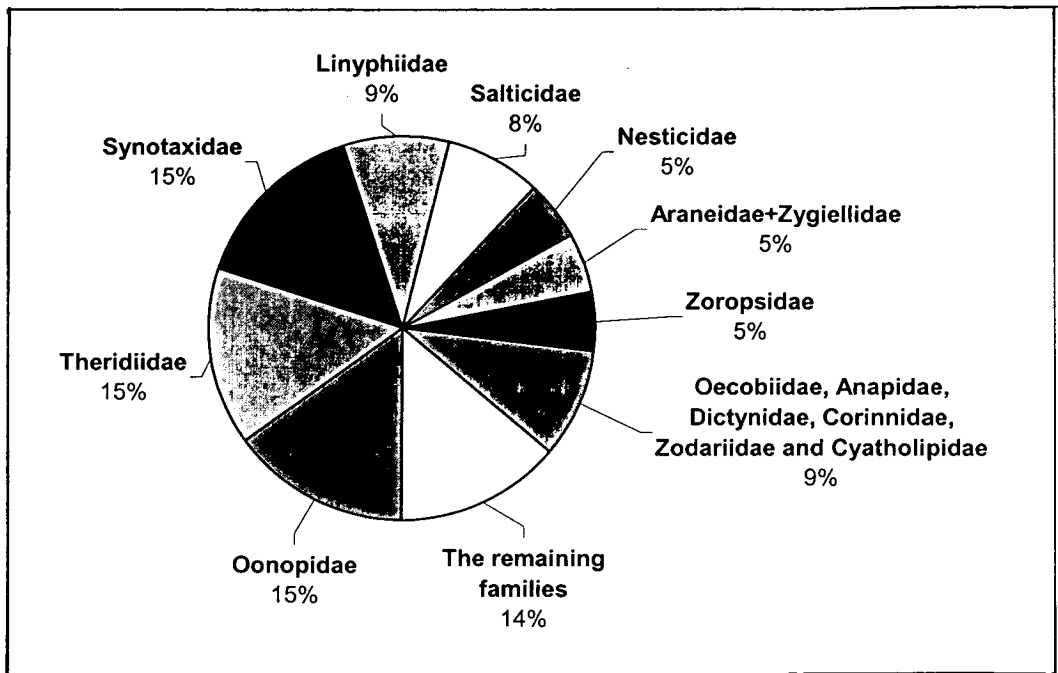


Diagram above: Rough abundances of adult specimens of the spider families, which are preserved in Baltic amber (valuation); based on my personal experiences - incl. some smaller collections of unsorted material. 1-2%: Anapidae s.l., Corinnidae, Cyatholipidae, Dictynidae s.l., Oecobiidae and Zodariidae.

Remarks on the diagram which is given by KUPRYJANOWICZ (2001: 60), which was probably based on adult as well as on juvenile spiders and mainly on small pieces of amber in which specimens of *Orchestina* are very frequent. Sparassidae (= Heteropodidae sensu KUPRYJANOWICZ) is unknown from Baltic amber; species of the genus *Sosybius* may be in fact members of the family Trochanteriidae. Most probably at least some of the Thomisidae sensu KUPRYJANOWICZ are members of other families (e.g. the Trochanteriidae, whose juveniles may be mistaken with Thomisidae). Most Clubionidae may be members of the families Corinnidae and Liocranidae. Members which were determined as Amaurobiidae may be taxa of the Zoropsidae (the genus *Eomatachia*). (Amaurobiinae (= Amaurobiidae s. str.) are extremely rare in Baltic amber). The frequent members of the family Synotaxidae (e.g.) are not shown in the diagram and may have been included mainly in the families Theridiidae and Linyphiidae.

See the chapter on biodiversity above!

Fossils are highly important regarding the study of the geographical distribution of animal and plants. Some of the new findings of the Eocene spider fauna are quite surprising and very helpful for the explanation of the today's distribution.

Today's distribution patterns of taxa are resulting from different events in the past - see REINHEIMER (1998: 287):

- (1) its origin,
- (2) its dispersal and
- (3) its extinctions

Remark: Biogeographical relationships are linked with taxonomical relationships and opinions. An example: If the spider family Archaeidae is regarded in a wide (and my personal) sense - incl. the Mecysmaucheniinae which occurs in South America in contrast to the Archaeinae - it is present in South America; if Archaeidae is regarded in a strict sense - excl. Mecysmaucheniinae - Archaeidae would be absent in South America. Because of a greater number of similar cases in spiders a differentiation of families and subfamilies is useful.

Cretaceous ambers on family level

Closer studies on the important Cretaceous amber spider faunas are just at the beginning - see ESKOV & WUNDERLICH (1995) and the papers on Lebanese amber and the families Oonopidae, Oecobioidae: Oecobiidae and Araneidae in this volume as well as PENNEY (1998, 2002).

Some preliminary results: The quota of the "primitive" superfamily Dysderoidea is high at least in the Taimyr ambers, but seemingly in the New Jersey amber, too, according to PENNEY (1998: 25). In a private collection of Spain - R. VIGIL in Vitoria - of Cretaceous amber from Alava I identified an probably adult female as a member of the genus *Orchestina* SIMON (Oonopidae) which also is known from several Tertiary ambers. The specimen has thickened femora IV which are typical in *Orchestina*. *Orchestina* is the only extant spider genus which is already known from the Cretaceous period. - The only family of the RTA-clade published from Cretaceous amber is Dictynidae, see PENNEY (1998: 25).

Dominican amber:

See WUNDERLICH (1986: 39-40, 1988: 13) as well as the papers on the Mygalomorpha, Dysderoidea and on fakes in this volume. - Reports of Nemesiidae and Symphytognathidae in Dominican amber - according to SCHAWALLER (1981) - are wrong determinations; material of the Anapidae: Symphytognathinae which is kept in the Mus. of Nat. Hist. in Stuttgart is really from the Theridiidae. The presence of the Miturgidae in Dominican amber is questionable to me because of the uncertain relationships of the genus *Strotarchus* SIMON 1888. - The Dominican amber fauna contains a larger number of strictly ("inner") tropical taxa than the fauna in Baltic amber - Barychelidae, Microstigmatidae, Tetrablemmidae, Caponiidae, Ochyroceratidae, Araneidae: Nephilinae, Trochanteriidae (questionable report), Selenopidae, Sparassidae: Sparianthinae and Salticidae: Cocalodinae and Lysso-maninae -, see below. The taxa Cyrtaucheniidae, Microstigmatidae, Ochyroceratidae, Tetrablemmidae, Hersiliidae, Anapidae s. l. (Anapinae and Mysmeninae) and Hahniinae (Dictynidae s. l.) are known from fossil but not from extant spiders, but extant members of some of these families have probably not yet been discovered on Hispaniola, which extant fauna is poorly known. PENNEY (1999) discussed biogeographical relationships of the Hispaniolan spider fauna. PENNEY (1999, 2001) and PENNEY & PEREZ-GELABERT (2002) compared the extant and Miocene (Dominican amber) faunas of Hispaniola. (On the Dominican copal and the Mexican amber: See WUNDERLICH (1986: 40-01)). In contrast to the Eocene fauna in Baltic amber - see below - there are no close relationships to regions far away but most taxa in Dominican amber have close relationships to the extant fauna of Hispaniola and Central America, see above (the diversity); few genera have a cosmopolitan distribution: *Ariadna* AUDOUIN 1827 (Segestriidae), *Scytodes* LATREILLE 1804 (Scytodidae), *Orchestina* SIMON 1882 (Oonopidae), *Oecobius* LUCAS 1846 (Oecobiidae), *Theridiosoma* O. PICKARD-CAMBRIDGE 1879 (Theridiosomatidae), ?*Achaeearanea* STRAND 1929 (Theridiidae), *Argyrodes* SIMON 1864 (s. l.) (Theridiidae), *Dipoena* THORELL 1869 s. l. (= *Lasaeola* SIMON 1881; further synonyms: See WUNDERLICH (1988: 148) and probably *Dipoenata* WUNDERLICH 1988) (Theridiidae), *Theridion* WALCKENAER 1809 (Theridiidae), *Mimetus* HENTZ 1832 (Mimetidae) (questionable proof in Baltic amber). Most genera are members of the family Theridiidae and are known from the Baltic amber fauna, too, but *Oecobius*, *Theridiosoma* and probably *Theridion* are absent in the Baltic amber fauna.

The differences between the extant and fossil taxa are most striking in the family Dictynidae: 4 of 5 (= 80%!) of the Hispaniolan genera are extinct (there are 16 extinct, but only 1 known extant species!). In the families Oonopidae, Pholcidae, Theridiidae and Corinnidae the number of extinct species is higher than the number of extant species.

Comparison of selected families and subfamilies in Baltic and Dominican amber:

Taxon		Baltic amber	Dominican amber
(3)	Oecobiidae: Oecobiinae	--	+
	Araneidae: Araneinae	?-	+
	Tetragnathidae: T'-inae	--	+
	-- : Aziliinae	--	+
	Linyphiidae: Micronetinae	?-	+
	Corinnidae: Castianeirinae	--	+
	-- : Trachelinae	--	+
	Theridiidae: Argyrodinae	--	+
	Lycosidae	--	+?
	Thomisidae: Thomisinae	--	+
	Salticidae: Euophrydinae	--	+
	-- : Lyssomaninae	--	+
	-- : Salticinae	--	+
(4)	Dysderidae	+	--
	Zoropsidae	+	--
(5)	Caponiidae: Nopinae	--	+
	Palpimanidae: Otiiothopini	--	+
(6)	Microstigmatidae	--	+
	Caponiidae: Nopinae	--	+
	Palpimanidae: Otiiothopini	--	+
	Corinnidae: Castianeirinae	--	+
	Tetragnathidae: Aziliinae	--	+
	Theridiidae: Argyrodinae	--	+
	Selenopidae	--	+
	Sparassidae: Sparianthinae	--	+
	Salticidae: Lyssomaninae	--	+
(7)	Archaeidae	+	--
	Cyatholipidae	+	--
(8)	Plectreuridae	+	--
(9)	Agelenidae	+	--
	Zodariidae	+	--

Remarks: (1) Not listed are the 10 extinct suprageneric taxa in the older Baltic amber (Microstigmatidae: Parvomysgalinae is the only suprageneric taxon in the younger Dominican amber which apparently is extinct). (2) All subfamilies of the Mygalomorpha are different in Baltic and Dominican amber.

Discussion of the groups above: (3) Oecobiidae: Oecobiinae, Araneidae: ?Aranei-nae, Tetragnathidae: Aziliinae and Tetragnathinae, Theridiidae: Argyrodinae, Linyphiidae: ?Micronetinae, Corinnidae: Castianeirinae and Trachelinae, Philodromidae, Thomisidae: Thomisinae s. l., Salticidae: Euophryinae s. l., Lyssomaninae and Salticinae are - according to my hypothesis - probably geologically young taxa which evolved - or radiated strongly - only after the disappearance of the Early Tertiary European amber forests. (4) Dysderidae and Zoropsidae are not known from the Neotropics (but e.g. from the Mediterranean) in contrast to (5) the Nopinae which are restricted to the New World. (6) The mainly tropical distribution of the Microstigmatidae, Nopinae, Castianeirinae, Aziliinae, Argyrodinae, Ctenidae, Selenopidae, Sparianthinae, Lyssomaninae and some other higher taxa may be the reason for their absence in Baltic amber. (7) Archaeinae and Cyatholipidae are not known from the Americas and their extant taxa are restricted to the Southern Hemisphere. (8) The family Plectreuridae is restricted today to America but unknown from Dominican amber. Most species occur in dry areas outside of amber forests, and therefore only a single specimen has ever been found. (9) The reason for the absence of Agelenidae and Zodariidae in the fossil and extant (!) fauna of Hispaniola is unknown, and probably due to the poorly known fauna of this island; both families are diverse and have a cosmopolitan distribution.

Comparison of families/subfamilies in Baltic and Dominican amber which have mainly - or nearly without exception: underlined - a tropical distribution:

	in Baltic amber	in Domini- can amber
(a) Suborder Mygalomorpha		
<u>Theraphosidae</u> : Ischnocolinae	--	<i>Ischnocolinopsis</i>
<u>Barychelidae</u>	--	<i>Psalistops</i>
Ctenizidae: Ctenizinae	2-3 genera	--
Family near Ctenizidae	--	<i>Bolostromus</i>
Dipluridae s. l.	<i>Clostes</i> ,	? <i>Ischnothele</i> , <i>Ma-</i>
incl. Hexathelinae	2 gen. indet.	<i>steria</i> , <i>Microsteria</i>
<u>Microstigmatidae</u>	--	<i>Parvomysgal</i>

(b) Suborder Araneomorpha

Plectreuridae: Plectreurinae	<i>Palaeoplectreurys</i>	--
Caponiidae: Nopinae	--	<i>Nops</i>
Oonopidae: Gamasomorphinae	? <i>Stenoonops</i>	<i>Fossilopopaea</i> , ? <i>Opopaea</i>
<u>Tetrablemmidae: Tetrablemmiinae</u>	<i>Balticoblemma</i>	? <i>Monoblemma</i>
Loxoscelidae	--	<i>Loxosceles</i>
Scytodidae	<i>Scytodes</i> , gen. indet.	<i>Scytodes</i>
Ochyroceratidae	--	<i>Arachnolithulus</i>
Palpimanidae: Palpimaninae	--	<i>Otiothops</i>
Archaeidae	5 genera	--
<u>Hersiliidae</u>	4 genera	<i>Fictotama</i>
<u>Deinopidae</u>	? <i>Menneus</i>	?
Araneidae: <u>Nephilinae</u>	--	<i>Nephila</i>
Tetragnathidae: <u>Diphyinae</u>	6 genera	--
Theridiosomatidae	4 genera	<i>Theridiosoma</i>
Anapidae s. l.: Anapinae	8 genera	<i>Palaeoanapis</i>
Anapidae s. l.: Mysmeninae	3 genera	<i>Dominicanopsis</i> , <i>Mysmenopsis</i>
Zoropsidae	3 genera	--
Zodariidae: ?Storenomorphinae	<i>Zodariodamus</i>	--
<u>Trochanteriidae: Trochanteriinae</u>	4 genera	? <i>Veterator</i>
Selenopidae	--	<i>Selenops</i>
Sparassidae: Sparianthinae	--	<i>Pseudosparianthis</i>
Borboropactidae: <u>Borboropactinae</u>	? <i>Borboropactus</i>	--
Borboropactidae: Succiniraptorinae	<i>Succiniraptor</i>	--
Thomisidae: <u>Stephanopinae</u>	?3 genera	--
Salticidae: <u>Cocalodinae</u>	9 genera	? <i>Phlegrata</i>
Salticidae: <u>Lyssomaninae</u>	--	<i>Lyssomanes</i>
<hr/>		
<u>Sum:</u>	20/21 families	62 genera 26 genera

The Eocene European ambers ("Succinite")

(a) The Ukrainian amber fauna(s)

There are several Tertiary amber deposits in the Northern Ukraine, here I consider only the amber from Rovno, see the paper on fossil spiders from the Ukraine in this volumes. I identified 13 families and 9 genera: *Acrometa* PETRUNKEVITCH 1942 (Synotaxidae), *Adorator* PETRUNKEVITCH 1942 (Zodariidae), *Balticonopsis* WUNDERLICH 2003 (n. gen.) (Anapidae), *Fossilanapis* WUNDERLICH 2003 (n.

gen.) (Anapidae), *Gorgopsina* PETRUNKEVITCH 1955 (Salticidae), *Mizalia* KOCH & BERENDT 1854 (Oecobiidae), *Orchestina* SIMON 1882 (Oonopidae), *Sosybius* KOCH & BERENDT 1854 (Trochanteriidae), and *Succinero* WUNDERLICH 2003 (n. gen.). Except members of *Balticonopsis* spiders of these genera are also frequent in the Samlandic amber. - The fossil spider fauna of the Rovno amber is very similar to the Bitterfeld and the Samlandic amber fauna but not identical: Although most species are identic other species are different.

(b) The Samlandic amber fauna

"Nor are the genera which are represented in both the Baltic Amber and the Recent fauna closely related to the present European fauna. On the contrary, genera which have European species are few and are widely distributed, while those which have no European species are more numerous and have now living species in distant countries, such as South Africa, Malay peninsula, Australia, South America. Moreover, entire families not found in Europe, are represented in Baltic Amber, namely Archaeidae and Psechridae." - PETRUNKEVITCH (1950: 259) on spiders of the Baltic amber fauna.

Half a century later I can confirm some of the previous findings of PETRUNKEVITCH on the spider fauna which is preserved in Baltic amber: There are various genera in the Baltic amber which have today a cosmopolitan distribution, only few have an European distribution, some have relationships to other continents - most foundations of such taxa by PETRUNKEVITCH are erroneous, see below -, and most genera are extinct. PETRUNKEVITCH (1942: 191) found 80.6% of the spider genera of the Baltic amber fauna to be extinct, according to my last findings the percentage is even higher, about 88%.

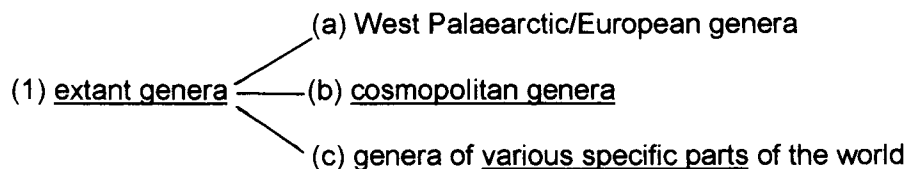
Fakes, confusions and wrong determinations lead to erroneous biogeographical conclusions:

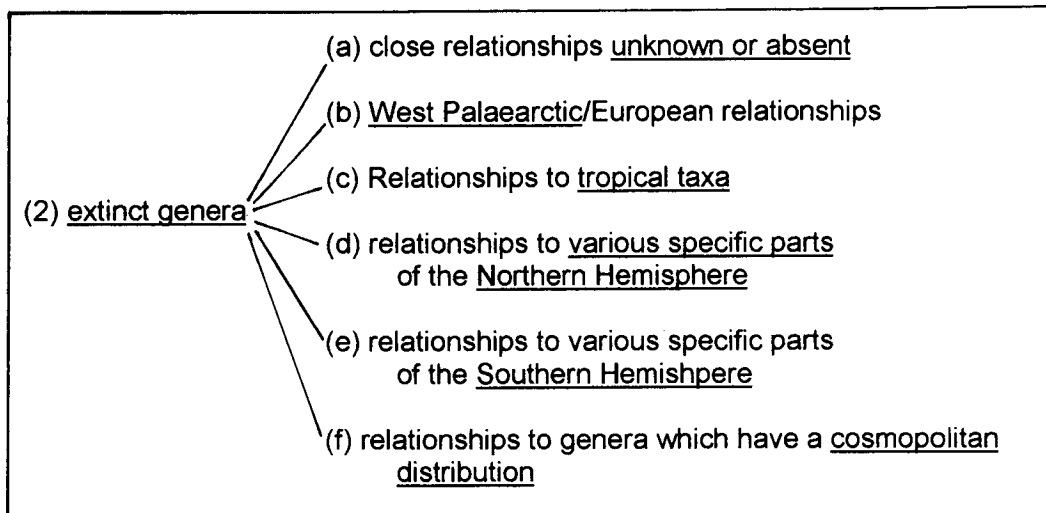
Fakes/confusions which are preserved in copal or artificial resin - see the chapter on fakes in this volume -, e.g. (1) a member of the genus *Parevophrys* PETRUNKEVITCH 1942 (Salticidae) which was placed by PETRUNKEVITCH (1942: 186) in the subfamily Heliophaninae which would be the unique report of this subfamily in Baltic amber, but the specimen is really preserved in East African copal, and (2) *Entomocephalus* HOLL 1829 - described by the geologist HOLL as a mixture of a spider and an ant (!) -, listed by PETRUNKEVITCH (1958: 372) as a questionable member of the family Archaeidae in Baltic amber, but the spider is really an extant member of the family Salticidae (!).

Examples of wrong determinations: Erroneous determinations of KOCH & BERENDT (1954) and MENGE in KOCH & BERENDT (1854): See the various families in this volume. In his list of Baltic amber spiders PETRUNKEVITCH (1958: 369-385) noted the families Eresidae, Erigonidae (now a subfamily of the Linyphiidae), Lycosidae, Philodromidae (sub Thomisidae) and Psechridae, but none of these taxa are known for safe from Baltic amber, only Philodromidae is questionable, see below and PETRUNKEVITCH (1942: 183). Examples on generic level: *Auximus* SIMON 1892 - listed by PETRUNKEVITCH (1958: 123) sub Amaurobiidae - see PETRUNKEVITCH (1942: 183) - is a synonym of *Dictyna* SUNDEVALL 1833 s. l. (Dictynidae).

The relationships of several genera which are noted by PETRUNKEVITCH (1942: 183, 188) are quite unsure: *Adamator* PETRUNKEVITCH 1942 (σ unknown!) was placed by PETRUNKEVITCH in the family Zoropsidae but is regarded by me as a member of *Sosybius* KOCH & BERENDT 1854, probably the family Trochanteriidae, not Sparassidae (sub Heteropodidae) as stated erroneously by me, see WUNDERLICH (1986: 24). According to PETRUNKEVITCH (1942: 188) *Adamator* "resembles most the genus *Zorocrates* known only from Central America"; in his catalogue of Araneae PLATNICK (1993: 586) placed *Zorocrates* SIMON 1888 in the family Tengellidae, while LEHTINEN (1968: 207) placed it in the Miturgidae: Uliodoninae. - *Anniculus* PETRUNKEVITCH 1942 (Zodariidae) (?= *Annarius* sensu PETRUNKEVITCH (1942: 183; probably a misspelling of *Anniculus*) is - according to the shape of the prosoma and the position of the eyes - not related to *Cycnethus* SIMON 1910 (= *Patiscus* SIMON 1893), see PETRUNKEVITCH (1942: 183). *Myro* PETRUNKEVITCH 1958: The familiar relationships - a member of the family Clubionidae? - of the holotype (σ) are quite unsure. The relationships of the remaining taxa which are published by PETRUNKEVITCH (1942: 183) - *Collacteus* PETRUNKEVITCH 1942, *Eostasina* PETRUNKEVITCH 1942, *Facundia* PETRUNKEVITCH 1942 and *Filiolella* PETRUNKEVITCH 1955 (= *Filiola* PETRUNKEVITCH 1942) - are absolutely uncertain because these taxa are described from exuvia (!), juveniles or probably inadult females only, but no male is known which could give more important information about their relationships.

In the biogeography of extant and extinct genera we can distinguish the following groups: the spiders in Baltic amber are members of...





(1) Extant genera: 24 genera (the determination of 9 of these is questionable):

(a) West Palaearctic/European genera:

Ummidia (Ctenizidae), *Harpactea* (Dysderidae), *Mastigusa* (Dictynidae: Cryphoeicinae). - Furthermore *Eopopino* (Nesticidae) is closely related to (or even synonym with) the extant genus *Carpathonesticus* LEHTINEN & SAARISTO, and *Eolabulla* (Linyphiidae) is closely related to the extant genus *Labulla* SIMON.

(b) widely spread or cosmopolitan genera:

Ariadna (Segestriidae), *Segestria* (Segestriidae), *Orchestina* (Oonopidae), *Scytodes* (Scytodidae), ?*Telema* (Telemidae), ?*Hersilia* (Hersiliidae) (probably widely spread), *Hyptiotes* (Uloboridae), ?*Mysmena* (Anapidae: Mysmeninae), *Dipoena* (= *Lasaeola*) (Theridiidae), *Episinus* (Theridiidae), *Phoroncidia* (Theridiidae), *Steatoda* (Theridiidae), ?*Mimetus* (Mimetidae), ?*Agelena* (Agelenidae) (widely spread), ?*Tegenaria* (Agelenidae) (widely spread).

(c) genera of various specific parts of the world:

?*Stenoconops* (Oonopidae) (the Americas), ?*Menneus* (Deinopidae) (Africa), *Balticoroma* n. gen. (Anapidae) (SE-Asia, Japan and Korea), *Pimoa* (Pimoidae) (Holarctic), *Apostenus* (Liocranidae) (Holarctic), ?*Borboropactus* (Borboropactidae) (SE-Asia).

Remarks: (1) Most of these genera are widely spread today. (2) About a quarter of the genera of (c) are members of the family Theridiidae, and the number of their genera may increase after a revision of the Theridiid fossils in Baltic amber. (3) No genus is known which has only survived in the Southern Hemisphere, but the extant genus *Tekella* URQUHART 1894 from New Zealand (Cyatholipidae) is closely related to *Spinilipus* WUNDERLICH 1993 which is preserved in Baltic amber. (4) KOCH & BERENDT and MENGE (1854) also published 24 extant genera of spi-

ders but most are wrong determinations; I only can confirm few of them: Surely *Mastigusa* and *Segestria*, with hesitation *Tegenaria*, with strong hesitation *Agelena* and *Hersilia*. Synonyms of extant genera which are treated by KOCH & BERENDT and MENGE are *Androgeus* = *Hyptiotes* and *Flegia* = *Episinus*.

(2) Extinct genera:

(a) close relationships unknown or absent:

Most genera.

(b) West Palaearctic/European relationships:

Eopopino (Nesticidae) - *Carpathonesticus* LEHTINEN & SAARISTO 1980,
Eolabulla n. gen. (Linyphiidae) - *Labulla* SIMON 1884,
Eoleptoneta (Leptonetidae) - *Leptoneta* SIMON 1872,
Paraspermophora n. gen. (Pholcidae) - *Spermophorides* WUNDERLICH 1992,
Gibbermastigusa n. gen. and *Protomastigusa* n. gen. (Dictynidae s.l.: Cryphoecinae) - *Mastigusa* MENGE 1854,
Adorator PETRUNKEVITCH 1942 (Zodariidae) - *Selamia* SIMON 1873.

(c) relationships to tropical taxa (see the map and the genera at the list above; see also d and e):

Compared with the tropical Dominican amber forest there is an impressive high number of tropical taxa of the Baltic amber fauna: 20 families and 62 genera. (Also various extant genera of the families Cyatholipidae - 5 fossil genera - and Synotaxidae - 10 fossil genera - occur in the tropics). But the number of the "true" tropical (sub)families is nearly the same as in the Dominican amber (8): Tetrablemmidae, Deinopidae, Hersiliidae (in fact a "true" tropical family?), Tetragnathidae: Diphysinae, Trochanteriidae, Borboropactidae, Thomisidae: Stephanopinae, Salticidae: Cocalodinae. Remarkable is the high number of Salticidae: Cocalodinae (8 genera, see especially the genus *Gorgopsina*): The whole subfamily is extinct in Europe and most extra-tropical parts of the Northern Hemisphere today.

(d) relationships to various specific parts of the Northern Hemisphere:

Palaeoplectreurys n. gen. (Plectreuridae) - *Plectreurys* SIMON 1893 - Neotropic,
Graea (Zygiellidae) - *Zygiella* F. O. PICKARD-CAMBRIDGE 1902 - Holarctic,
Chrysometata n.gen. (Zygiellidae) - probably *Chrysometa* SIMON 1895 - Americas,
Balticocryphoea n. gen. (Dictynidae s.l.: Cryphoecinae) - *Cryphoea* THORELL 1870 and *Neocryphoea* ROTH 1970) - Holarctic,
Protoorthobula n. gen. (Corinnidae) - *Orthobula* SIMON 1899 and *Sphingius* THORELL 1890 Orientalis (SE-Asia).

(e) relationships to various specific parts of the Southern Hemisphere:

Genera of the families Archaeidae (e.g. *Archaea*) - South Africa and Australia,
Cyatholipidae (especially *Spinilipus* WUNDERLICH 1993 - *Tekella* URQUHART 1893 and *Succinilipus* WUNDERLICH 1993 - *Tekellatus* WUNDERLICH 1978) (see above) - Australian Region,
Mimetidae: Oarcini (*Praeoarces* n. gen.) - probably South America,

Spatiatoridae (*Spatiator* PETRUNKEVITCH 1942, extinct) has most probably its closest relatives (Huttoniidae: *Huttonia* O. PICKARD-CAMBRIDGE 1879) in New Zealand,

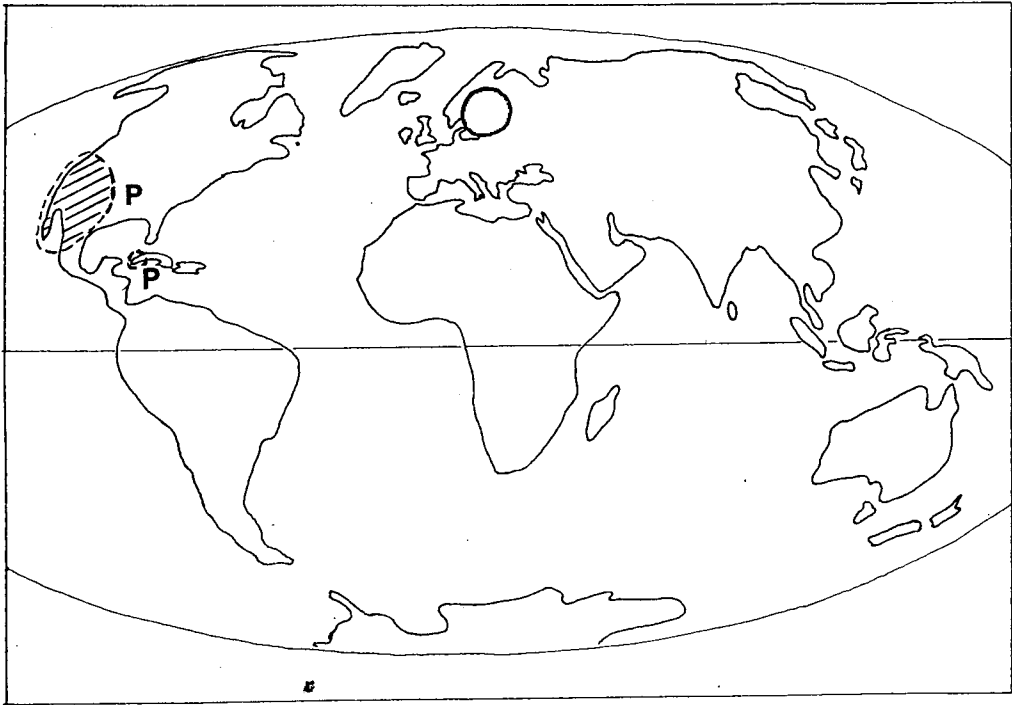
Synotaxidae (diverse genera) - Australia, ?South America,

Salticidae: Cocalodinae: Especially *Gorgopsina* PETRUNKEVITCH 1955 - *Tomocyrba* SIMON 1900 in the Ethiopian Region (South Africa, Madagascar).

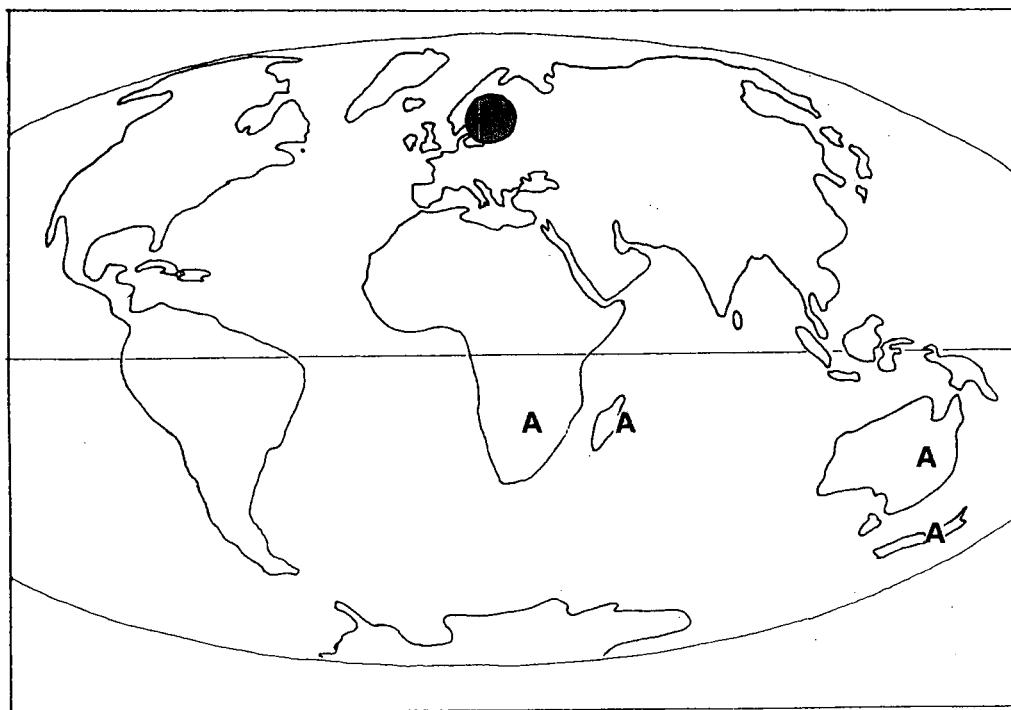
(f) relationships to genera which have a cosmopolitan distribution:

e.g. *Succinero* n. gen. (Mimetidae) - *Ero* C. L. KOCH 1837.

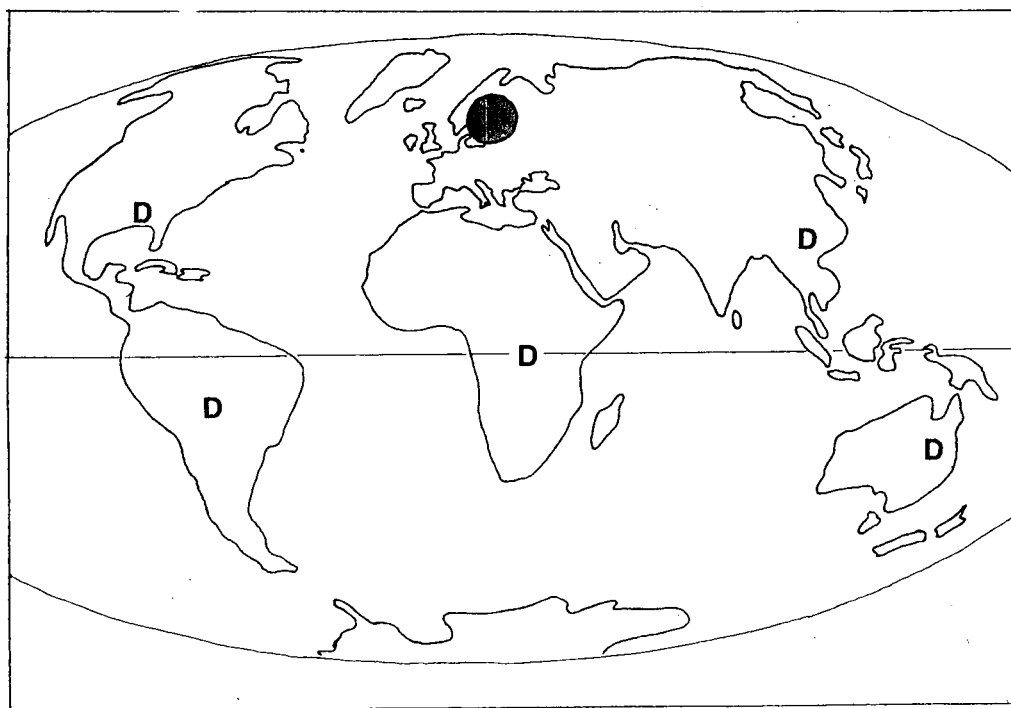
Impressive examples of biogeographical relationships of the Baltic amber Arthropods - and other animals and plants -, including maps of the distribution are given e.g. by ANDER (1942). WEITSCHAT & WICHARD (2002: 38, 74) give only short notes on biographical aspects but discussed more questions of the climate.



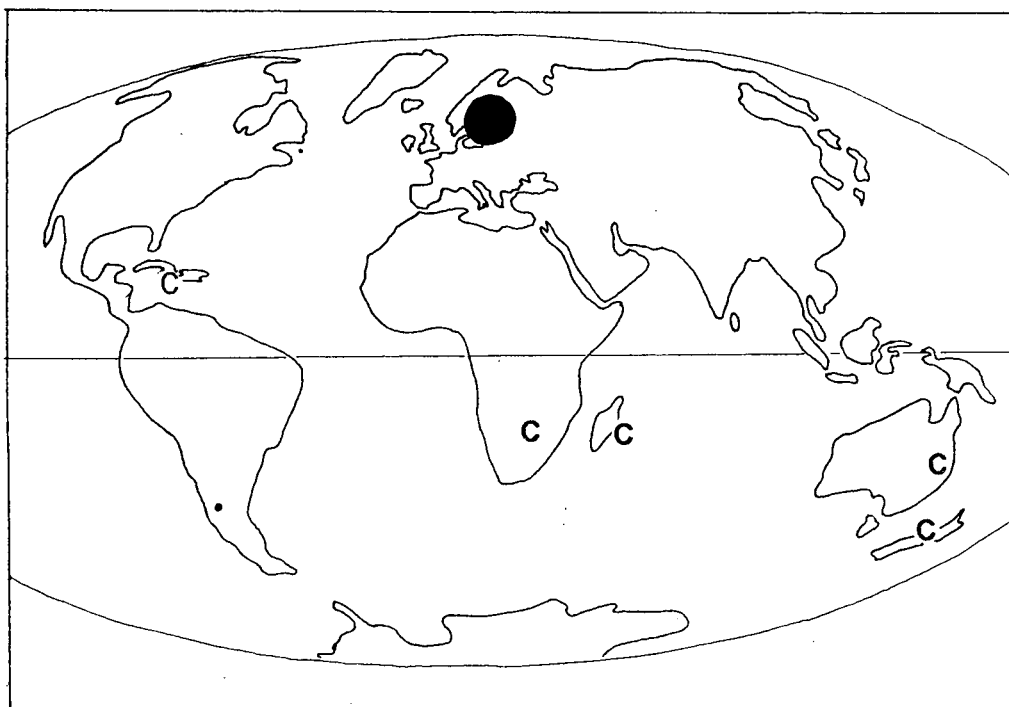
Distribution of the subfamily **Plectreurinae** (Araneae: Plectreuridae) at the Baltic deposit (black circle) and extant in the Americas (P)



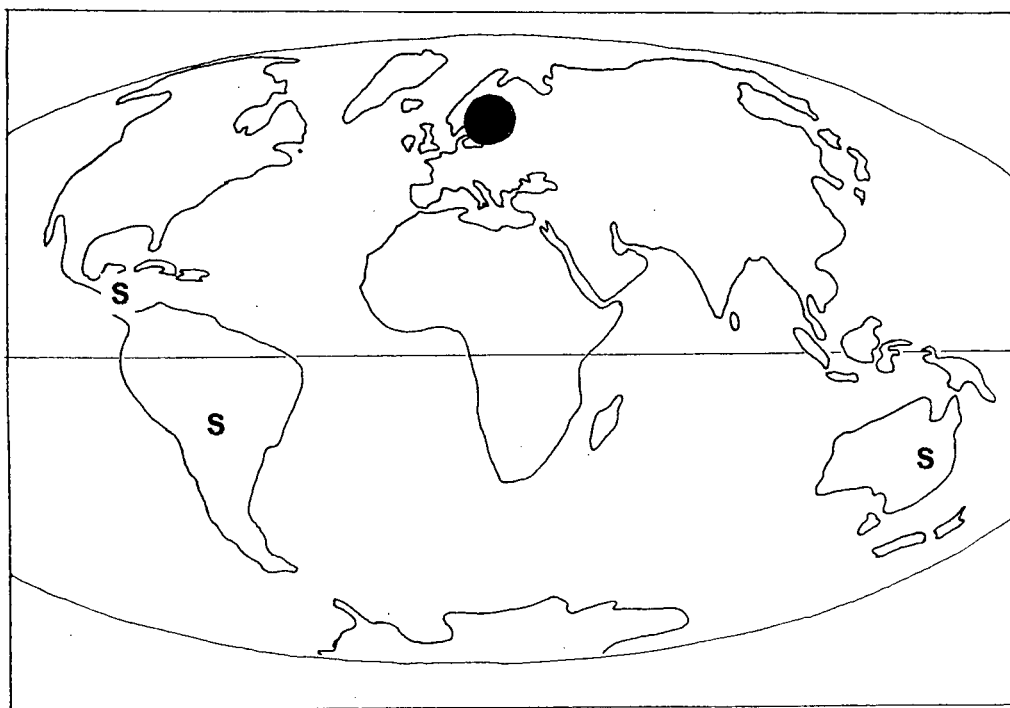
Distribution of the subfamily **Archaeinae** (Araneae: Archaeidae) at the Baltic amber deposit (black circle) and extant (A) in the Southern Hemisphere:



Distribution of the family **Deinopidae** (Araneae) at the Baltic amber deposit (black circle) and extant (D)



Distribution of the family **Cyatholipidae** (Araneae) at the Baltic amber deposit (black circle) and extant in the Southern Hemisphere (C)

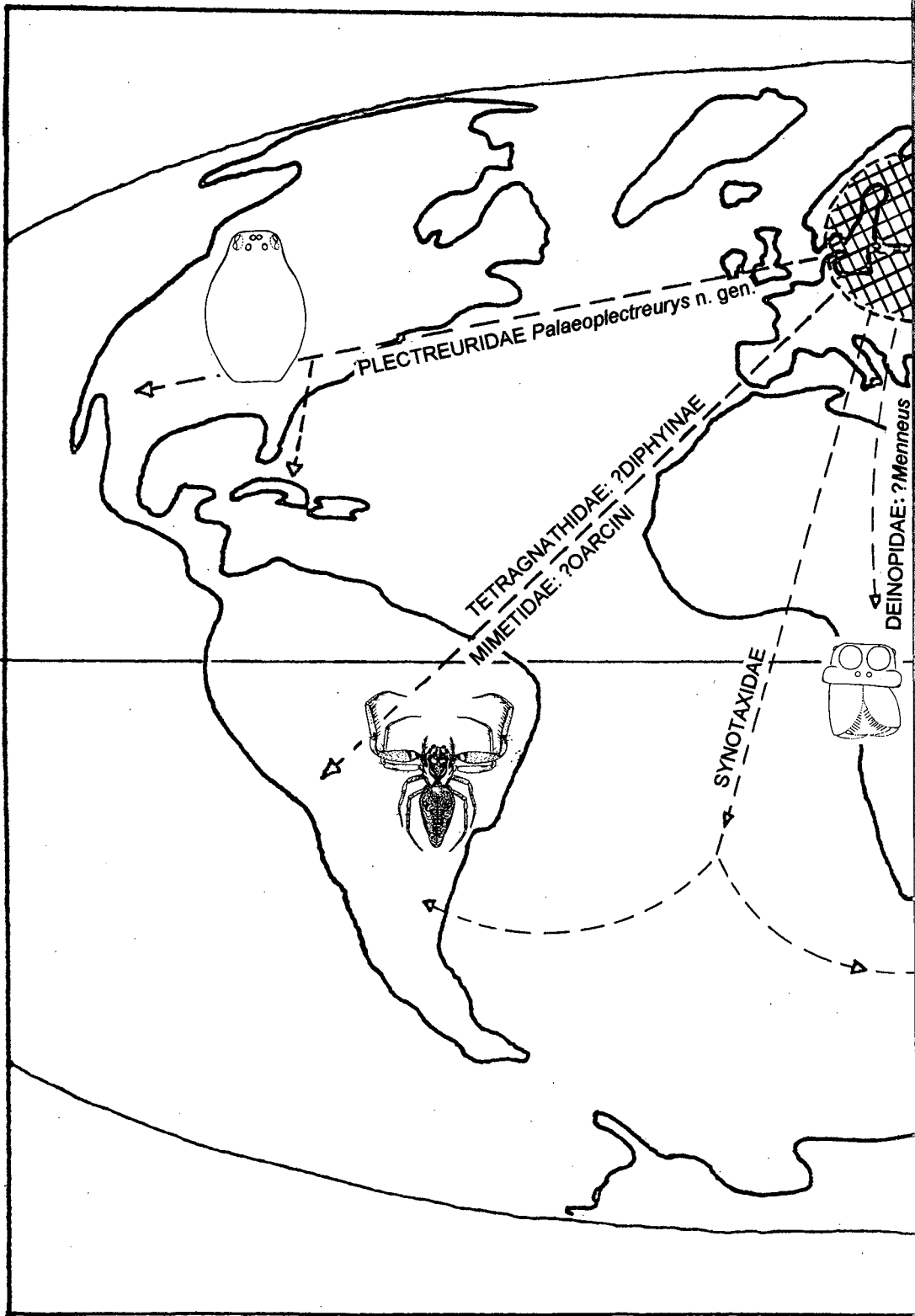


Distribution of the family **Synotaxidae** (Araneae) at the Baltic amber deposit (black circle) and extant mainly in the Southern Hemisphere (S)

WORLDWIDE BIOGEOGRAPHICAL RELATIONSHIPS of selected taxa which are related to the Eocene European fauna 50 million years ago.

WELTWEITE BIOGEOGRAPHISCHE BEZIEHUNGEN ausgewählter Spinnen-Gruppen, die verwandt sind mit der europäischen Fauna im Bernstein des Frühen Tertiärs (Eozän) vor 50 Millionen Jahren.

Taxa of more than a dozen spider families of the Eocene European (incl. the Baltic amber) forests (hatched) show relationships (arrows) to tropical and South hemispherical taxa of the Australian, Ethiopian, Oriental and Neotropical (partly questionable) Regions: Anapidae s. l.: Comarominae, Archaeidae: Archaeinae, Borboropactidae, Corinnidae, Cyatholipidae, Deinopidae, Mimetidae, Plectreuridae: Plectreurinae, Salticidae: Cocalodinae, Spatiatoridae, Synotaxidae, Tetrablemmidae: Tetrablemminae, Tetragnathidae: Diphyinae and Thomisidae: Stephanopinae. - Mitglieder von mehr als einem Dutzend Spinnen-Familien der Frühen Tertiären Europäischen Bernstein-Wälder (incl. dem Baltischen Bernsteinwald, schraffiert) zeigen Beziehungen zu tropischen Verwandten und solchen der Südlichen Halbkugel (Pfeile).



Changes in the range, "Gondwanaland taxa", relict taxa and the origin of selected taxa

COOPE et al. (1971) published impressive examples regarding the change in the beetle fauna of Great Britain in the last 100 000 years; the ranges of species which lived at the site of Trafalgar Square are today from the Iberian Peninsula up to Asia; see also HENGELFELD (1990) and TAYLOR & TAYLOR (1996). These examples of "fossil Coleoptera as indicators of climatic fluctuations during the last glaciation in Britain" are much more recent than the existence of the Baltic amber forest.

HOFFEINS & HOFFEINS (1995: 207-210) published fossil members of the family Nymphomyiidae (Diptera) from Baltic amber which are today found in North America, Japan and the Himalaya. The genus *Caddo* (Opiliones: Caddidae) is restricted at the present to North America and Japan, and has also been found in Baltic amber. The Anapidae: Comarominae are known today from North America, Europe and SE-Asia (Japan, Korea), altogether three to four species, but members of this subfamily were not rare in Baltic amber. ZWEDO (2002) described a species of the Cixiidae (Hemiptera) in Baltic amber which is related to taxa which are restricted today to the New World. A fossil member of the family Thaumstocoridae (Heteroptera) in Baltic amber is closely related to an extant species from Cuba, see BECHLY (2001: 54). Like these findings a member of the family Plectreuridae (Araneae) in Baltic amber - the first fossil record of this spider family which is restricted today to the New World, see the paper on the Plectreuridae: Plecteurinae (Dysderoidea) in this volume - indicates the much wider range of various groups of animals in the Early Tertiary and got extinct in this region latest during the coldness of the Oligocene. Members of the tropical to subtropical subfamily Plecteurinae had probably a Laurasian distribution at the end of the Cretaceous and were separated in two fractions when North America and Europe separated 60 million years ago (see the fig. below). The genus *Plectreurys* survived in North America, the genus *Palaeoplectreurys* became extinct in Europe during the Oligocene.

The importance of fossil spiders regarding conclusions on the biogeography has been underestimated. The discovery of fossils can found new hypothesis on biogeographical relationships of taxa. Many animal and plant groups are nowadays restricted to the southern continents and have been found as fossils in Eurasia and/or North America, e.g. the conifer genus *Araucaria*, the mammals Monotremata (German: Kloakentiere), most Marsupialia (German: Beuteltiere), "Xenarthra" ("Zahnarme"), the lower primates Prosimii (Halbaffen), the birds Palaeognathae/Ratitae (Straußenartige Vögel), etc., see e.g. ESKOV & GOLOVATCH (1986: 266). The primitive termite genus *Mastotermes* lives today only in Australia but fossils of this genus have turned up in Mexican, Dominican and Baltic ambers, see ROSS (1998: 34). Certain bees in Baltic amber have extant relatives in South Africa, others in the Oriental Region, see ENGEL (2001). A spectacular example was the find of a member of the Myrmecophagidae (Edentata) (German name: Amei-

senbären) in the German Eocene of the Grube Messel near Darmstadt, a group of Mammals which was only known from South America (it is the oldest fossil of this group). Where was the origin of the Myemcophagidae - the Gondwanaland, South America or the Northern Hemisphere, Europe? - Various authors conclude from the extant distribution of a taxon rush on its Gondwanan origin and a spreading to the north, but the reverse may be the case of the taxa which are known today only from the southern parts of the Southern continents (the "southern semicircle") may be relicts of taxa which had a much wider range in the past, see e.g. the criticism on "mobilistic biogeography" and the explanation of today's distributions of organisms in relation to the continental drift by ANDER (1942: 57-68), ESKOV & GOLOVATCH (1986), the papers of KRAUS (1978: Fig. 3) and WUNDERLICH (1995) as well as the papers on the Archaeidae (Eresoidea s. l.) and Cyatholipidae in this volumes.

Changes in the range of spiders: The distribution/range of members of several families/subfamilies as Plectreuridae (extinct), Terablemmidae, Archaeidae, Oecobiidae: Mizaliinae (extinct), Deinopidae, Tetragnathidae: Diphyinae, Araneidae: Nephilidae, Cyatholipidae, Synotaxidae, Baltsuccinidae (extinct), Protheridiidae (extinct), Zoropsidae: Eomatachiini and Eoprychiini, Spatiatoridae (extinct), Trochanteriidae, Borboropactidae, Thomisidae: Stephanopinae and Salticidae: Coccolodinae - which apparently preferred subtropical climates in the Early Tertiary and which became extinct during the Oligocene in Europe as well as in parts of the Northern Hemisphere but survived in the Southern Hemisphere - changed probably mainly because of the coldness in the Oligocene, see below. Plectreuridae is a relict in the Americas today. Archaeinae and Cyatholipidae are completely extinct in the Northern Hemisphere, only members of a single genus of the Synotaxidae are known at present from the Northern Hemisphere. Archaeinae was more diverse in genera in the amber forest as today worldwide (they are absent in South America), Synotaxidae were as diverse as today in genera (they are absent in Africa). The reasons for the extinctions on the Northern Hemisphere is not known with certainty. One reason regarding the Cyatholidae and Synotaxidae was probably the competition with members of the subfamily Erigoninae (family Linyphiidae); this subfamily is mainly distributed in moderate climates; it is not known from Baltic amber and it radiated probably only in the Oligocene when the Baltic amber forest already was gone. (All the families in question are not known from earlier than Tertiary deposits).

Change of distribution/range of some spider families and subfamilies

Taxa which are pre-served in Baltic amber:	Today's distribution:
Plectreuridae	Mainly tropical Americas

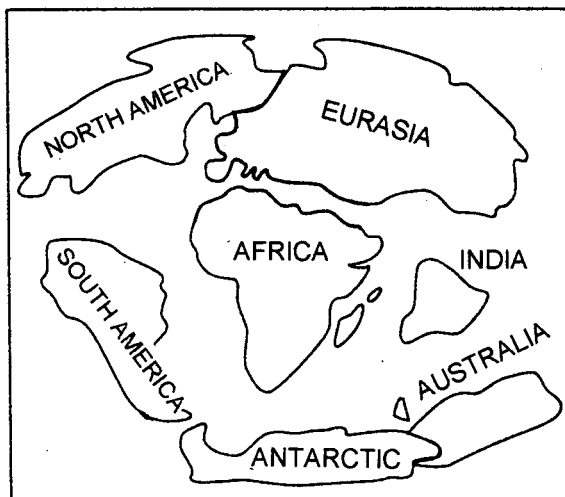
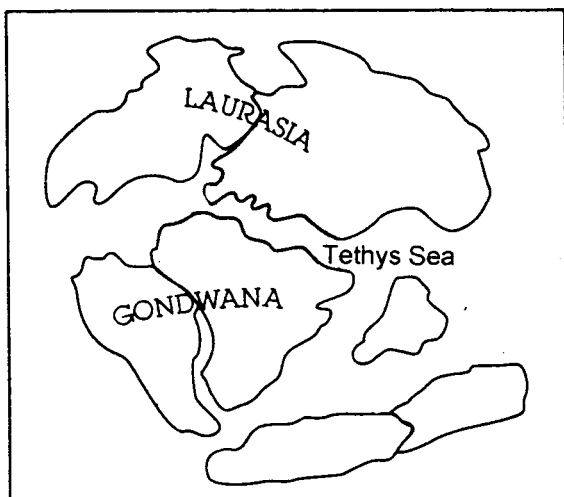
Tetrablemmidae	Tropics
Archaeidae: Archaeinae	Ethiopian and Australian Regions
Deinopidae	Tropics
Tetragnathidae: Diphyinae	Tropics and Southern Hemisphere
Cyatholipidae	Ethiopian ?Oriental and Australian Regions, the Southern Hemisphere
Synotaxidae	Americas and Australian Region, mainly the Southern Hemisphere
Thomisidae: Stephanopinae	Tropics
Salticidae: Cocalodinae	Tropics and Southern Hemisphere

To summarize: The relationships of the Baltic amber spider fauna in these higher taxa is closer to the Australian and the Ethiopian Regions than to the Oriental Region; there are only few certain relationships to the Americas

What is the explanation for the totally different distribution of spiders if we compare the Eocene European with today's distribution? What are the reasons for the disjunctions nowadays?

The distribution of many Baltic amber taxa is restricted to the Southern Hemisphere, mainly Australia (including New Zealand) and South Africa (including Madagascar). This fact is not new for authors of the "Old World" - see below - but is occasionally ignored by some authors of the "New World" who may be restricted to their language or on American publications. GRISWOLD (1987) wrote regarding the spider family Cyatholipidae: "... representing former parts of the Gondwanaland"; see the paper on the Cyatholipidae in this volumes.

I do not want to exclude the Gondwanan origin of families as Archaeidae, Cyatholipidae and Synotaxidae but the records of the Early Tertiary fossils in Baltic amber does not give proof for such an origin, and the absence of the Archaeinae in South America does not indicate a Gondwanan origin of this subfamily. Surely the extant + fossil ranges of these taxa are much wider than the extant ranges. Both subfamilies of the Archaeidae s. l. - Archaeinae (absent in South America) and Mecysmaucheniinae (absent in Africa) - occur together only in the Australian Region. Hence the origin of the Archaeidae may have been in the Australian Region probably during the Lower Cretaceous. A dispersal of the Archaeidae to Euramerica occurred probably during the Cretaceous, and an extinction in North America - or both Americas - happened probably during the Early or Middle Tertiary. - According to ES-KOV & GOLOVATCH (1986: 282) "The proposed mechanism imply: (1) the gradual reduction of a pancontinental to a bipolar ... range, (2) a 'Gondwanan' distribution due to the disappearance of the northern 'semicircle'." - See the worldwide distribution of the family Prosopistomatidae (Ephemeroptera), STANICZEK & BECHLY (2002).



Position of the continents at the beginning (130 million years ago, left side) and the end (65 million years ago) of the Cretaceous Period. Only about 10 million years later was the origin of the "Eocene European amber forests" incl. the Baltic amber forest. - Taken from UB, 139 (1988), modified.

Distribution and probable areas of origin of some (sub)families

The case of the sister groups Linyphiidae and Pimoidae is quite different from the families which are treated above. Linyphiidae has a cosmopolitan distribution and is mainly distributed in moderate climates of the Northern Hemisphere, the archaic Pimoidae is restricted to the Northern Hemisphere and has a holarctic distribution. Members of both families are known from Baltic amber but not (yet?) from Cretaceous deposits. Nearly all of the taxa of the Linyphiidae in Baltic amber are "archaic" genera of the subfamily Linyphiidae. These facts indicate an origin of these families in the Northern Hemisphere. (One has to keep in mind that Early Tertiary fossils of these families of the Southern Hemisphere are completely unknown!).

Remark: The following (sub)families of the infraorder Araneomorpha are known only from the Northern Hemisphere (reports in Baltic amber are undelined, * = extinct taxa): Hypocheilidae, Dysderidae, Harpacteinae and Rhodinae, Plectreuridae s. l.: Diguetinae and Plectreurinae, Leptonetidae, Archoleptonetinae and Leptonetinae, *Spatiatoridae, Oecobiidae, *Lebanoeobiinae and *Mizaliinae, Zygiellidae:

Zygiellinae, Araneidae: *Miraraneinae, *Juraraneidae, Anapidae: Comarominae and Synaphrinae, *Baltsuccinidae, *Protheridiidae, Pimoidae, Zoropsidae s. l.: Zoropsinae, Titanoecidae, Dictynidae s. l.: Cryphoecinae and Mizagallinae, *Insecutoridae, Trechaleidae: *Eotrechaleinae, Zodariidae s. l.: Homalonychinae, *Ephal-matoridae, Borboropactidae: ?Borboropactinae and *Succiniraptorinae, Zoridae.

Hypochilidae, Titanoecidae and Zoridae are the only extant families in this list which are unknown from Baltic amber.

Known from the New World are only the following taxa (the underlined taxa are restricted to North America): Digueatinae, Archoleptonetinae, Leptonetinae, Zygiellinae, Comarominae, Pimoidae, Cryphoecinae and Homalonychinae.

Borboropactidae and Zoridae are the only members of the classical Dionycha in the list. Besides the Linyphiidae and Pimoidae (see above) several (sub)families may have been originated in the Northern Hemisphere, e.g. Harpacteinae, Rhodinae, Plectreuridae, Leptonetidae, Comarominae, Zoropsinae (all its subfamilies?), Titanoecidae, Homalonychinae and Zoridae.

(c) The Bitterfeld (= Saxonian) amber and its spider fauna

According to the erroneous conclusions of BARTHEL & HETZER (1982) and various papers of KRUMBIEGEL the age of the amber from the Bitterfeld deposit is about 22 million years (Miocene), less than half the age of the Samlandic amber. Various authors doubted the young age of the Bitterfeld amber - see e.g. WEITSCHAT (1997), WUNDERLICH (1982) - and regard(ed) both of about the same age. Faunas and floras of both kinds of amber are very similar and have subtropical and tropical elements which would be absent in a fauna of a younger and colder Oligocene climate (see below).

Several authors found both faunas very similar or even identical, but other authors noticed differences, too: E.g. PERKOVSKY (pers. commun.) found differences in the faunas of the Formicidae, KOTEJA (pers. commun.) found the 3 specimens of *Matsucoccus saxonicus* KOTEJA (Coccina) only in Bitterfeld amber although he studied much more material of the Coccina in the Samlandic amber. ARNOLD (1998) found significant differences in the composition of pollen grains between Bitterfeld and Samlandic amber.

Remark: Occasionally amber from Bitterfeld and the Samland (Kaliningrad) is mixed in the collections of dealers. Furthermore: After the end of the former DDR some amber material from Bitterfeld was transported to Russia (HOFFEINS & HOFFEINS, pers. commun.) and some inclusions may have come back to Germany as "Samlandic amber". Most of the material which was studied by me is kept in the Palaeontological Museum of the Humboldt University or comes from private collectors who collected themselves at Bitterfeld or got material directly from this

locality, e.g. H. GRABENHORST, C. GRÖHN, H. KRÜMMER, M. KUTSCHER, W. LUDWIG, A. & O. PAULSEN and M. SCHIPPLICK.

The fossil spider fauna

(a) Taxa which are common to Samlandic deposits and the Bitterfeld deposit: I investigated the spider faunas of Bitterfeld amber and Samlandic amber and found identical genera, families and subfamilies, inclusively the tropical Tetrablemmidae, Deinopidae and Salticidae: Cocalodinae. The frequency of the investigated genera and the two most frequent (subdominant to dominant) species (*Orchestina breviembolus* and *Acrometa cristata*) are identical.

From the Bitterfeld amber I studied e.g. more than 250♂ from my private collection (CJW) and about 100 specimens (35♂) from the collection M. SCHIPPLICK (CMS) in Braunschweig and numerous males from other collections. Members of the genus *Orchestina* SIMON (Oonopidae) and *Acrometa* PETRUNKEVITCH (Synotaxidae) are most frequent in Baltic amber. I found 20/30% of the males and 7.6% of the specimens of the CMS being members of *Orchestina*. This is similar to finds in collections of the Samlandic amber. 10% of the males are members of *Acrometa* PETRUNKEVITCH (Synotaxidae) in the CJW but only about 2% in the CMS. Furthermore present in the CMS are: 4% Salticidae, 2% Linyphiidae and Theridiidae, 1.6% Archaeidae and Dictynidae: Hahniinae.

Selected common species:

Oonopidae: *Orchestina baltica* PETRUNKEVITCH 1942, *breviembolus* WUNDERLICH 1983, *cochlembolus* WUNDERLICH 1983, *crassimbolus* 1983, *forceps* WUNDERLICH 1983 and *furcata* WUNDERLICH 1983;

Archaeidae: *Archaea paradoxa* KOCH & BERENDT 1854, *Eoarchaea hyperoptica* (MENGE in KOCH & BERENDT 1854);

Anapidae: Anapinae: *Balticoroma serafinorum* n. gen. n. sp., *Flagellapis voigti* n. gen. n. sp.;

Anapidae: Mysmeninae: *Mysmena groehni* n. sp.;

Synotaxidae: *Acrometa cristata* PETRUNKEVITCH 1942;

Zoropsidae s. l.: Eomatachiini: *Eomatachia latifrons* PETRUNKEVITCH 1942;

Dictynidae s. l.: Hahniinae: *Eohahnia succini* PETRUNKEVITCH 1958;

Liocranidae: *Apostenus spinimanus* (KOCH & BERENDT 1854);

Corinnidae: *Ablator triguttatus* (KOCH & BERENDT 1854), *Protoorthobula deele-manni* n. gen. n. sp.;

Salticidae: *Gorgopsina frenata* (KOCH & BERENDT 1854).

Remark: Numerous species of fossil spiders are known from a single specimen only, hence the percentage of species which is common to both kinds of ambers/faunas will increase when more material has been studied.

(b) Differences in the fossil resins/faunas - indications to an independent "Bitterfeld amber forest"?

See the papers in this volume e.g. on the families Telemidae - ?*Telema moritzi* n. sp. is more frequent in the Bitterfeld deposit than in the Samlandic deposits although I studied twenty times more spiders of Kaliningrad material -, Archaeidae, Theridiosomatidae, Anapidae, Synotaxidae, Cyatholipidae, Zoropsidae and Salticidae. Members of the *Spinilipus kerneggeri*-group (Cyatholipidae) - 2 species, 18 specimens - are not known from the Bitterfeld deposit; in contrast to that: more than 50% of 20 males of the *Spinilipus bispinosus*-group come from the Bitterfeld deposit. One species (*S. curvatus*) is only known from the Bitterfeld deposit.

Remarkable is the composition of the species of the genus *Balticoroma* n. gen. (Anapidae): The most "plesiomorphic" species - *gracilipes* n. sp. - comes from the Bitterfeld deposit, the remaining - derived - species are preserved in the Samlandic ambers, too; see the paper on the family Anapidae in this volume.

There is a high number of spider species which are only known from the Bitterfeld deposit (**BiD**) or from Samlandic Baltic amber deposits, e.g., Kaliningrad (Königsberg) -, which are here summarized as **SD**. I focus here on the spiders in BiD: Is there an indication for the existence of "true BiD-species" or are these species accidental findings caused by the small number of specimens? - In my opinion there is no way to verify the hypothesis of the existence of "true BiD-species" - we have to wait for more and more material from the SD to probably falsify this hypothesis. Or - quite another procedure - Thus I will provisionally assume that there are no "BiD species", see below (statistics). *If this hypothesis is in contrast to the findings in fossil spiders there might really exist "true BiD-species" (!).*

Remarks: (1) The species-specific and free observable male spider genitalia allow a comparison of spiders from Bitterfeld and Samlandic deposits on species level. (2) In the following I will concentrate on such species as are known from two or more specimens from the BiD but not known from the SD. (3) For statistic handling I will concentrate on my private investigations: From the SD I studied - mostly adult males - of about 80 000 specimens, from the BiD about 4 000 specimens - mostly males, too -, altogether about 400 species. That means that only 1/20 of the specimens comes from the BiD.

Findings: From the BiD I have got four species which I know from two specimens each (of the families Archaeidae (see figs. 1-2), Anapidae and Salticidae (see figs. 3-5)), and one species which I know from three specimens (of the family Zoropsidae s. l.). See the addendum!

Reflections on statistics: If I find the same species in two specimens solely in the BiD and suppose this species not to be a "true BiD-species" - the hypothesis which is founded above - there should be found about 20 times more specimens of this species in the collections from SD (see above), that means 40. Let us go on with the help of an experiment in our mind: We use a collection of two kinds of marbles (red and blue ones) in a pot and pick up the marbles one after the other by chance.

The chance to get two red marbles (BiD specimens) from the sum of 42 *before* getting one of the 40 blue marbles (SD specimens) is 1: 861 (i. e. $1/41 \times 2/42$) (probability calculus). The chance to get three of the red marbles before getting one of the blue marbles is nearly 1/40 000 (!) (i. e. $1/61 \times 2/62 \times 3/63 = 1/39\,711$).

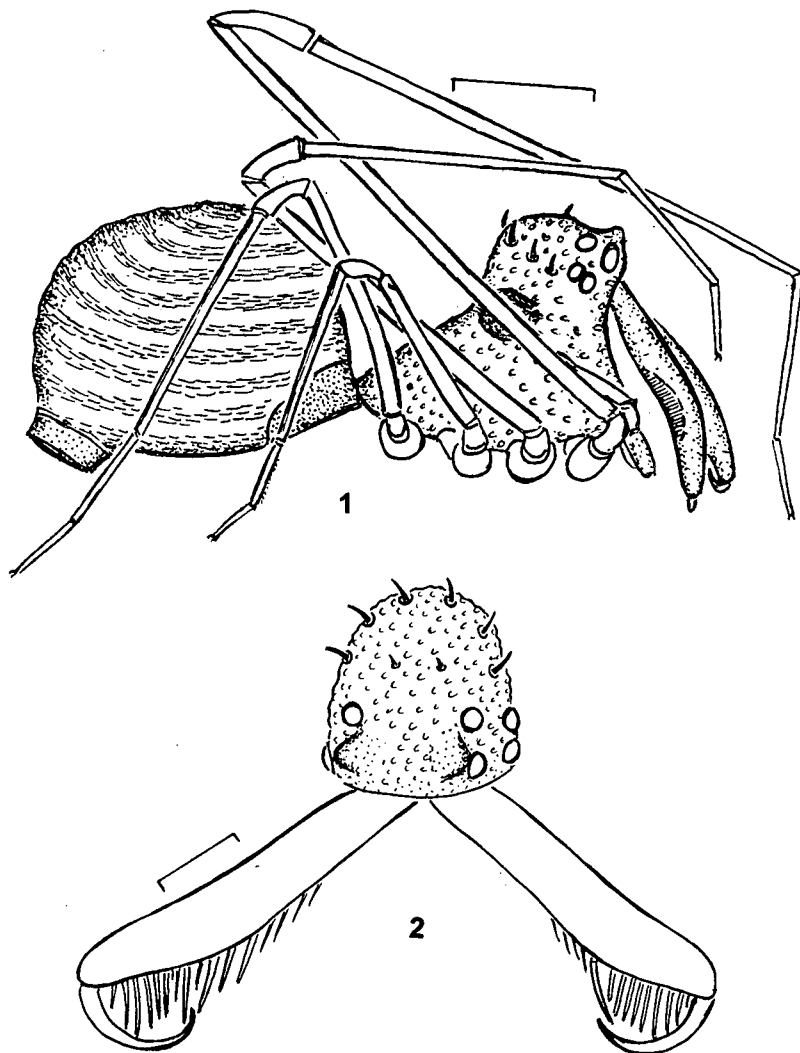
Conclusions: Within the about 400 spider species in Baltic amber (BiD + SD) which were studied closely by me there should - theoretically - exist less than one species (400/861) in two specimens which originate from the Bitterfeld deposit exclusively. Most likely not a single species (1/39 711) with three species should be found. *Actually* I found four "BiD-species" with two specimens each and two species with three specimens, see above ("findings" and the addendum). *The findings are in contrast to the hypothesis "absence of BiD species"*. Therefore - with reference to qualitative differences in the fossil spider faunas - there is indication to the existence of a partly particular Bitterfeld amber fauna and an independent "Bitterfeld amber forest". The true "BiD species" are likely to be endemics of the Tertiary Bitterfeld amber forest as probably is the species of the Coccina, *Matsucoccus saxonicus*, see above.

Arguments against these conclusions: (1) Probably the small to tiny spiders - which are treated in this study - were more carefully studied and more rarely overlooked in the amber from Bitterfeld than tiny spiders in Samlandic ambers, and therefore the statistic may be incorrect. (2) When I investigated the spider fauna of the tiny island "Pfaueninsel" in Berlin (size only 2/3 square kilometers) I found - among about 300 species and more than 100 000 specimens - two species which were new to science. Were/are these species to regard as endemics? Certainly not: In the meantime - nearly 40 years later - one of these species was discovered near Berlin and in Hungary, the other species has been found at several localities in Germany. Specimens of both species - compared with their relatives - are rare and live in particular habitats.

Final speculations: The number of known endemic spider species of the Bitterfeld amber forest should increase during further studies of spiders of the Bitterfeld deposit, probably to far more than 20 of several hundred - or even few thousand - species (= few percent). For a comparison: 10% of the 73 known spider species of Lanzarote, Canary Islands, are endemics of this island, see WUNDERLICH (1992: 179). - The most simple explanation for the evolution of endemics is the (former) existence of an isolated Bitterfeld amber forest - as a separate island or peninsula? - at the margin or within the large Baltic amber forest *sensu lato* (the large Eocene European amber forests) for a longer geological period; see RÖSCHMANN (1997).

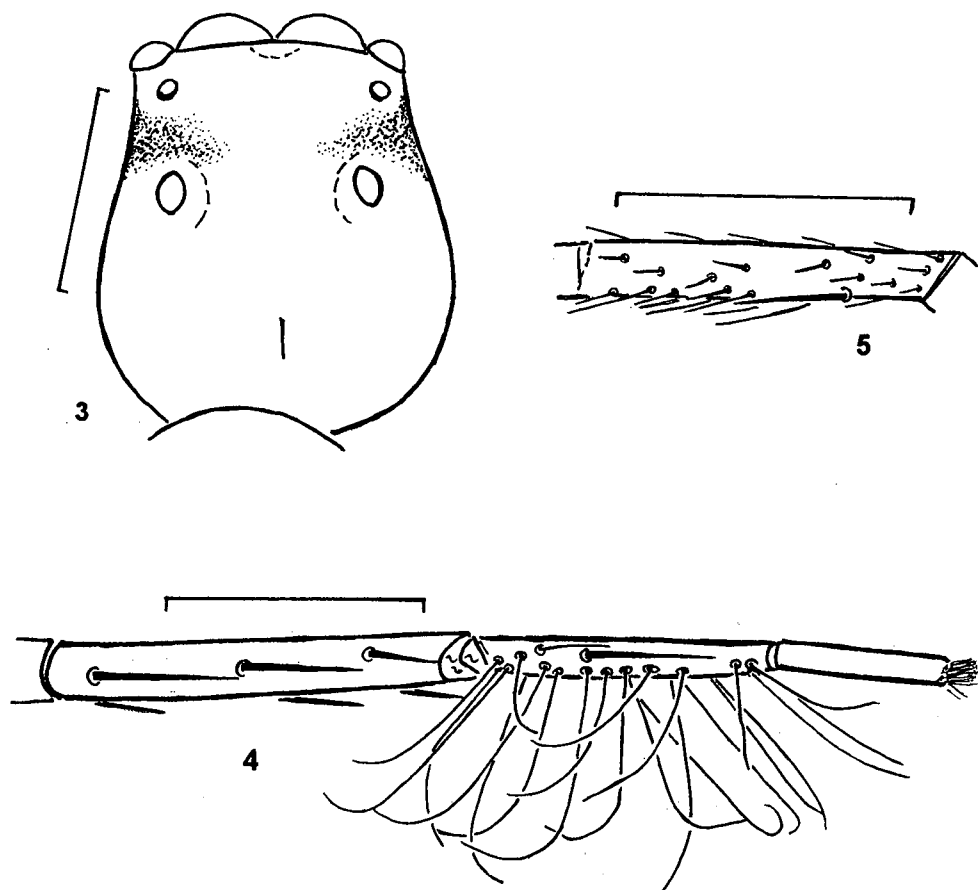
Addendum: Recently I got some more - seven - specimens of two species of the genus *Saxonarchaea* n. gen. (Archaeidae; see the paper on this family in this volume), three or four specimens of the first and all the three specimens of the second species are preserved in Bitterfeld amber, one or none specimen comes from the Samlandic amber (!). Thus probably *Saxonarchaea* may have been an endemic genus of the Bitterfeld amber forest.

Oonopidae: I saw several thousand specimens of this family in Baltic and Bitterfeld amber, probably twenty times more in Baltic amber than from Bitterfeld. Almost all of these spiders are members of the genus *Orchestina* SIMON; the only member of a different genus is the single male of the genus *Stenoonops* SIMON (the determination is not sure), and this male comes from the Bitterfeld deposit (!).



Figs. 1-5: Structures of two spider species (Araneae) which are preserved in Baltic amber and only found at the Bitterfeld deposit - two males each - and one relative.

Figs. 1-2: *Saxonarchaea dentata* n.gen.n.sp., ♂, family Archaeidae (Long-necked Spiders); 1) body, lateral view (the left legs are not drawn); 2) prosoma, frontal view (slightly from the left); note the spines on the prosoma and the paired humps between the anterior eyes which are absent in the frequent relative *Archaea paradoxa* KOCH & BERENDT 1854.



Figs. 3-5: *Almolinus* sp., ♂, family Salticidae (Jumping Spiders); 3) *Almolinus* sp., ♂, prosoma dorsally with the typical Salticid eye position; 4) *Almolinus bitterfedensis* n. sp., distal articles of the second left leg retroventrally (normal hairs are not drawn). Note the extremely long ventral sensory hairs of the metatarsus - unique in this species - in contrast to the normal hairs of the second metatarsus of a related *Almolinus* sp. which is shown in fig. 5). - M = 0.2 mm in fig. 2), 0.5 mm in the remaining figs.

PHYLOGENETICS (ABSTAMMUNG UND EVOLUTION)

See the paper on the superfamily Araneoidea in these volumes.

I focus on the taxa in Baltic amber and occasionally compare with Dominican amber.

Speciation, subspecies and "chronospecies" (Artwandel, Unterarten)

If the large Eocene European amber forests existed for 5 or 10 or even more million years, and in probably isolated areas - Bitterfeld, Ukraine -, too, there may well have been cases in which speciation can be traced in "fossilized lineages" as well as in subspecies of fossils. WUNDERLICH (1986: 53ff) described some questionable subspecies of the spider genus *Eopopino* PETRUNKEVITCH 1942 (Nesticidae) in Baltic amber and discussed questions regarding possible "chronospecies".

Extinct and extant taxa; rates of extinction (Ausgestorbene und heutige Gattungen; Aussterberaten)

There is no proof of the existence of a fossil species of the Early Tertiary which still exists today, although arthropod species may probably live for some million years; the apparently fossil fly in Baltic amber is a fake: a specimen of an extant species, see e.g. RÖSCHMANN (1997). According to SCHUMANN & WENDT (1989: 404) several "recent fossil forms" of Baltic amber insects are conspecific with extants. These authors did not confirm this opinion by studies of their own. According to my own investigations of male spider genitalia not a single species has survived up to now although there are several related species of nearly twenty genera like *Segestria* (Segestriidae), *Dipoena* (Theridiidae) and *Mastigusa* (Dictynidae s.l.).

The percentage of extinct taxa in Baltic and Dominican amber is as follows (see the lists in the chapter palaeodiversity):

Taxon category	Baltic amber	Dominican amber
species	100	100
genera	88	33
subfamilies	6*	0
families	10	0

* besides the extinct families.

Discussion: (1) In contrast to the Dominican amber exists a great percentage of extinct subfamilies and families exist in the Baltic amber.

(2) Striking is the similar proportion of both amber types (a) of the percentages of extinct genera - $88 : 33 = 2.7$ and (b) of their ages - ca. 50 million years of the Baltic amber and in ca. 22 million years of the Dominican amber = 2.3; there is a positive connection.

(3) The extinct spider families in Baltic amber are: Baltsuccinidae, Ephalmatoridae, Insecutoridae (probably not extinct), Praetheridiidae and Spatiatoridae. (Arthroditynidae PETRUNKEVITCH 1942 is not a family of its own, Inceptoridae PETRUNKEVITCH 1942 is a dubious taxon, see WUNDERLICH (1986: 24, 25)). - In comparison the number of extinct insect families in the Baltic amber is low; according to ANDER (1942: 57) only the Lepidotrichidae (Thysanura) (a synonym of the Lepismatidae?) and the Pelecinopteridae (Ichneumonoidea) are probably extinct; furthermore the Archipseudophasmatidae (Phasmatodea) and two families of the Strepsiptera are extinct: The Mengeidae and a new family which will be described by KINZELBACH & POHL. Thus the number of extinct families in the smaller group of spiders is about the same as in the huge class Insecta - what are the reasons for this disproportion?

The rate of extinction of genera in four superfamilies and one family:
(excl. the Theridiidae (Araneoidea) in Baltic amber)

	<u>Baltic amber</u>	<u>Dominican amber</u>
Dysderoidea.....	62% (8 of 13 genera)	23% (3 of 13 genera)
Eresoidea.....	100% (6 genera)	-- (absent)
Araneoidea s. l.	93% (56 of 60 genera)	23% (7 of 31)
Dictynoidea s. l.	94% (15 of 16 genera)	80% (4 of 5 genera)
Salticidae.....	100% (8 genera)	10% (3 of 31 genera)
sum	93 of 103 genera = 90%	17 of 80 genera = 21%

Results and discussion: (1) In both kinds of amber the rate of extinction is highest in the superfamily Dictynoidea s. l.. (2) For biogeographical reasons Eresoidea is absent in the Dominican amber. (3) The ratio of extinction of the Salticidae in the Baltic amber is ten times higher than in the Dominican amber. The reason: In Baltic amber only members of the "plesiomorphic" subfamily Cocalodinae are present. This subfamily has a mainly tropical distribution; it is extinct in Europe and most parts of the Northern Hemisphere, very rare in the Dominican amber. In contrast to this most Salticidae in Dominican amber are members of more derived taxa. (4) Within the Baltic amber fauna the more "plesiomorphic" superfamily Dysderoidea has the lowest rate of extinction. (One third of its genera has a cosmopolitical distribution).

Geologically "old" ("primitive", "archaic") and geologically "young" (derived) taxa (Geologisch alte und junge Gruppen)

See ANDER (1942: 38) as well as the chapters on "Evolutionary trends and missing links" and the addendum.

In the middle of the 20th century some authors hopefully thought that animal fossils from the Early Tertiary - which are only 10-15 million years younger than the end of the "age of the Dinosaurs" at the Cretaceous limit 65 million years ago - would give information about evolutional processes. According to BACHOFEN-ECHE (1949: 65) "This raised hopes that studies of the insects of that time would also give fundamental conclusions about their evolution. Such expectations were disappointed. The deeper the knowledge of the species was unfolded, the clearer it became that all the living orders and a considerable part of families had already been extant in the Early Tertiary, as far as their inclusion in amber was possible, that former primitive forms can be compared with mostly equivalent living families of today." Some fossils which are described in these volumes have made me reconsider the former opinion.

There is no doubt that there are higher spider taxa in the Tertiary Baltic amber fossils - even on the family level - which possess "primitive" (plesiomorphic) characters, see e.g. the papers on the Araneidae, Ephalmatoridae, Linyphiidae, Protheridiidae, Oecobioidea, Tetragnathidae, Trochanteriidae and Zoropsidae in these volumes. If we compare Early Tertiary Arthropoda and extant relatives we find distinct evolutionary changes/adaptations, e.g. in the family Paussidae (Coleoptera) and in

the new family of the insect order Strepsiptera; a description is prepared by KINZELBACH & POHL. Thus findings on organic inclusions in amber can be really helpful in the reconstruction of the process of the evolution, see below: evolutionary trends, the origin of myrmecomorphy, radiations and coevolutions, and the paper of GOLUB (2001) on the family Tingidae (Heteroptera).

The radiation/diversification of most Angiospermae and the co-evolution of numerous groups of flying insects - e.g. the bees, see ENGEL (2001: Fig. 121) - happened in the Lower Cretaceous period, 90-130 million years ago. Because of the kind of its prey - most members of the spider superfamily Araneoidea capture flying insects in higher strata of the vegetation - the main radiation of the Araneoidea happened also in the Lower Cretaceous, depending indirectly on the diversification of the Angiospermae. So it was not unlikely to discover geologically old spider taxa which probably originated in the Lower or Middle Cretaceous and became extinct - at least in the area of the Baltic amber forests - in the Early Tertiary during the coldness of the Oligocene. Such taxa are probably the rare members of the (sub)families Baltsuccinidae, Ephalmatoridae, Miraraneinae (Araneidae) and Protheridiidae. Were these strange spiders the last survivors of their families in the Tertiary period which lived only about 10 million years after the Cretaceous-Tertiary boundary event? According to my expectation members of these taxa will be discovered in Cretaceous ambers.

Ancestral higher - and extinct - insect taxa in Baltic amber are e.g.: Archipseudophasmatidae ZOMPRO 2001 (Phasmatodea), a new subfamily of the Hemiptera: Cicadellidae, recently reported by ZWEDO & GEBICKY (2002); a new family of the Strepsiptera whose description is in preparation by KINZELBACH & POHL.

Selected ancestral ("primitive"/"plesiomorphic") fossil higher spider taxa in the Eocene Baltic amber (see the chapters on various families in these volumes):

Scytodidae: In some inadult members of this family in Baltic amber the prosoma is flat but not domed as in extant taxa, see the paper on the Dysderoidea: Scytodidae in these volumes. Scytodidae possess two different functional parts of poison glands: The smaller part produces poison, the larger part a fluid for the production of threads; mainly the latter causes the domed prosoma of the extant - and most fossil - Scytodidae. The fossil spiders in question probably possessed the plesiomorphic low prosoma which was not yet provided with large silk-producing glands. They may well be members of an undescribed primitive subfamily; an adult fossil male is needed for closer studies.

Oecobioidea: Structures of the male pedipalpus, see below, "Evolutionary trends...". (The advanced taxa: See below, young taxa").

Tetragnathidae: Members of the "plesiomorphic" tropical subfamily Diphyinae are present in the Baltic amber; advanced members as Tetragnathinae - see below - in which femoral trichobothria are present, a cymbial outgrowth is absent (lost) and the strongly enlarged chelicerae bearing clasping teeth are absent.

Protheridiidae: See below ("missing links").

Linyphiidae: Mainly members of the "plesiomorphic" subfamily Linyphiinae are present in Baltic amber which usually possess an unfolded scapus of the epigyne. (The derived subfamily Erigoninae: See below, "young taxa").

Thomisidae: Only members of the ancestral tropic subfamily Stephanopinae are present in Baltic amber in which several cheliceral teeth and claw tufts are still present (plesiomorphic characters).

Salticidae: Only members of the ancestral ("plesiomorphic") and mainly tropical subfamily Cocalodinae are present in Baltic amber - in which a median apophysis of the bulbus and frequently a prosomal inclination are present, distinct sexual dimorph large chelicerae and large legs I of the males are absent -, but not a single one of the numerous extant higher taxa has yet been found.

Further ancestral taxa which were diverse in the Baltic amber forests but are relict taxa today are e.g. the Comarominae (Anapidae) and the Nephilinae (Araneidae).

To summarize: Most of the ancestral taxa of the Baltic amber forests are replaced by derived taxa, e.g., already in the Miocene Dominican amber forest and in Europe today.

Geologically "young"/derived taxa which were **absent** in the Baltic amber forests

Remarks: If there is no report of a taxon in Baltic amber it does not mean that this taxon did not exist at that time - there is basically no negative proof; this taxon may have existed somewhere else in the former world or has probably not yet been found in the Baltic amber, e.g. because of its large body size or rareness or special habitat. I know only two specimens of each of the families Baltsuccinidae, Oxyopidae and Borboropactidae, only one specimen of the Amaurobiinae, only very few questionable adult specimens of the Clubionidae, Gnaphosidae, Philodromidae and Thomisidae (juvenile Thomisidae are not so rare). - See the chapters above: "Palaeodiversity and Palaeogeography, Gaps in the faunas".

Findings: The following families/subfamilies are (still?) completely absent in the Baltic amber forest although most are known as extant from Europe and from the younger Dominican amber forest (except Erigoninae and Lycosidae): Oecobiidae: Oecobiinae, Linyphiidae: Erigoninae, Araneidae: Argiopinae and probably Araneinae, Tetragnathidae: Tetragnathinae, Lycosidae, Sparassidae (= Heteropodidae), Thomisidae: Dietinae, Salticidae: Lyssomaninae, Euophryinae s. l. and Salticinae s. l. as well as some questionable taxa, see below.

Discussion: Most Argiopinae, Tetragnathinae, Lycosidae and Sparassidae are large spiders which are difficult to capture in a resin and thus are absent in Baltic

amber. Lyssomaninae - absent in Europe today - has an "inner tropical" distribution. (But other tropical (sub)families - as the Deinopidae - are present in the Baltic amber).

Conclusion: The remaining taxa - Oecobiinae, Erigoninae, Dietinae, Thomisinae, Euophryinae, Salticinae and some of the questionable taxa - are good aeronauts (as well as juvenile Lycosidae, but probably not the Oecobiinae), they are frequent, have a cosmopolitical distribution and thus should have been found in Baltic amber at least as juveniles. Therefore I conclude that these taxa - and probably the Tetragnathinae, Lycosidae, Dictynini, Sparassidae and Philodromidae, too - may be geologically "young" taxa or did not yet have an expressive diversification at that time.

The following subfamilies are among others apparently the most advanced taxa of their family:

The Oecobiidae: Oecobiinae possess the most complicated/advanced structures of the male genital organs within their family, see the figures below.

The Tetragnathidae: Tetragnathinae are characterized by the following apomorphic characters: The presence of "clasping spurs" at the strongly enlarged chelicerae, secondary haplogyne female genitalia and the absence (loss) of a cymbial outgrowth besides the paracymbium. (Furthermore they have femoral trichobothria in common with their sister group, the Leucauginae, which may be a "young" taxon, too). Members of this subfamily are frequent, known from all continents and known as aeronauts.

The Linyphiidae: Erigoninae are characterized e.g. by their dwarfishness, the loss of most leg bristles, the presence of tibial apophyses of their male pedipalpi and their special - advanced - respiratory system. Today members of this family are very frequent, extremely good aeronauts and spread all over the world. The absence of endemic genera in Australia - which has been isolated for nearly the whole Tertiary - may be a further indication for the geologically late origin or diversification of this subfamily.

The Salticidae: Euophryinae and Salticinae, which are characterized by the complete absence (loss) of the median apophysis; see the paper on the family Salticidae in these volumes, the "chronocladogram" of the subfamilies.

Probable "young" taxa of insects: The oldest record of a calyptate fly - family Anthomyiidae - was recently reported from the Baltic amber, see MICHELSEN (2000). This is the only known member of the Calyptatae from the Baltic amber forest. Why are these flies so extremely rare in the Baltic amber? This is a mystery like the rareness of members of the spider subfamily Amaurobiinae in Baltic amber. Probably some calyptate families are in fact "young" taxa in a geological sense. MICHELSEN (2000: 12) writes on the derived taxa of the order Diptera: "One obvious explanation for the paucity of "higher" Diptera in Baltic amber could be that they are relatively young and thus happened to be poorly diversified by the beginning of the Cenozoic era."

Evolutionary "trends" (Evolutionäre "Trends")

In chapter "VI. Evolutionary trends in spiders" PETRUNKEVITCH (1942: 144-178) treated more general aspects than explicit examples of fossil spiders.

There are numerous changes in single and/or simple body structures of fossil arthropods in Baltic amber compared to extant taxa - see below -, but only few examples of distinct changes in body structures, behaviour and/or ecology are known to me; the example no. 1 is most spectacular, nos. 1 and 3-5 regard insects, the remaining spiders, nos. 6 and 13 are of interest in the phylogeny of families, 7, 8, 10, 12 and 13 (Nephilinae) are of interest in intrafamilial or intrasubfamilial changes, nos. 8 and 9 may be of interest in various families, no. 12 regards an intrageneric change within the Eocene European amber forests:

(1) In the beetle (Coleoptera: Carabidae) subfamily Paussinae (in German: Fühlerkäfer) - whose members live as "guests" in ant nests - especially the mouth parts and the antennae evolved within about 50 million years; see WASMAN (1929), WEITSCHAT & WICHARD (2002: 155, figs. g-h). BACHOFEN-ECHE (1949: 178) wrote (in German):

"Diese Ameisengäste haben im Bernstein, wo wir sie erstmalig finden, noch einen Mund, der zur Fütterung durch die Ameisen, aber nicht mehr zu selbständiger Nahrungsaufnahme geeignet ist. Derselbe hat seither eine vollständige Umgestaltung erfahren und dient nunmehr zum Aussaugen von Ameisenlarven. Gleichzeitig haben sich die Fühler (sie scheiden ein Sekret aus; JW) vielfältig verändert und bieten den Ameisen durch bedeutende Vergrößerung der Fläche, welche zum Ablecken der Ausscheidungen frei liegt, eine wesentliche Erleichterung der Aufnahme dieses Genußmittels. Daneben haben sich ganz wesentliche Veränderungen des Körpers in vielen Richtungen ergeben. Alle freiliegenden Organe sind bedeutend widerstandsfähiger gegen Bisse der Ameisen geworden, die Beine können in entsprechende Vertiefungen der Körperoberfläche eingezogen werden, die Fühler sind außerordentlich zäh. Es ist ein einzigartiger Fall in der Insektenwelt, in der wir eine so vollständige Umgestaltung der Familie in geologisch kurzer und junger Zeit feststellen können."

Translation into English: "These guests of the ants still have in amber, where they have been found for the first time, a mouth, suitable for feeding through the ants but not for taking food on their own. The very same has been completely transformed since and now serves for sucking out the ant larvae. Simultaneously the antennae (which discharge some secretion; JW) have changed in various ways and through the expansion of the surface for licking off the secretion have enormously facilitated taking in of this luxury by the ants. Besides essential changes of the

body in various directions have occurred. All exposed organs have become much more resistant to ant-bites, the legs can be drawn up into particular hollows of the body surface, the antennae are extraordinarily tough. This is a unique case within the world of insects in which we can ascertain such a complete transformation of a family in a geologically short and young time."

(2) Extant members of the European spider genus Mastigusa MENGE 1854 (Dictynidae s. l.) are also known as guests in ant nests, see WUNDERLICH (1986) and the paper on the family Dictynidae s. l. in these volumes. Behavioural or morphological/anatomical adaptations to their mode of life are unknown with a single exception: The eyes of most extant spiders are reduced as in numerous spiders which live in ant nests - in contrast to all congeneric spiders in Baltic amber in which the eyes are large. Members of Mastigusa in Baltic amber are not too rare, and therefore - and corresponding with their large eyes - I suppose that these spiders most probably did not yet live in ant nests at the time of the Baltic amber forest.

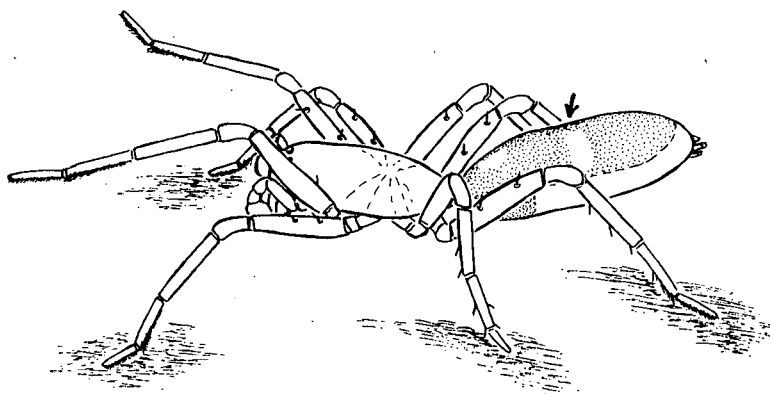
(3) In extant members of the insect order Strepsiptera (German name: Fächerflügler) - compared with genera which are preserved in Baltic amber - changes in the body structure and the behaviour occurred, see POHL & KINZELBACH (in prep.). The larvae of this order live as endoparasites in larvae of various orders of insects, only the short-living males are winged. According to LARSSON (1978: 112) the extinct Mengeidae differ in significant points from the other Strepsiptera and present in particular a series of primitive characteristics.

(4 and 5) Also the extinct taxa of insects in Baltic amber Pelecinopteridae (Ichneumonoidea) and Lepidothrix MENGE (family Lepidothrichidae but probably a synonym of the Lepismatidae) possess primitive features, see ANDER (1942: 38, 57) and LARSSON (1978: 115, 139).

(6) According to my hypothesis the members of the new spider family Protheridiidae in Baltic amber may possess plesiomorphic features; see below, "missing links".

(7) Modified densely hairy/spiny and frequently powerful anterior legs in numerous male Salticidae - a sexual dimorphism - are known from extant spiders and from fossils in Dominican amber, see Fig. 683 in the book of WUNDERLICH (1988) - but not from fossils in Baltic amber. In the Salticidae the modified anterior male legs are used during the mating behaviour (weaving), see the chapter on the courtship behaviour above. So the leg structure and the mating behaviour must have changed - evolved - from the Early Tertiary up to now. - In extant males of this family the pedipalps are frequently used in a similar way to the anterior legs. In the fossil Salticidae in Baltic amber I found only a single species (photo) in which the cymbium bears striking hairs and whose members probably used their pedipalps during the mating behaviour. - The only family in which Early Tertiary males are already known to possess strongly modified anterior legs in connection with the mating behaviour - thickened articles, clasping spurs and probably pheromone glands - is Anapidae, see the figure below and the paper on this family in these volumes.

(8) Myrmecomorphy (an ant-shaped body, ant-mimicry) occurs in various extant spider families, most expressive in the Corinnidae, Gnaphosidae and Salticidae and Zodariidae, but also e.g. in the Araneidae, Theridiidae, Linyphiidae and Thomisidae; see the chapter on myrmecomorphy above as well as below: The chapter on coevolution and WUNDERLICH (1995). The earliest cases of myrmecomorphy, representing Batesian mimicry, are described from spiders in Baltic amber, from the Zodariidae (photos) and the Corinnidae (photos, the figure below), see WUNDERLICH (2002). Remarkably ant-shaped members of the Salticidae are absent in this kind of amber, but are known from Mid Tertiary (Miocene) Dominican amber - see WUNDERLICH (1988) and are not rare in extant spiders. The diversification of ants probably happened in the Late Cretaceous or/and in the earliest time of the Tertiary. Did myrmecomorphy in Salticidae evolve later than in other families and only after the existence of the Baltic amber forests during the Upper Oligocene or even in the Miocene - or earlier in an area away from the Baltic amber forests?



Reconstruction of an ant-shaped (myrmecomorph) spider in Baltic amber, lateral aspect of the male of *Eomazax pulcher* PETRUNKEVITCH 1958, family Corinnidae, body length 3mm. The first pair of legs is shown in a hypothetically raised position as in numerous extant myrmecomorph spiders, imitating insects' antennae. Notice the slender shape of body and legs, the saddle-shaped constriction of the long opisthosoma (arrow), bands and patches of white opisthosomal hairs which are characteristic of numerous extant myrmecomorph spiders.

(9) Body size and sexual size dimorphism. We do not know the largest spiders of the Baltic amber forest because (most of) such spiders could escape from the sticky resin. Furthermore our knowledge about the probable existence of size dimorphism in fossil spider taxa is weak: Most fossil spider species - and even genera - are only known from one sex, usually the male; the genera *Orchestina* SIMON (Oonopidae), *Balticoroma* n. gen. (Anapidae) and *Acrometa* PETRUNKEVITCH 1942 (Synotaxidae) - which are occasionally preserved in both sexes - are three of the rare exceptions.

In some cases a distinct sexual size dimorphism - small or even dwarf males, mainly in reference to the prosoma and to members of the superfamily Araneoidea

- may be an "evolutionary strategy" to reduce the intra-specific competition: Members of both sexes capture prey of different classes of size. (Remark: Only in few spider taxa the male is usually larger than the female, e.g. in *Argyroneta* LATREILLE 1804 (Argyronetidae) and some species of *Centromerus* DAHL 1886 (Linyphiidae); relatively large male are known to me also from the genera *Linyphia* LATREILLE 1804 (Linyphiidae) and *Cheiracanthium* C. L. KOCH 1839 (Clubionidae)).

Within extant taxa of the superfamily Araneoidea a sexual size dimorphism is distinct e.g. in the family Araneidae but not e.g. in the related families Tetragnathidae and Zygellidae in which the male even may be larger than the female. Within the fossils in Baltic amber I can confirm this fact for the members of the family Zygellidae which I found in both sexes.

Regarding the body size of fossil members of a whole subfamily, 4 extant and 2 extinct genera of the Zygellidae: Zygellinae - see the paper on this family in these volumes - it became clear that the fossil Zygellinae in Baltic amber were distinctly smaller than their extant relatives of related genera: The body length of the fossil males is 3-4mm but the extant spiders are twice in size on average (except some specimens of a species of the Canary Islands which is very variable in its body size). Apparently there was a tendency to increase in length. The reason may have been the adaptation to larger prey - an example of co-evolution? See also below: The Urocteini. - Remark: I studied several hundred fossil Zygellinae in Baltic amber, but I never found a larger specimen although fossil spiders of more than 4mm of other genera are not too rare.

In various taxa of the family Araneidae probably both happened: Dwarfishness in males and gigantism in females. Unfortunately there is no proof from fossil spiders in Baltic amber: Dwarf fossil males are known, but no very large or even giant females; such females may have existed but were probably too large to be kept in the fossil resin.

Compared with all other known fossil and extant suprageneric taxa of the family Oecobiidae - see the paper on this family in these volumes - the members of the tribus Urocteini are the "giants" within the family. They are only known from extant spiders whereas all known fossil spiders of this family are small. Large - subadult and adult - Urocteini prefer beetles, Myriapods and large ants as prey (pers. observ. in the Mediterranean area), but the small spiders of the Oecobiini (which are strongly related) feed mainly on smaller ants. Apparently here we have a case of ecological separation between tribus which is connected with the body size.

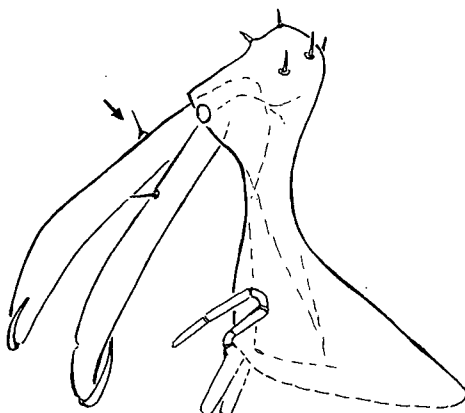
(10) Changes of the leg autotomy. In the Early Cretaceous subfamily Lebanoneocobiinae the patella-tibia leg autotomy - this kind of autotomy is plesiomorphic in this superfamily - was still present as it is in the extant Oecobiinae: Oecobiini, but in the strongly related extant Oecobiinae: Urocteini the autotomy has been lost. In the subfamily Mizaliinae of the Baltic amber forest a coxa-trochanter autotomy existed. See the papers on the superfamily Oecobioidea and on leg autotomy in these vol.

(11) Within extinct taxa (4 genera) and extant taxa (2 genera) of the subfamily Archaeinae a difference in the spination of the chelicerae in both sexes existed: In the extant taxa a bristle is present in an anterior position of the chelicerae (arrow in the fig. below), but in all the fossil and extinct taxa of the Baltic amber forest such a

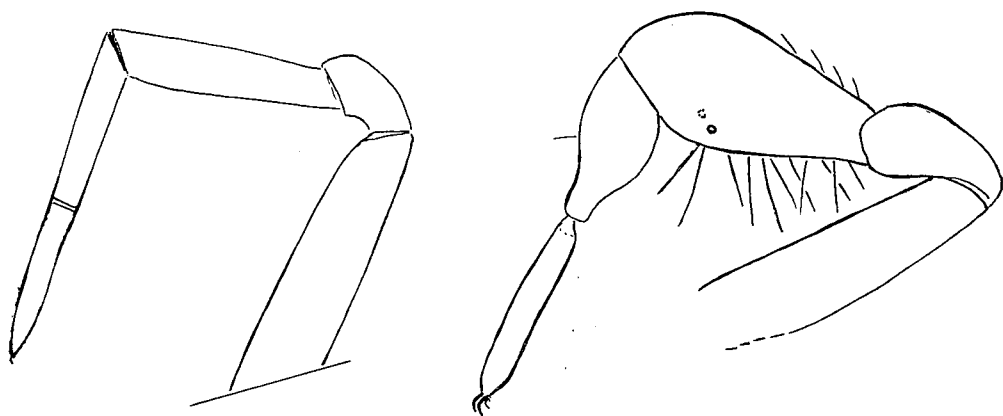
bristle is absent. Therefore the ancestor of the extant Archaeinae most probably evolved this bristle during the Tertiary.

Prosoma of an extant member of the family Archaeinae.

Note the cheliceral bristle (arrow) which was still absent in the spiders of the Baltic amber forest



(12) It may be possible to reconstruct the evolutionary way of the diversification within the genus *Balticoroma* n. gen. (Anapidae) based on the shape of the male anterior leg I - see the paper on the family Anapidae in these volumes -: In the most "plesiomorphic" *B. gracilipes* an unmodified/slender leg exists (see the fig. below), in the "advanced" species the male leg I is modified/thickened e.g. as in the right fig. below. (In contrast to the remaining species *B. gracilipes* occurred mainly in the Bitterfeld amber forest). A similar "tendency" occurs e.g. in the fossil genus *Balticonopsis* n. gen. and numerous extant genera of this family.

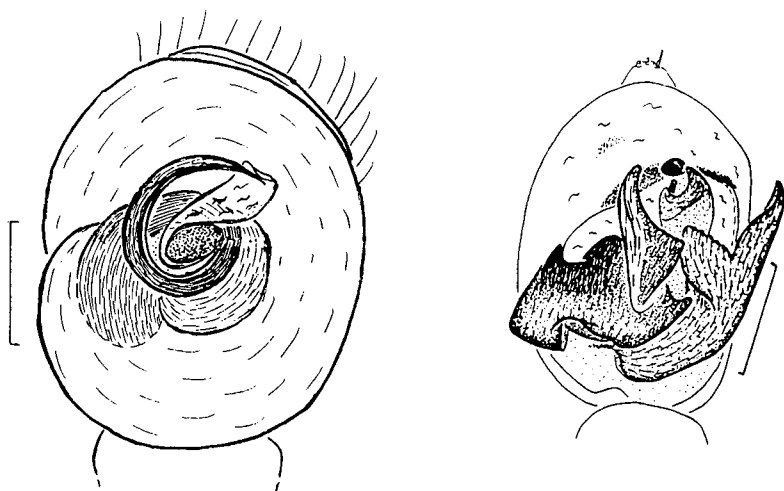


A modified and powerful anterior male leg I of the derived species *Balticoroma reschi* n. gen. n. sp. (Anapidae) in Baltic amber in which the metatarsus is distinctly shortened and the tarsus is distinctly lengthened (at the right side) - which is known from the Samland amber -, and a slender male leg I of the "plesiomorphic" *Balticoroma gracilipes* n. sp. in which metatarsus and tarsus are about equal in length, and which is mainly known from the Bitterfeld deposit

(13) Evolution of spider genitalia. In contrast to most parts of the female genitalia - the structures of the vulva - the (secondary) male genitalia of spiders are freely observable, and therefore I focus on these structures, with the exception of the family Linyphiidae: In all Linyphiidae of the Baltic amber forest - see the paper on this family in these volumes - a scapus of the epigyne is present and unfolded (stretched) which is a plesiomorphic feature in this family. In the extant derived Erigoninae - which are absent in the Baltic amber - such a scapus is usually absent/lost (tendency 1). In most extant Linyphiidae besides the Erigoninae - the Micronetinae - the scapus is folded (tendency 2), but in almost all of the fossil Linyphiidae in Baltic amber the scapus is still unfolded. Thus the diversification of the Micronetinae (and Erigoninae) most probably happened in the Middle Tertiary when the Baltic amber forests were gone, but the diversification of the Linyphiinae already took place in the Early Tertiary.

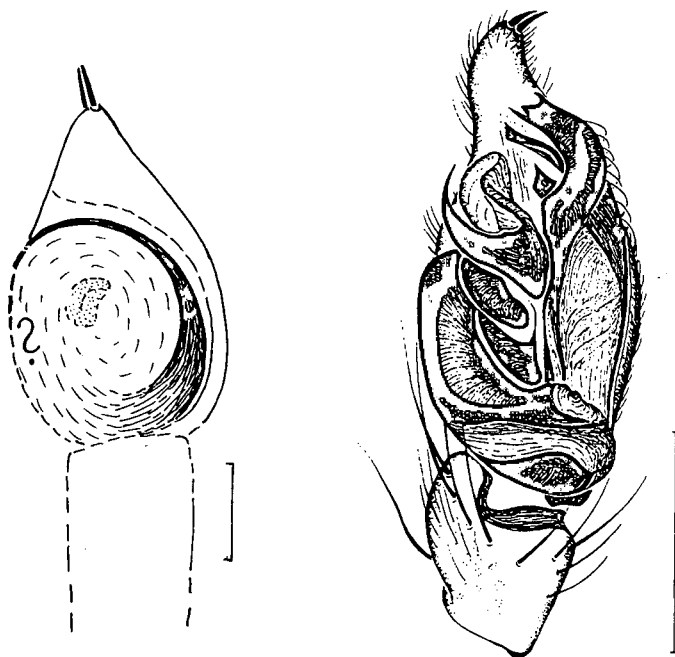
The secondary male genitalia - see also the papers on the taxa Eresoidea: Archaeeidae and Pimoidae in this volume -: In some fossil spiders of the Baltic amber forest the male genitalia are as complicated as in extant congeners, e.g. in the genera *Episinus* WALCKENAER 1809 (Theridiidae) and *Mastigusa* MENGE 1854 (Dictynidae s. l.); in *Mastigusa* the male has to carry its extremely large pedipalpus above its "back", the prosoma. In contrast to this feature in the fossil taxa of the Nephilinae (Araneidae) - see the paper on this family in these volumes - the bulbus structures are distinctly more complicated than in spiders of today: Here simplifications/reductions of these structures happened during the Tertiary, e.g. the median apophysis of the tegulum disappeared.

In other taxa - e.g. in the families Oecobiidae and Hersiliidae - complicated structures of the bulbus evolved from quite simple ones, see the figs. below. In these relatively "archaic" spiders - see the paper on the superfamily Oecobioidea in these volumes - several complicated tegular structures appeared during the Tertiary which may be even more complicated than in "advanced" taxa of the superfamily Araneoidea or of the retrolateral "tibial apophysis" (RTA) clade.



Simple and complicated male pedipalpi of fossil and today's (extant) members of the family Oecobiidae. Left: Ventral aspect of the simple bulbus of an extinct mem-

ber of the subfamily Mizaliinae, *Mizalia spirembolus* n. sp. of the Baltic amber forest; right: Ventral aspect of the complicated bulbus of an extant member of the subfamily Oecobiinae (tribus Oecobiini), *Oecobius aculeatus* WUNDERLICH 1987 from the Canary Islands. M = 0.2mm.



Simple and complicated male pedipalpi of fossil and today's (extant) members of the family Hersiliidae. Left: Ventral aspect of the simple bulbus of the extinct species *Gerdiopsis infrigens* n. gen. n. sp. of the Baltic amber forest; right: Ventral aspect of the complicated bulbus of an extant species, *Tamopsis hirsti* BAEHR & BAEHR 1998 from Australia, taken from BAEHR & BAEHR (1998). M = 0.2mm.

To summarize: Several Early Tertiary spider taxa - see nos. 7, 8, 11 and 13 - and insect taxa - see nos. 1 and 3 - show more primitive patterns of behaviour and structures than younger Tertiary fossil and extant relatives. The structures of the secondary male genital organs may be distinctly more complicated in today's spiders of the same family, e.g. in the Hersiliidae and in the Oecobiidae, although such cases are rare. Contrarily in taxa of the Araneidae: Nephilinae the reverse - a structural simplification during the Tertiary - is the case. In certain spider taxa - e.g. of the family Salticidae - a special mating behaviour and connected structures/ sexual dimorphism evolved most probably not before the Early Tertiary, after the Cretaceous/Tertiary boundary event; members of the Salticidae are unknown from the Cretaceous and a sexual dimorphism in the anterior leg is unknown in spiders from the Early Tertiary. Cheliceral stridulating organs - e.g. in the families Archaeidae and Linyphiidae - were already as well developed in the Early Tertiary as in extant relatives, see the papers on these families in these volumes.

"Missing links" ("Zwischenglieder" in der Evolution)

Recently SELDEN (2002) found a Miocene spider taxon being a "missing link" between an Eocene fossil taxon - both taxa are not preserved in amber - and the extant European water spider *Argyroneta aquatica* (CLERCK 1757) (family Argyronetidae). Remarkable is (e.g.) the different position of the tracheal spiracle of the taxa in question and its intermediate position. As a result of his investigations this author synonymized the monotypic family Argyronetidae with the Cybaeidae.

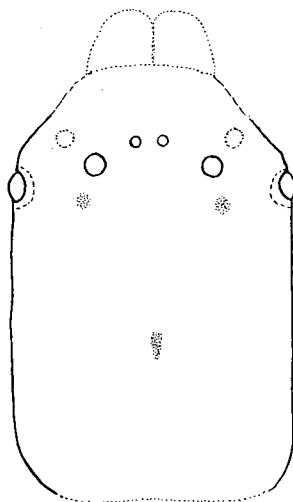
Plesiomorphic features - fossil "links" to derived extant structures and taxa - are present in certain Tertiary amber taxa. Besides a "missing link" of the family Segestriidae in Baltic amber - the description is in preparation - I choose here four examples from spiders in Baltic and Dominican amber (see the papers on these families in these volumes):

(1) Members of the new family Protheridiidae (superfamily Araneoidea) may be somewhat like "missing links" between the derived "spineless femur clade" and the "archaic" "coxa-trochanter autotomy clade", in which numerous leg bristles are present, including femoral bristles, which are absent in the Theridiidae and its relatives; see the paper on the superfamily Araneoidea.

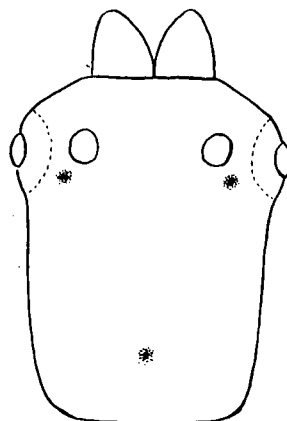
(2) In most fossil taxa of the family Trochanteriidae a short trochanter is still present in contrast to most extant members of this family.

(3) Family Uloboridae: In the pantropical extant genus *Miagrammopes* O. PICKARD-CAMBRIDGE 1869 - which is also known from Dominican amber - the eyes of the anterior row have been completely lost (see the fig. below). In the related fossil genus *Eomiagrammopes* n. gen. in Baltic amber the eyes of the anterior row are strongly reduced but still present (fig. below). Thus *Eomiagrammopes* may be a fossil "link" in this structure - or at least a model of it - between an unknown extinct taxon and the extant genus *Miagrammopes*.

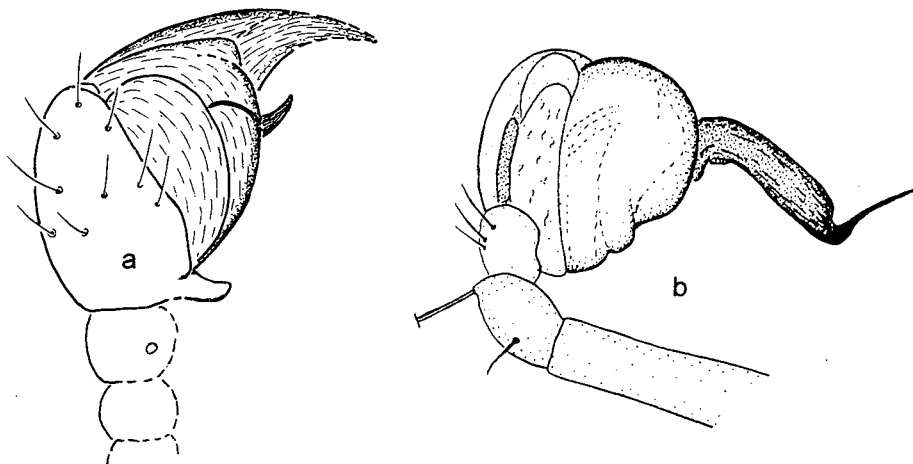
Prosoma of the fossil species *Eomiagrammopes singularis* n. gen. n. sp. (♂) in Baltic amber, dorsal aspect of the prosoma. Note the reduced eyes of the anterior row and compare the following figure.



Prosoma of the fossil species *Mia-grammopes dominicanus* n. sp., ♂ in Dominican amber, dorsal aspect of the prosoma. Note the complete absence of the eyes of the anterior row.



(4) In fossil males of the subfamily Nephilinae (Araneidae) a well developed - plesiomorphic - median apophysis is present (fig. below) in contrast to all fossil taxa in Dominican amber (fig. below) and all extant taxa (fig. below) in which this apophysis has been lost. The loss apparently happened during the era between the Eocene (Baltic amber) and the Miocene (Dominican amber). According to my hypothesis the presence of such an apophysis - besides other characters - in the fossil taxa indicates the membership of the Nephilinae in the Araneidae and not in the Tetragnathidae, see the paper on the family Araneidae in these volumes.

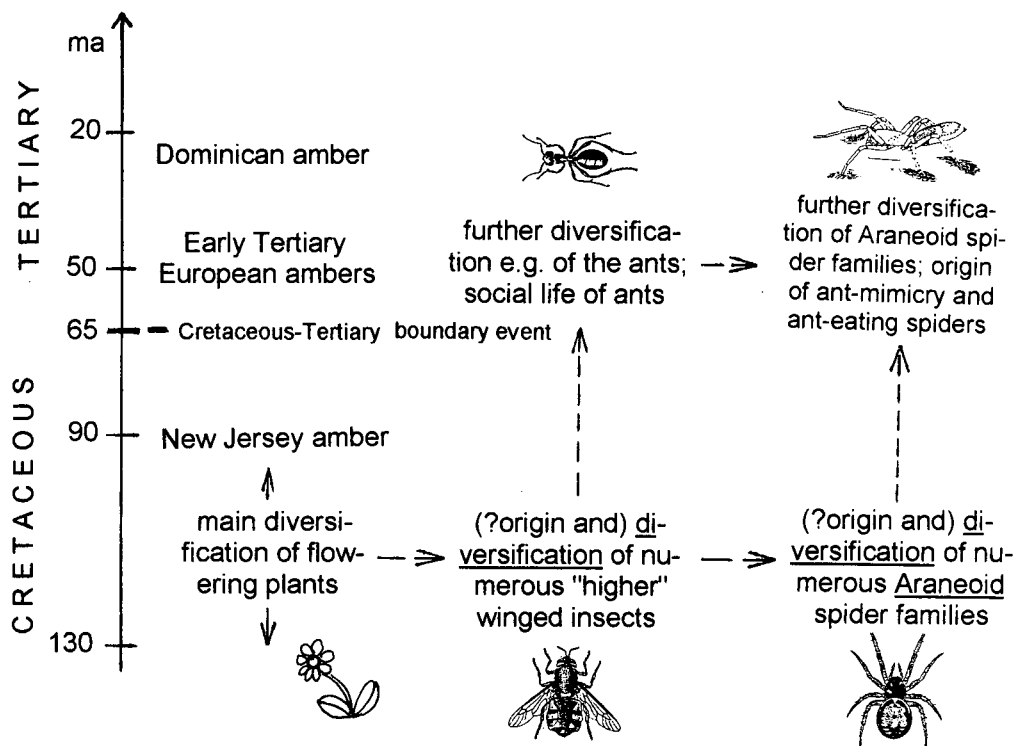


Male right pedipalpus of fossil and extant members of the subfamily Nephilinae (Araneidae): (a) *Eonephila longembolus* n. gen. n. sp. in Baltic amber (M = median apophysis), (b) *Nephila dommeli* WUNDERLICH 1982 in Dominican amber, (c) *Nephila clavipes* (LINNAEUS 1767), extant, neotropical.

Radiations/diversifications and coevolutions (Evolutionäre "Vervielfältigungen" von Gruppen und Wechselwirkungen von Gruppen während der Evolution)

Radiations/diversifications in spiders and other Arthropoda happened in various geological periods. Our knowledge on the dating of such events as the origin or radiations of spider families is weak, see PENNEY & SELDEN (2002) (I doubt the earliest records of the families Tetragnathidae and Linyphiidae by these authors, see the papers on these families in these volumes), as well as the papers on the Araneoidea, Oecobioidea and Salticidae in these volumes, in which I give chronocladograms, too.

Depending on our knowledge of today three periods are of special interest in this matter: (a) the Cretaceous amber from New Jersey, USA, (b) the Early Tertiary European ambers (mainly the Samlandic - Baltic) amber - and (c) the Miocene Dominican amber, see the fig. below. (In the future the study of the Early Cretaceous Mediterranean ambers - e.g from the Lebanon, Spain and France - will be of great interest because their origin falls in the early time of the Angiosperm diversification, 120-130 million years ago! Only few inclusions have been studied of this kind(s) of amber).



Geological eras, the age of three kinds of amber and the probably main diversifications of flowering plants, "higher" winged insects as well as spiders of the superfamily Araneoidea (Orb-web spiders and their relatives) which are most frequent in Tertiary ambers. Ants played an important role in the evolution/diversification of Tertiary spiders.

(a) According to ENGEL (2001: 153) bees originated about 125 million years ago and their main diversification (radiation) took place in the Cretaceous Period between 90 and 130 million years ago during the "dramatic increase in angiosperm diversity". Within this period a coevolution of several winged insect groups happened, too, which - as various bees and ants - were connected with angiosperms. Most probably also the ants originated in this period, but probably did not yet evolve a social behaviour and a strong diversification, as only very few records from the Cretaceous period indicate.

First of all the members of the superfamily Araneoidea - the Orb weavers and their relatives - profited in the second half of the Cretaceous Period from the diversification of flying insects, mainly Diptera, Coleoptera and Hymenoptera, see ESKOV & WUNDERLICH (1995: Figs. 8-9). Thus the spiders' evolution/diversification indirectly depended on the angiosperm diversification. According to the fossil records and to my hypothesis the main radiation of the superfamily Araneoidea - and probably even their origin - happened in the second half of the Cretaceous and the main diversification in the Early Tertiary, (similar, e.g., to the Corinnidae, Salticidae and Zodariidae), depending on the geologically late diversification. Other taxa - as the extinct Protheridiidae, Baltsuccinidae and Ephalmatoridae which were rare in the Baltic amber forest - may have been frequent in the Cretaceous, but became extinct during the Early/Middle Tertiary.

(b) Probably a global warming at the Early Tertiary, at the end of the Palaeocene, caused the appearance - and the spreading - of (e.g.) the Gramineae and some orders of mammals as the Artiodactyla (in German: Paarhufer) - the most diverse order of mammals - and the Primates (in German: Herrentiere, Affen) in this period. That means that the diversification of these groups happened in a geologically young era; see the chapters above, e.g. about geologically "young" and "old" taxa. According to my hypothesis only after the Cretaceous-Tertiary event and during the warm Eocene most families of the Araneoidea diversified strongly, as did the Dictynidae s. l., Corinnidae, Zodariidae and others which were already diverse in the Baltic amber forests. The diverse Salticidae is of special interest because only one - the most "ancestral" subfamily Cocalodinae - was present in the Early Tertiary European amber forests, but all subfamilies were already present in the Miocene Dominican amber forest. Thus apparently the radiation/diversification of the Cocalodinae took place in the Early Eocene, but the diversification of the remaining subfamilies - as well as the origin of some subfamilies? - happened later, probably during the Oligocene and Miocene. - Similar to the Salticidae in the families Oecobiidae, Araneidae and Linyphiidae the "ancestral" taxa were present in the Baltic amber forest - and derived taxa were absent - but the advanced taxa were present and frequent in the Dominican amber forest while "ancestral/plesiomorphic" taxa were absent or rare. - We do not yet know the effect of the C-T event on the late Cretaceous spider fauna, but if more "ancestral" families were pushed back - according to my hypothesis - the members of more derived families as Theridiidae, Linyphiidae, Zodariidae, Corinnidae and Salticidae could diversify - as did the Gramineae, Artiodactyla and Primates. The era of diversification in the Early Tertiary of the Cocalodinae (in German: Ur-Springspinnen, family Salticidae, Jumping Spiders) may have been nearly the same as of the suborder Prosimii (in German: Halbaffen) (Primates).

(c) In the Young Tertiary (Miocene) Dominican amber we find several fossil higher spider taxa which are absent in the Early Tertiary Baltic amber fauna (see above: "gaps of the Baltic amber fauna"), e.g. Oecobiinae: Oecobiini (Oecobiidae), Tetragnathinae and probably Leucauginae (Tetragnathidae), probably Lycosidae, Trachelinae (Corinnidae), Sparianthinae (Sparassidae), Selenopidae, probably Thomisinae (Thomisidae) as well as the Lyssomaninae, Euophryinae and Salticinae (Salticidae). So in this respect the Dominican amber fauna is something like a "stepping stone" between the Baltic amber fauna and the extant fauna and may indicate geologically "young" taxa.

Coevolution

I focus on one important family of insects, the ants (Formicidae). Members of this family are rare in Cretaceous ambers - see the page before, HÖLDOBLER & WILSON (1990: 23) - but very frequent, diverse and social living in the Eocene European ambers forests. According to my hypothesis this family diversified at the same - geologically late - time (Palaeocene/Eocene) as several families of the Araneioidea (the Orb weavers and their relatives) as well as certain other spider families. Already in the Early Tertiary ants belonged to the most frequent Arthropods in various biotopes (except in water); their enormous biomass surely was to spiders "a grist to their mill" (in German: "Ein gefundenes Fressen"). The frequency of ants in the Baltic ambers - as their frequency today - indicates an important ecological role of this family. Ants may hunt spiders and some spiders hunt ants.

Several higher spider taxa show intensive connections to ants: (a) The main prey of members of the Oecobiidae: Oecobiini, of members of the whole family Zodariidae and of various genera, e.g., of the Theridiidae, Corinnidae, Gnaphosidae, Thomisidae and Salticidae are ants. (b) Myrmecomorphy (ant mimicry) is known from numerous extant spider taxa as well as from fossil Salticidae in Dominican amber, and from Corinnidae and Zodariidae in Baltic amber. Thus - mainly the wingless walking - ants had an important role of "setting course" (in German: "Weichenstellung") in the evolution of numerous taxa of spiders from the Early Tertiary up to now.

(a) Ant- hunting spiders. Hunting ants may be dangerous to spiders, see below - mimicry - but numerous spiders were perfect in hunting this kind of prey already in the Early Tertiary: Ants are by far the most frequent spiders' prey which is preserved in Baltic amber, more than 90% of spiders' prey - held by threads of capture webs or spun in - see the photos - are ants. Members of (1) the Oecobiidae: Oecobiinae evolved (a) a special web which is a protection for ants, and (b) a special encircling behaviour of fixing the ants. Such members - of the genus *Oecobius* LUCAS 1846 are preserved in Dominican amber. From Baltic amber the genus *Mizalia* KOCH & BERENDT 1854 (subfamily Mizaliinae) is known whose prey is unknown; see the paper on the Oecobiidae in these volumes. (2) Certain Combfooted spiders (Theridiidae) evolved special tangled threads; with their help ants are lifted and thus they hang freely below a platform from where the spider can bite the ant. (3) Also known from Baltic amber - diverse and not rare - are members of the family Zodariidae, at least members of the advanced subfamilies

feed on ants and are the most frequent ant hunters, see the paper on this family and the photos. Injured members of the Zodariidae, their amputated legs, the remains of ants near fossil spiders in Baltic amber and a piece of amber in which a fight of ants with a member of the Zodariidae is preserved indicate that Zodariidae feed on ants already in the Early Tertiary. Apparently in adaptation to their dangerous prey the Zodariidae evolved a special healing system which may be unique in spiders. If the diversification of the ants did not happen before the end of the Cretaceous the adaptations of the Zodariidae to their prey took only 10 to 15 million years.

(b) Ant mimicking spiders. Ants are dangerous to most arthropods and vertebrates, most birds beware of ants - the ants' soldiers may possess stings and powerful jaws, they may use ants acid, too. If a spider looks like an ant - and moves among numerous socially living ants - they may be protected in a special way (Batesian mimicry). Ant-shaped spiders are known in extant members of various spider families, most expressive in the Corinnidae, Gnaphosidae, Salticidae and Zodariidae. The geologically earliest cases of myrmecomorphy, representing Batesian mimicry, are described from spiders in Baltic amber (Early Tertiary, about 50 million years old), from members of the Zodariidae (photos) and of the Corinnidae (photos and the fig. above), see WUNDERLICH (2002) and the chapter on myrmecomorphy. So myrmecomorphy was distinct only 15 or 20 million years after the ants' diversification. Fossil ant-shaped members of the family Gnaphosidae are unknown. Fossil ant-shaped Salticidae are reported from Dominican amber - see the paper on the family Salticidae in these volumes -, but unknown in Baltic amber, although Salticidae are not rare in this kind of amber.

The slender body and legs, a saddle-shaped constriction of the opisthosoma and white hairs in this area give the illusion of a three-segmented body (ant-like). One may speculate if the forelegs of the spider were raised in antenna-like fashion, but the opisthosoma was raised, too, as in numerous extant ants.

The resemblance of the spiders to its ant model(s) is more distinct in the fossil Corinnidae (fig. above) than in the Zodariidae, it may be placed between grades 2 and 3 in the sense of WUNDERLICH (1995).

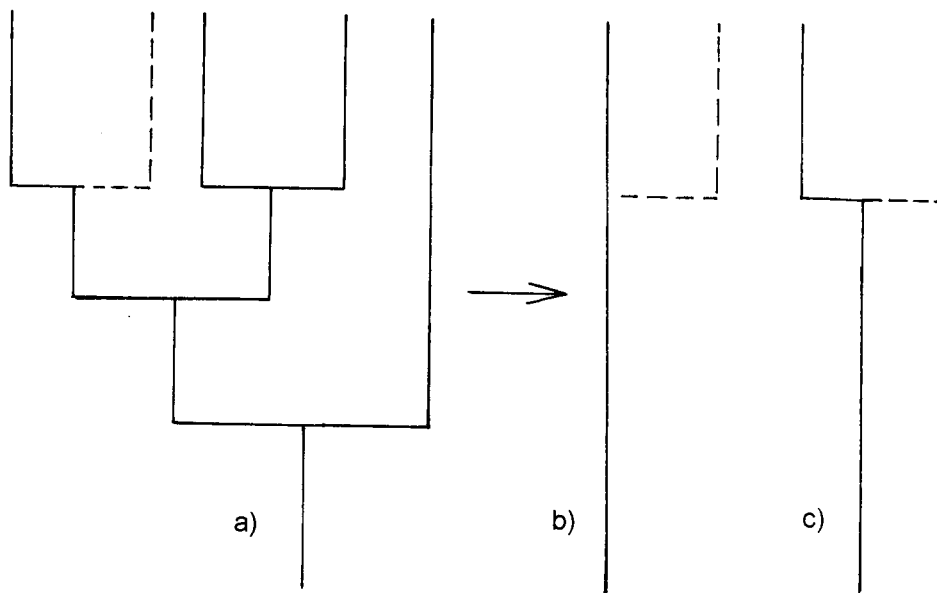
Addendum

Remarks on the geological age of two subfamilies of spiders and on "sister groups"

I suppose that the subfamily Tetragnathinae (Tetragnathidae) in the traditional sense is nothing else than one of several branches of the diverse subfamily Leucauginae; see the paper on the Tetragnathidae. (Corresponding birds are actually nothing else than one branch of the diverse Dinosaurs, "flying Dinosaurs").

Simply because of their conspicuous apomorphies Tetragnathinae - and birds - are raised to a higher level (rank). If this is true the name Tetragnathinae has to replace the name Leucauginae, and Tetragnathinae in the traditional sense has to downgrade to Tetragnathini.

From that follows that the presence of Leucauginae in the Early Tertiary Baltic amber forest does not allow the conclusion that "formalistic biologists" have that Tetragnathinae - which is regarded as sister group to Leucauginae in a simplified cladogram (see the figs. b-c) - must already have been present at that time (!).



Figs. a-c): Three phylogenetic graphics of the taxon "Leucauginae" with the branch "Tetragnathinae" (dotted lines). a) = probably correct cladogram (schematic and incomplete), b) and c) simplified, "formal cladograms" in which Tetragnathinae is regarded as "formal sister group" to Leucauginae, and is - incorrectly but ingeniously - raised to subfamilial level.

Apparently it is impossible to press all the results of diversification in a practicable and useful system.

Most probably Erigoninae of the Linyphiidae is a corresponding case: Its sister group (Linyphiinae + Micronetinae) was already present in the Baltic amber forest but we wonder about the absence of the Erigoninae which had probably not yet evolved at that time. - See also the subfamilies of the Salticidae.

LIST OF AND KEYS TO THE EXTANT ORDERS OF THE CLASS ARACHNIDA AND ITS ORDERS IN BALTIC AND DOMINICAN AMBER

List of the orders and presence in the ambers:

Order	Baltic amber	Dominican amber
Acari (Milben).....	+	+
Amblypygi (Geißelspinnen).....	--	+ (!)
Araneae (Spinnen).....	+	+
Opiliones (Weberknechte).....	+	+
Palpigradi (Palpenläufer).....	--	--
Pseudoscorpiones (Pseudoskorpione).....	+	+
Ricinulei (Kapuzenspinnen).....	--	--
Schizomida (Zwerg-Geißelskorpione).....	--	+ (!)
Scorpiones (Skorpione).....	+	+
Solifugae (Walzenspinnen).....	+	+
Uropygi (Thelyphonida) (Geißelskorpione).....	--	--

Remarks on the list above: See SCHLEE & GLÖCKNER (1978) and POINAR & POINAR (1999). - Members like the cave dwelling Palpigradi or the rare ground-living Ricinulei I do not expect in amber. - We are waiting for the first members of the Amblypygi and Schizomida in Baltic amber, which are already known from Dominican amber.

Key to the extant orders of the class Arachnida and fossils in Baltic and Dominican amber, based on "simple" morphological characters (figs. 1-18):

Remark: The habitus of members of the Acari (figs. 14-18!), Araneae and Opiliones is quite variable in contrast to members of the remaining orders; thus the determination of some of their taxa may be more difficult.

1 Opisthosoma ("abdomen") posteriorly elongated in a usually long "tail" (an opisthosomal "flagellum") (figs. 1, 3-5) (in Schizomida the "tail" may be short but not tiny, fig. 4). Except Palpigradi larger animals, extremely rare in amber or even absent (Palpigradi). 2

- Opisthosoma posteriorly blunt or with a rudimentary appendix only (figs. 2, 8-9), in Araneae with paired spinnerets (fig. 6). Tiny to larger animals, not rare in amber 5

2(1) Powerful "tail" present with a thickened poisonous sting (telson); pedipalpi with large chelate pincers at the end (fig. 1) similar to Pseudoscorpiones (fig. 2). Larger animals of a uniform body shape. Baltic and Dominican amber, very rare. **Scorpiones**

- The "tail" is a slender "flagellum", a poisonous sting is absent (figs. 3-5); subchelate pincers at the end of the pedipalpi - of a quite different shape - are present in the Uropygi (Thelephonida) only (fig. 5). Not reported from Baltic amber. 3

3(2) Pedipalpi slender (fig. 3); eyeless, body of a uniform shape, its length - in addition to the flagellum - less than 3mm. Not reported from amber. **Palpigradi**

- Pedipalpi thickened (figs. 4-5); eyes present or absent, larger animals. 4

4(3) Eyes absent, pedipalpi without a pincer but with a claw, flagellum with 3-4 segments only and shorter than the diameter of the opisthosoma (fig. 4). Dominican amber, extremely rare. Photo 694. **Schizomida**

- Eyes present (fig. 5), pedipalpi with a pincer at its end, flagellum with numerous segments and longer than the diameter of the opisthosoma (fig. 5). Not reported from amber. **Uropygi (Thelephonida)**

5(1) Body with a "waist": Prosoma and opisthosoma are distinctly divided and connected by a narrow stalk, a petiolus (figs. 6-8). 6

- Body undivided, prosoma and opisthosoma are widely fused (figs. 9-18). 7

6(5) Spinnerets present (fig. 6), in some taxa short and indistinct; anterior leg pair usually not or only slightly longer and thinner than the second pair, its tibia unsegmented (figs. 6-7, photos). The pedipalpi of adult males function as copulatory organs, they are thickened at the end and usually complicated. Body length of adults 0.33mm to about 10cm. Baltic and Dominican amber, not rare. **Araneae**

- Spinnerets absent, leg I much longer and thinner than the other legs (antenniform) and the tibia with numerous segments, body depressed (fig. 8). The pedipalpi build a powerful and spiny "catching basket" in both sexes. Larger animals (body length 10-45mm) of a uniform body shape. Dominican amber, very rare. Photos 695-696 . . . **Amblypygi**

7(5) Pedipalpi very large and with thick pincers at the end (fig. 2) similar to scorpions (fig. 1). Small animals which have usually a long and uniform body. Baltic and Dominican amber, not frequent, occasionally phoretic **Pseudoscorpiones**

- Pedipalpi without thickened pincers at the end (figs. 9-17) (tiny pincers are present in Ricinulei, fig. 9). Body shape very diverse. 8

8(7) Habitus uniformly as in fig. 9, an undivided anterior "hood" (cucullus) is present, opisthosoma with four dorsal plates (tergites) which usually are divided longitudinally two times (fig. 9); large leg I, eyes absent. Not reported in amber. **Ricinulei**

- Habitus otherwise, very variable, e.g. as in figs. 10-18; leg I large or small, eyes usually present but often small/indistinct. Baltic and Dominican amber. 9

9(8) Body uniform as in fig. 13: Long, with a constriction in front of the middle, powerful chelicerae and a pair of median eyes on a low elevation. Pedipalpi very large, leg-shaped, the first leg pair is shorter than the other legs. (A "flagellum" and "malleoli" are typical structures). Extremely rare, only a single adult specimen is known both in Dominican and Baltic amber. Photos 688-689 **Solifugae**

- Body: Shape very variable (figs. 10-12, 14-18), often short, no constriction in front of the middle. In most Opiliones a pair of large median eyes is present on a distinct tubercle (fig. 10b; but see figs. 11-12); in most Acari the first leg pair is distinctly larger than the small pedipalpi, a pair of median eyes is only rarely present (fig. 17). (Flagellum and malleoli are absent). Frequent in Baltic and Dominican amber. 10

10(9) **(a)** A pair of large lateral prosomal tubercles bearing stink glands is present in mite-shaped Opiliones (fig. 12, Sironidae) and the anterior prosomal margin is cross-cut or (extremely rare in Baltic amber) or **(b)** body strongly flattened (fig. 11, Trogulidae; comp. fig. 9!), bearing an anterior divided "hood", the first legs are the shortest legs (not reported in amber) or **(c)** most taxa in amber: Usually with a pair of large median eyes on a common elevation (figs. 10a, 10b) and very long second legs which possess numerous segments. - Leg autotomy frequent. Mostl often larger animals. Baltic and Dominican amber, not frequent. **Opiliones**

- Combination of characters different. If the shape of the body is similar: **(a)** (fig. 14, Opilioacarida): Stink glands and lateral prosomal elevations absent, anterior prosomal margin protruding, pedipalpi small; **(b)** a divided "hood" is absent and the first legs are the longest legs; **(c)** if median eyes are present (rarely: The solifugae-shaped Rhagidiidae, fig. 17, photo): Eyes situated on low elevations only, the second leg is short and has no segmentation of the articles. - The body shape of Acari (figs. 14-18) is very variable, the body is frequently short, the opisthosoma is usually not segmented but a secondary segmentation may be present. Autotomy is rare. Frequently tiny animals and

body length of adults less than 1mm. Juvenile (larval) and some adult Acari (fig. 18) have less than 4 pairs of legs, 3 leg pairs are present in most juveniles (fig. 15), the first leg pair is usually the longest and is frequently antennae-shaped raised. Baltic and Dominican amber, very frequent, the most diverse order of animals (some are araneae-, opiliones-, solifugae-, beetle-, worm- or star- shaped); there are land and water dwellers, decomposers, predators, parasites, phytophagous and phoretic animals which may be attached e.g. on Opiliones or beetles. **Acari**

Bestimmungs-Tabelle für die heutigen Ordnungen der Spinnentiere (Arachnida)
nach "einfachen" morphologischen Merkmalen; mit Hinweisen auf fossile Nachweise in Baltischem und Dominikanischem Bernstein (Abb. 1-18):

Anmerkung: Das Aussehen von Vertretern der Milben (Abb. 14-18!), Spinnen und Weberknechten ist im Gegensatz zu demjenigen der übrigen Ordnungen sehr variabel, die Zuordnung einiger Gruppen dieser Ordnungen kann daher entsprechend schwierig sein.

1 Der Hinterkörper (Opisthosoma, "Abdomen") trägt am Ende einen schwanzartigen Anhang ("Flagellum") (Abb. 1, 3-5) (bei den meisten Schizomida ist dieser Anhang kurz, aber nie winzig, Abb. 4). Außer den Palpenläufern größere Tiere. Im Bernstein extrem selten oder sogar fehlend (Palpenläufer) 2

- Hinterkörper am Ende abgerundet oder mit winzigem Anhang (Abb. 2, 8-9), bei den Spinnen (Araneae) mit paarigen Spinnwarzen (Abb. 6). Winzige bis größere Tiere, im Bernstein nicht selten. 5

2(1) Es existiert ein sehr großer "Schwanzanhang", der am Ende einen verdickten Giftstachel trägt (Abb. 1); die Pedipalpen tragen am Ende große Scheren (Abb. 1) ähnlich denjenigen der Pseudoskorpione (Abb. 2). Größere Tiere. Baltischer und Dominikanischer Bernstein, sehr selten. *Skorpione*. **Skorpiones**

- Es existiert ein schlanker "Schwanzanhang", ein Giftstachel fehlt (Abb. 3-5); "Scheren" der Pedipalpen - deutlich anders - existieren nur bei den Geißelskorpionen (Uropygi) (Abb. 5). Im Baltischen Bernstein nicht nachgewiesen. 3

3(2) Pedipalpen schlank (Abb. 3); augenlos, Körper uniform, Länge ohne Flagellum weniger als 3mm. Im Bernstein nicht nachgewiesen. *Palpenläufer*. **Palpigradi**

- Pedipalpen verdickt (Abb. 4-5); Augen fehlend oder vorhanden, größere Tiere. 4

4(3) Augenlos, Pedipalpen ohne "Schere", aber mit einer Klaue, Flagellum mit nur 3-4 Segmenten und kürzer als der Durchmesser des Hinterkörpers (Abb. 4). Dominikanischer Bernstein, extrem selten. *Zwerg-Geißelskorpione*. Foto 694. **Schizomida**

- Augen vorhanden (Abb. 5), Pedipalpen am Ende mit einer "Schere", Flagellum mit zahlreichen Segmenten und länger als der Durchmesser des Hinterkörpers (Abb. 5). Im Bernstein nicht nachgewiesen. *Geißelskorpione*. **Uropygi (Thelyphonida)**

5(1) Körper mit einer "Taille": Vorderkörper und Hinterkörper sind deutlich geteilt und durch einen dünnen "Stiel" (Petiolus) miteinander verbunden (Abb. 6-8). 6

- Körper einteilig, Vorder- und Hinterkörper breit miteinander verbunden (Abb. 9-18). . . 7

6(5) Spinnwarzen vorhanden (Abb. 6), gelegentlich sehr kurz; erstes Beinpaar gewöhnlich nicht oder kaum länger als das zweite Beinpaar, seine Tibia nicht segmentiert (Abb. 6-7, Fotos). Die Pedipalpen des Männchens fungieren als Kopulations-Organ, sie sind am Ende deutlich verdickt und meist kompliziert gebaut. Körper-Länge 0.33m bis etwa 10cm. Baltischer und Dominikanischer Bernstein, nicht selten. *Spinnen*. **Araneae**

- Spinnwarzen fehlen, Bein I viel länger als die anderen Beine (antennenförmig) seine Tibia mit zahlreichen Gliedern (Abb. 8). Die Pedipalpen bilden in beiden Geschlechtern einen mächtig entwickelten, stacheligen "Fangkorb". Größere Tiere von recht gleichförmigem Aussehen, Körper-Länge 10-45mm. Dominikanischer Bernstein, sehr selten. *Geißelspinnen*. Fotos 695-696 **Amblypygi**

7(5) Pedipalpen sehr groß und am Ende mit stark verdickten "Scheren" (Abb. 2) ähnlich denjenigen der Skorpione (Abb. 1). Kleine Tiere mit recht uniformem und meist langgestrecktem Körper. Baltischer und Dominikanischer Bernstein, nicht häufig, gelegentlich phoretisch. *Pseudoskorpione*. **Pseudoscorpiones**

- Pedipalpen am Ende ohne verdickte "Scheren" (Abb. 9-18) (winzige "Scheren" existieren bei Kapuzenspinnen, Abb. 9). Körperform sehr variabel. 8

8(7) Körper recht gleichförmig wie in Abb. 9, "Kapuze" (Cucullus) vorhanden, Hinterkörper oben mit 4 "Schildchen" (Tergiten), die gewöhnlich zweimal längs geteilt sind. Großes Bein I. Augenlos. Im Bernstein nicht nachgewiesen. *Kapuzenspinnen*. . . . **Ricinulei**

- Körper anders, sehr variabel, z. B. wie in Abb. 9-18. Bein I groß oder klein, Augen gewöhnlich vorhanden, oft klein/undeutlich. Baltischer und Dominikanischer Bernstein. . . 9

9(8) Aussehen gleichförmig wie in Abb. 13: Körper langgestreckt, mit einer Verengung vor der Mitte, mächtig entwickelten Cheliceren und einem Paar Mittelaugen auf einer flachen Erhebung. Pedipalpen sehr groß, bein-förmig, das erste Bein-Paar ist kleiner als die übrigen Beine. (Typische Strukturen sind "Flagellum" und "Malleoli"). Fossil äußerst selten, es ist jeweils nur ein einziges geschlechtsreifes Exemplar im Dominikanischen und im Baltischen Bernstein bekannt. *Walzenspinnen*. Fotos 688-689, **Solifugae**

- Aussehen sehr variabel (Abb. 10-12, 14-18), Körper oft kurz, eine Verengung vor der

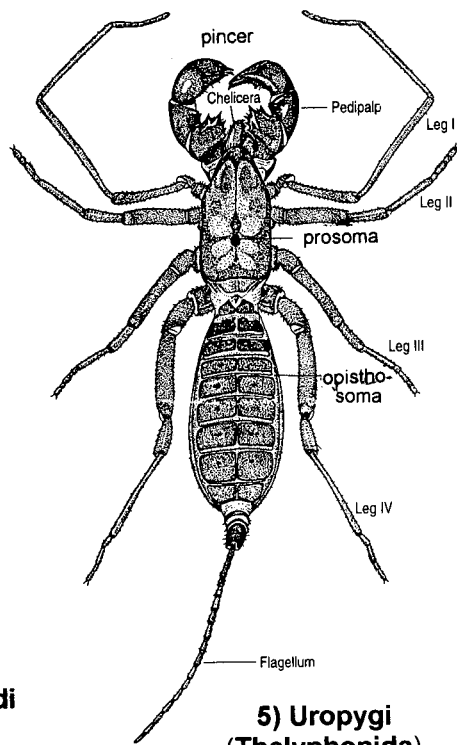
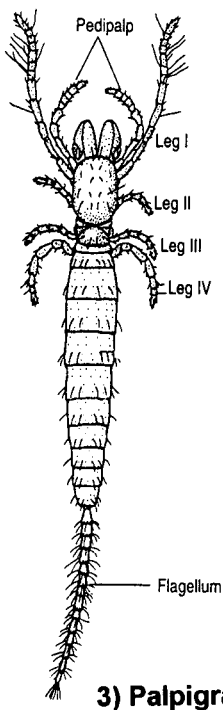
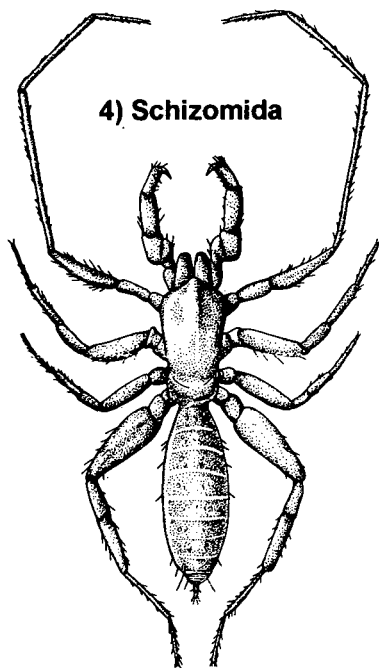
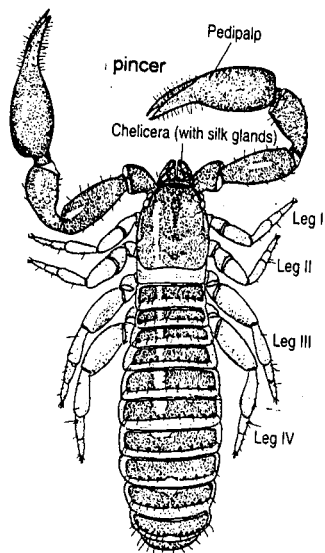
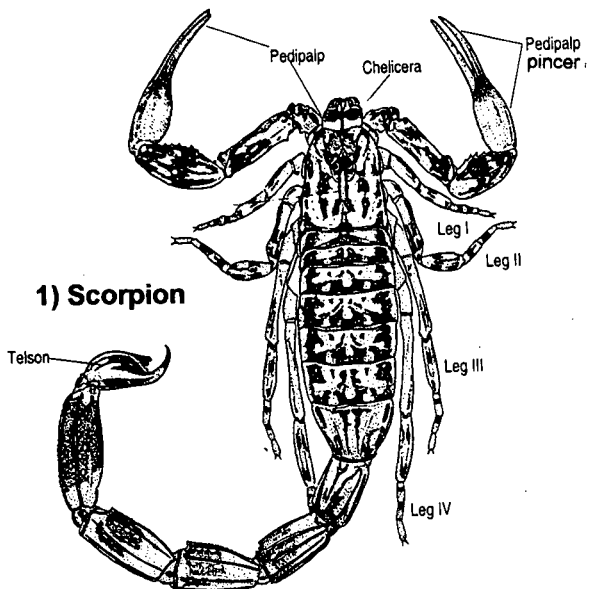
Mitte fehlt. Bei den meisten Weberknechten existiert ein Paar großer Mittelaugen auf einem deutlichen Hügel (Abb. 10b; vgl. aber Abb. 11-12); bei den meisten der gewöhnlich wesentlich kleineren Milben ist das erste Bein-Paar deutlich größer als die kleinen Pedipalpen, ein Paar Mittelaugen ist nur sehr selten vorhanden (Abb. 17). (Flagellum und Malleoli fehlen). Häufig in Baltischem und Dominikanischem Bernstein. 10

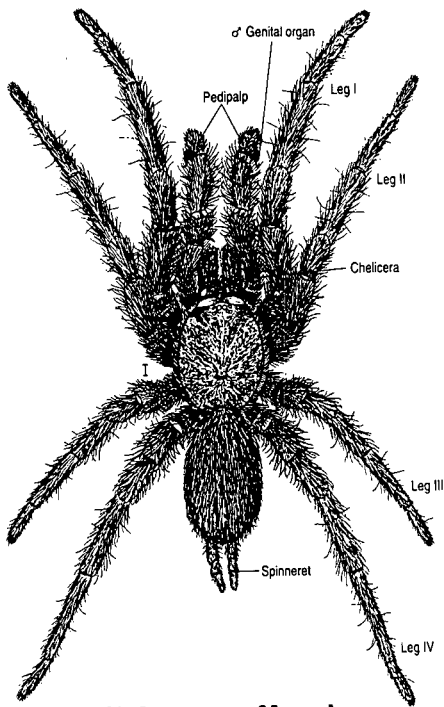
10(9) (a) Bei den milben-ähnlichen Weberknechten (Abb. 12, Sironidae) existiert ein Paar großer seitlicher Hügel des Vorderkörpers, die Stinkdrüsen tragen, und der vordere Rand des Vorderkörpers ist wie quer abgeschnitten (extrem selten im Baltischen Bernstein); oder (b) der stark abgeflachte Körper der Brettkanker (Trogulidae) (Abb. 11, vgl. Abb.9!) trägt vorn eine geteilte "Kapuze", das erste Bein-Paar ist das kürzeste (im Bernstein nicht nachgewiesen) oder (c) (die allermeisten Arten im Bernstein!): Gewöhnlich mit einem Paar großer Mittelaugen auf einem deutlichen Hügel (Abb. 10a, 10b) und mit ungewöhnlich langem zweiten Bein-Paar, das zahlreiche Segmente trägt. Meist größere Tiere; Autotomie ("Abwerfen" der Beine) häufig; oft liegen abgetrennte Beine neben dem Fossil. Baltischer und Dominikanischer Bernstein, nicht häufig. *Weberknechte*. **Opiliones**

- Merkmals-Kombination anders. Sofern ähnlich: (a) (Abb. 14, Opilioacarida) fehlen Stinkdrüsen und seitliche Hügel des Vorderkörpers, der Vorderrand des Vorderkörpers ist vorgezogen, die Pedipalpen sind klein; (b) eine geteilte Kapuze fehlt und das erste Bein-Paar ist am längsten; (c) sofern - sehr selten! - Mittelaugen vorhanden sind, sitzen diese auf flachen Erhebungen, das zweite Bein-Paar ist kurz und besitzt keine Segmentierung der Glieder: Die solifugen-ähnlichen Vertretern der Familie Rhagidiidae (Abb. 17, Foto). - Körper der Milben oft kurz und winzig, häufig weniger als 1mm lang, Form sehr variabel, Hinterkörper selten gegliedert. Autotomie selten (außer bei den Opilioacarida). Juvenile und manche geschlechtsreife Milben (Abb.18) besitzen weniger als 4 Bein-Paare, Jungmilben meist 3 (Abb. 15). Baltischer und Dominikanischer Bernstein, sehr häufig, artenreichste und diverseste Tiergruppe überhaupt, einige sind spinnen-, weberknecht-, walzenspinnen-, käfer-, wurm oder stern-förmig, meist an Land lebend, manche leben im Wasser, andere sind Kompostierer, leben räubersich, als Pflanzenfresser oder als Parasiten, gelegentlich als "Mitreisende" (phoretisch) - auch im Bernstein - z. B. an Weberknechten, Zweiflüglern oder Käfern. *Milben*. **Acari**

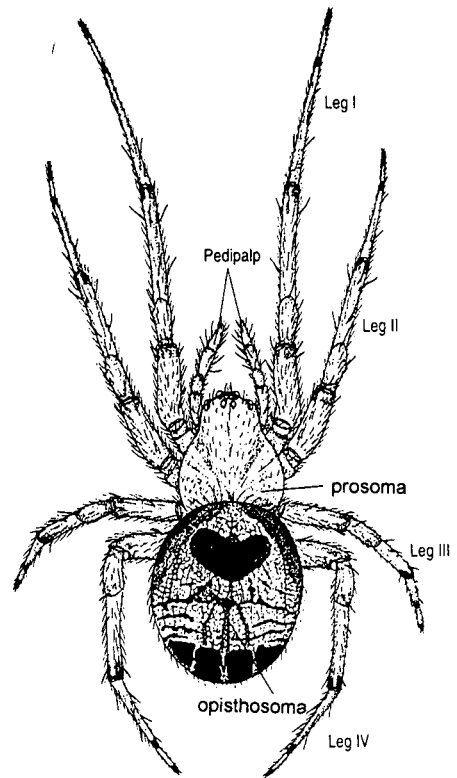
Pedipalpi in the arachnid orders and their modifications:

- (a) Weakly modified, more or less leg-shaped: Most Acari (figs. 14-18), female Araneae (fig. 7) (large in most Mesothelae and Mygalomorpha) (male Araneae: See (d)), most Opiliones (figs. 10-12) (large and spiny like a "capture basket" in Laniatores, see (c)), Palpigradi (fig. 3), Schizomida (fig. 4), Solifugae (fig. 13) (long, fairly thickened, blunt, with a terminal adhesive organ, terminal claw absent).
- (b) Pincers (in German: Scheren): Small: Ricinulei (fig. 9); large: Pseudoscorpiones (fig. 2), Scorpiones (fig. 1) and Uropygi (fig. 5) (see (c)).
- (c) Spiny "capture baskets" (in German: "Fangkörbe"): Amblypygi (fig. 8); similar: Uropygi (fig. 5) and Opiliones: Laniatores (see (a)).
- (d) Secondary copulatory organs (the metatarsus has been lost, the tarsus has changed to cymbium with bulbus, embolus): Male Araneae (fig. 6), sexual dimorph, see (a).

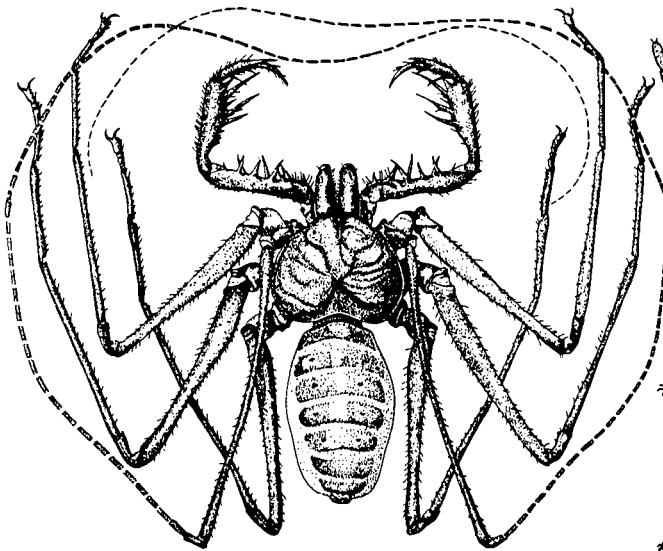




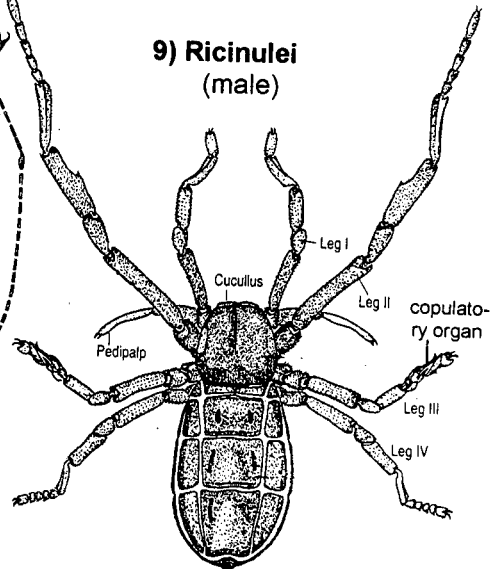
6) Araneae: Mygalomorpha, male spider



7) Araneae: Araneomorpha, female spider (spinnerets not observable)

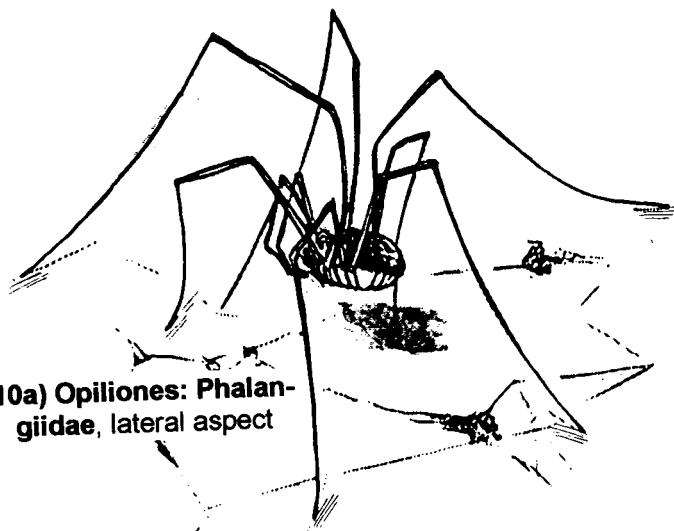


8) Amblypygi

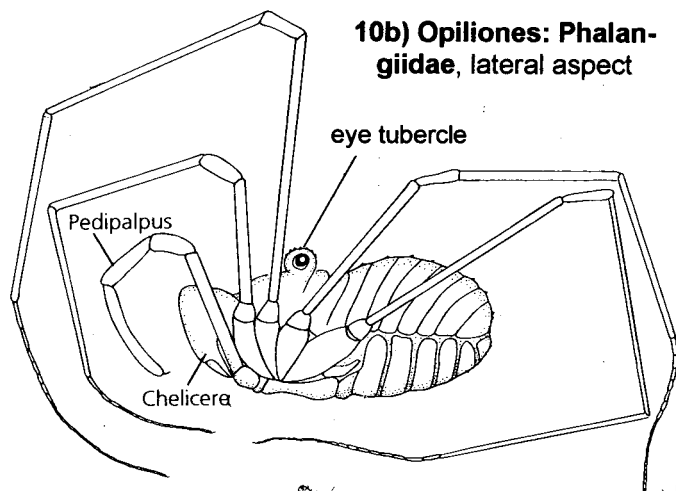


9) Ricinulei (male)

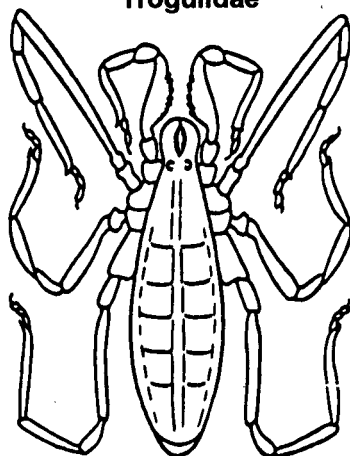
10a) Opiliones: Phalangidae, lateral aspect



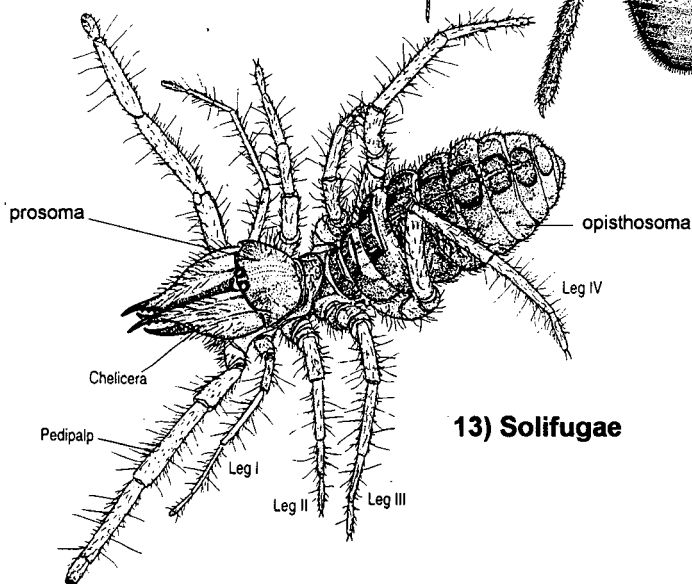
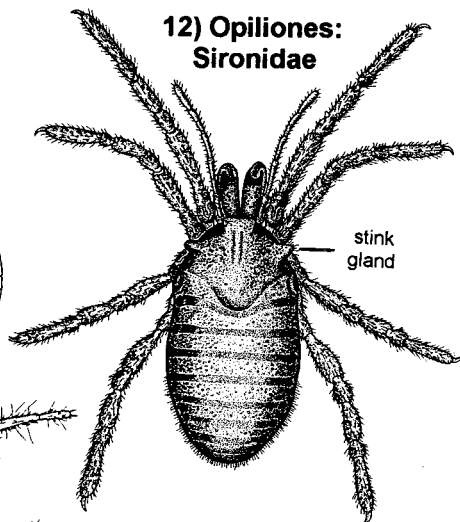
10b) Opiliones: Phalangidae, lateral aspect



11) Opiliones: Trogulidae



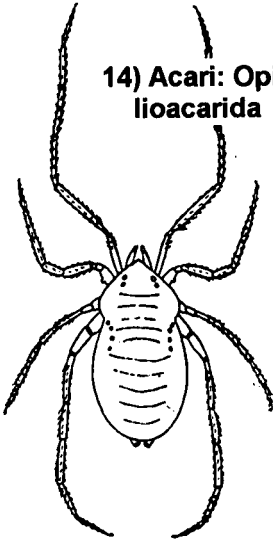
12) Opiliones: Sironidae



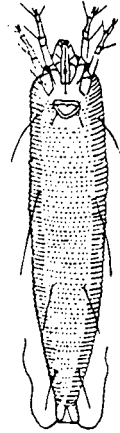
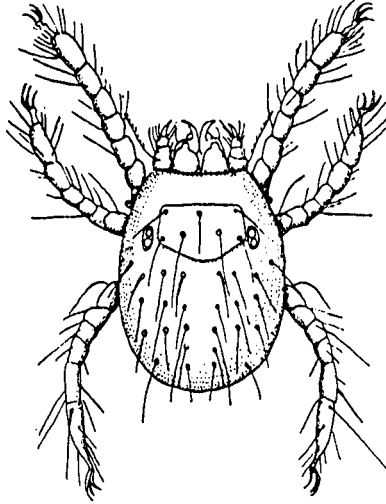
13) Solifugae

Acari (Milben)

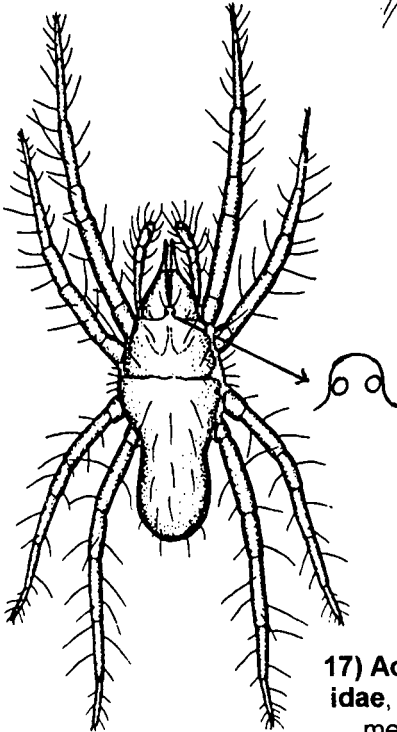
14) Acari: Opi-
lioacarida



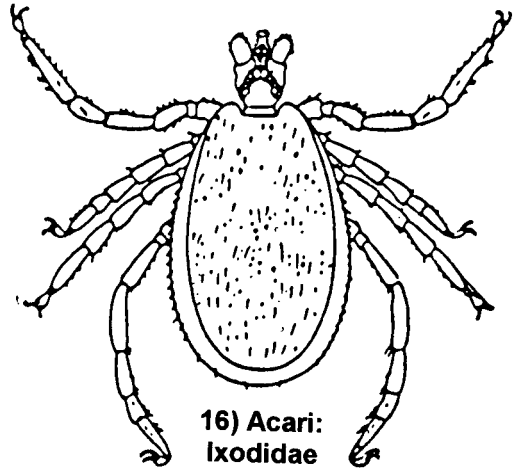
15) Acari: Trom-
biculidae, juv.



18) Acari: Erio-
phyidae, ven-
tral aspect



17) Acari: Rhagidi-
idae, with enlarged
median eyes



16) Acari: Ixodidae

Remarks: Some - beautiful - figures are taken from ROBERTS in MURPHY & MYRPHY (2000): An Introduction to the Spiders of South East Asia. - If not otherwise noted the dorsal aspect of the body is shown.

IDENTIFICATION KEYS to the spiders in Baltic amber (BESTIMMUNGSTABELLEN für die Spinnen im Baltischen Bernstein)

Keys to the spiders in Dominican amber: See WUNDERLICH (1988).

In contrast to certain authors I use the correct terms of the spiders body parts: Prosoma (not carapax or cephalothorax), opisthosoma (not abdomen) and gnathopodae (not maxillae or endites). (The terms in brackets are mainly used in crabs and other Crustacea but not in Arachnida).

At the **first step of the identification of a fossil spider** one may search for a striking character of the spider. About 80% of the spiders may be members of one of the following families or even of these genera (see the photos, too):

Salticidae (Jumping Spiders; in German: Springspinnen) (photos 411-430, figs. 4-5) have special eyes on a case-shaped high prosoma, which bears three eye rows and extremely large anterior median eyes which are directed forwards. (Large posterior median eyes are present in the Deinopidae, fig. 7). Members of the genera *Eolinus* and *Gorgopsina* are not rare.

Oonopidae (Oonopids, photos 29-35; in German: Zwerg-Sechsaugenspinnen) possess a strongly thickened femur IV (fig. 6) and only 6 eyes (fig. 8; their position is similar to the Segestriidae), the bulb is simple and pear-shaped. Their body length is only 1-1.5mm. Fossil members of the genus *Orchestina* are very frequent.

Mimetidae (Pirate Spiders, photos 242-246; in German: Spinnenfresser-Spinnen) possess rows of long and strong prolateral bristles on the first and second tibia and/or metatarsus (and usually short curved bristles between them) (fig. 9); e.g. *Succinero*.

Theridiidae (Combfooted Spiders; in German: Kugelspinnen) (revision in preparation) frequently have a high prosoma which may bear deep dorsal folds: Most species of the genus *Dipoena* (figs. 23-25) or may possess a long and spiral embolus: Members of the genus *Clypea* (= *Nanomysmena*) or they may have a rather long opisthosoma: Members of the genus *Episinus*. Femoral, metatarsal and lateral tibial bristles are absent in this family as in the Cyatholipidae, Nesticidae and Synotaxidae. Specimens are frequent in all Tertiary fossil resins.

Synotaxidae (Synotaxids, photos 210-233; in German: Kugelhöhlenspinnen) may possess a brush of prosomal hairs and two spiral structures of the bulb (fig. 27) (frequent members of the genus *Acrometa*) or simple and very small bulbi (the genus *Anandrus*, photo 20). Excepts ventrally (fig. 226) femoral, metatarsal and lateral tibial bristles are absent as in the similar Cyatholipidae, Nesticidae and Theridiidae.

Linyphiidae (Sheet web weavers, photos 249-263; in German: Baldachinspinnen) have slender legs which bear numerous bristles on femora, patella, tibia and metatarsus. In almost 40% of the fossil specimens a leg is broken off between patella and tibia (autotomy) and lost or situated near the spider in the amber (photo 674). (This kind of autotomy also occurs e.g. in the similar Pimoidae, in the Leptonetidae which have only 6 eyes, and in the Hersiliidae which have very long posterior spinnerets). Their lateral cheliceral stridulating files (fig. 20) are usually hard to observe in the fossils. Frequent are members of the genus *Custodella* in which the cymbium bears distinct outgrowth(s).

Archaeidae (Archaeids, photos 56-78; in German: Urspinnen) usually have an elevated "head-shaped" part of the prosoma as well as long and diverging chelicerae which bear spiny "teeth" (fig. 10); e.g. the genus *Archaea* of which juveniles are not so rare.

Zoropsidae (photos 314-323): Females are rare but males are not too rare in the Baltic amber, especially members of the genus *Matachia*; their body length is usually 4-5mm. The tibia of the male pedipalpus bears several long and outstanding apophyses. Occasionally hidden in the fossils is the typical basal tibial suture of the male legs (photo 318).

Trochanteriidae (photos 389-394): If the legs are stretched out to the side a spider in Baltic amber is most often a member of the genus *Sosybius* (or probably Thomisidae). Juvenile *Sosybius* are not rare in Baltic amber, but adults - their body length may be more than 1cm - are rare. In adult spiders the tarsi and metatarsi bear a dense scopula and the lenses of the posterior median eyes are reduced and oval.

In most males of the small or even tiny Anapidae (photos 143-176) and Cyatholipidae (photos 189-209) the leg I may be modified: thickened, more or less bent or bearing spurs or spines. E.g. members the genera *Spinilipus* (photos 193-195) and *Succinilipus* (photo 204) (Cyatholipidae) as well as *Balticoroma* (photos 146-149) (Anapidae) are not too rare.

In the Zygiellidae (photos 123-124, 474) the legs bear numerous bristles which are standing out from their leg articles - as in the Araneidae and the Linyphiidae - in contrast to members of several other families in which the ventral tibial bristles are paired and near to the article and in which several tarsal trichobothria are present (there is none in the Zygiellidae). An autotomy between coxa and trochanter is frequent. Members of the genus *Graea* (eye position fig. 19) are usually 3-4mm long.

A second step in the identification of a fossil spider - if necessary - may be to find out (a) if it is adult or inadult (juvenile), e.g. subadult, and (b) the sex. Adult spiders possess completely evolved genital (copulatory) organs and are larger, but some adults are tiny - body length far less than 1mm - and certain juveniles on the other hand - e.g. of *Sosybius* (Trochanteriidae) - may possess a body length of 1cm. In both sexes the shape of the pedipalpi is also different (the most striking sexual dimorphism in spiders, see the figs. below). They originate in front of the legs and

are leg-shaped in females and juveniles of both sexes; with the exception of the Mygalomorpha they are distinctly smaller than legs, a metatarsus is completely absent, only a single tarsal claw may be present. (In adult males the pedipalpus functions as a copulatory organ: With the help of the embolus of the bulbus the sperm is transported to the female epigyne). A spider can most easily be recognized as an adult male (fig. 1(b), photos 14, 57, 263): (a) The tibia of the pedipalpus may bear one or several apophyses, (b) the terminal article of the pedipalpus, the bulbus, is distinctly thickened, most often it is built in a complicated way as well as usually bearing ventral apophyses, and (c) a cymbium is present which is a separate and usually shovel-shaped article; it is situated above the bulbus and is completely absent in the juvenile males. In various members of the Mygalomorpha and Dysderoidea apophyses of the bulbus are absent and only a pointed embolus is present (photo 14). In the juvenile male the terminal article of the pedipalpus may be more or less thickened. In the subadult male - the last moulting stage before being adult - the terminal article of the pedipalpus is distinctly thickened (fig. 3, photos 457, 465) (with the exception of the Mygalomorpha and Mesothelae), frequently pear-shaped, at first sight similar to the adult male, but - in contrast to the adult male - it has no apophyses and a bulbus is absent. (The identification on the species level usually the ventral aspect of the bulbus is needed which unfortunately is frequently hidden by a white emulsion or by parts of the spider's body).

The female spider has a slender pedipalpus like a juvenile spider (in few extant species e.g. of the Dictyninae the terminal article is thickened similarly to a subadult male). The legs and the opisthosoma - which may bear eggs and larger spinning glands! - are stouter than in the male. In most groups - except the Mygalomorpha and Dysderoidea - the external female genital organ, the epigyne, is a sclerotized plate which is situated ventrally on the opisthosoma and which may bear one or two grooves (photo 297) and/or an outgrowth (photo 252). Unfortunately the epigyne of fossil females - except many Linyphiidae - is most often covered by a white emulsion, and thus it may be hard to distinguish them from juveniles. The proportions of prosoma, legs and opisthosoma as well as the position of the leg articles may be different in the juveniles, e.g. the opisthosoma may be smaller, the leg articles may be less sclerotized and more strongly bent in the dead spiders.

In numerous families the determination of juvenile spiders to family level is difficult or even impossible. (Unfortunately the descriptions of most fossil species of spiders which were described in former times are based on juveniles or females and thus their identification is usually not sure). If dorsal femoral, dorsal metatarsal and lateral tibial bristles are absent most juvenile spiders in Baltic amber are members of the - most frequent - families Theridiidae (e.g. the genera *Dipoena* and *Clya* (= *Nanomysmena*)) and the Synotaxidae (e.g. the genus *Acrometa*). If the hind femur is strongly thickened (fig. 6, photos 32-33) a tiny spider in Baltic amber is a member of the genus *Orchestina* (Oonopidae); if the legs are stretched out to the side, most of such juvenile spiders in Baltic amber are members of the genus *Sosybius* (Trochanteriidae) (photo 390) in which the adults are large spiders and possess a well developed tarsal scopula as well as a large dorsal opisthosomal scutum in contrast to the young spiderlings (a case of stage dimorphism).

In a **third step** - if necessary - one has to use the identification keys below.

Spider Structures

Fig. 1(a) Ventral View

(♀)

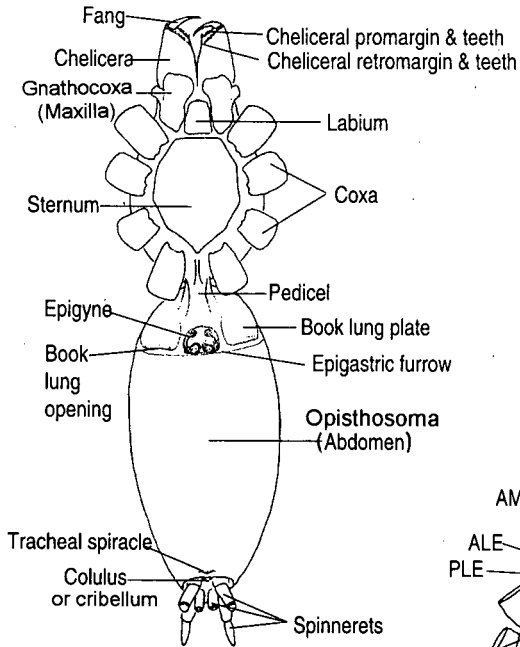
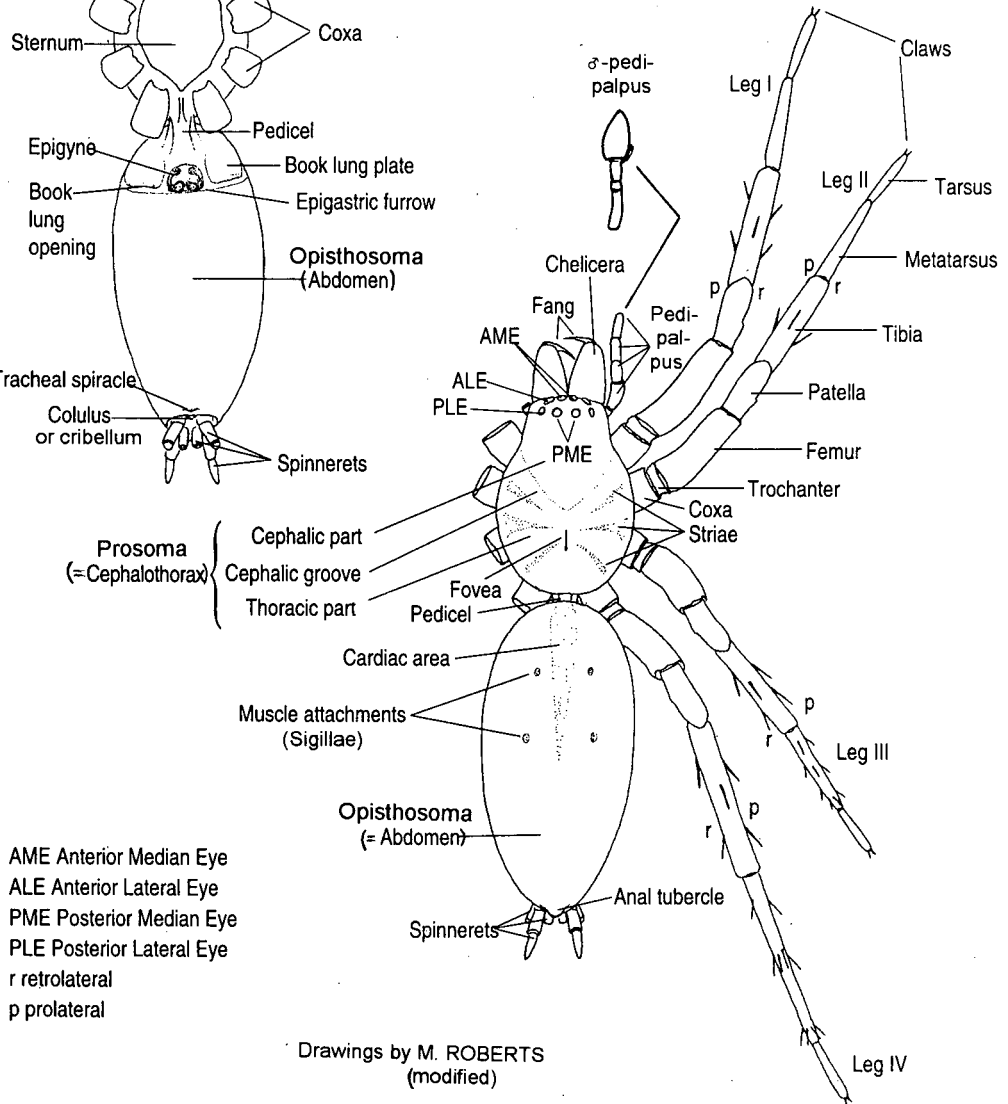
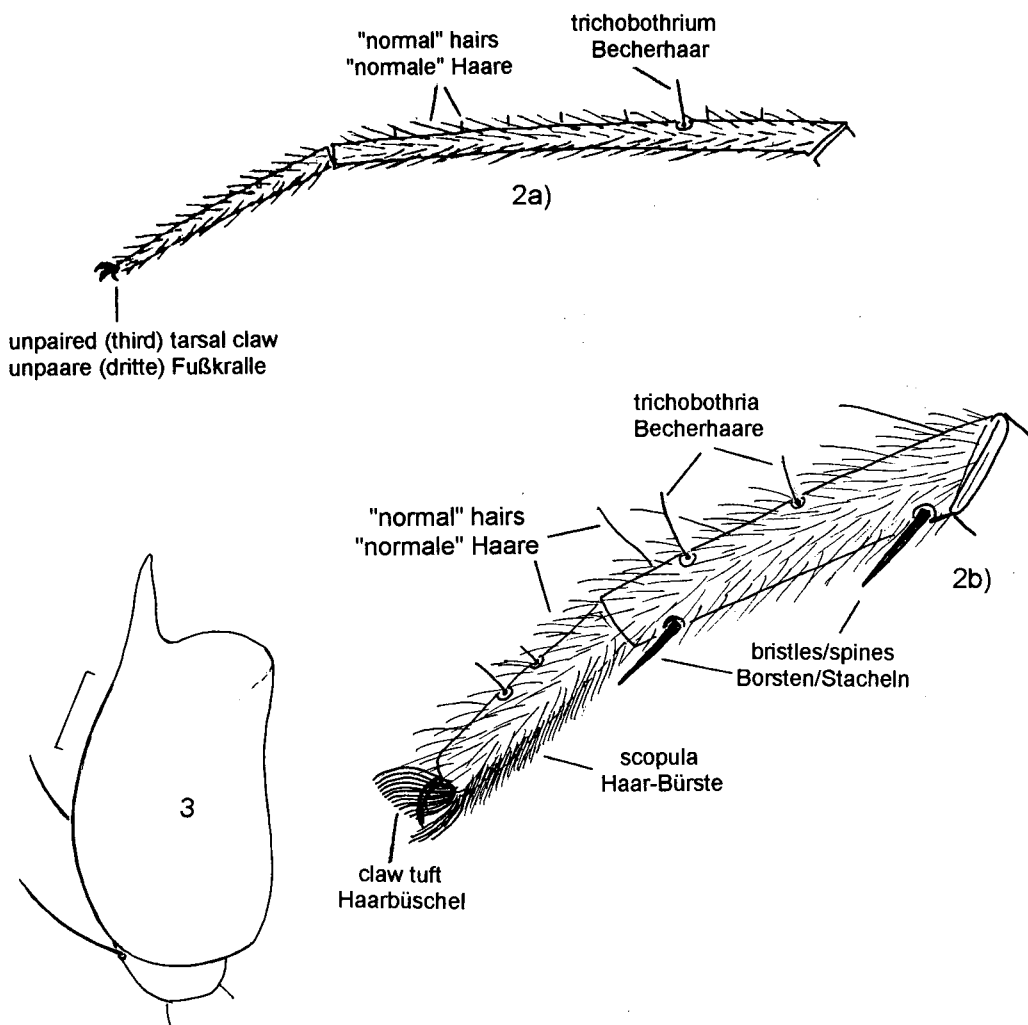


Fig. 1(b) Dorsal View

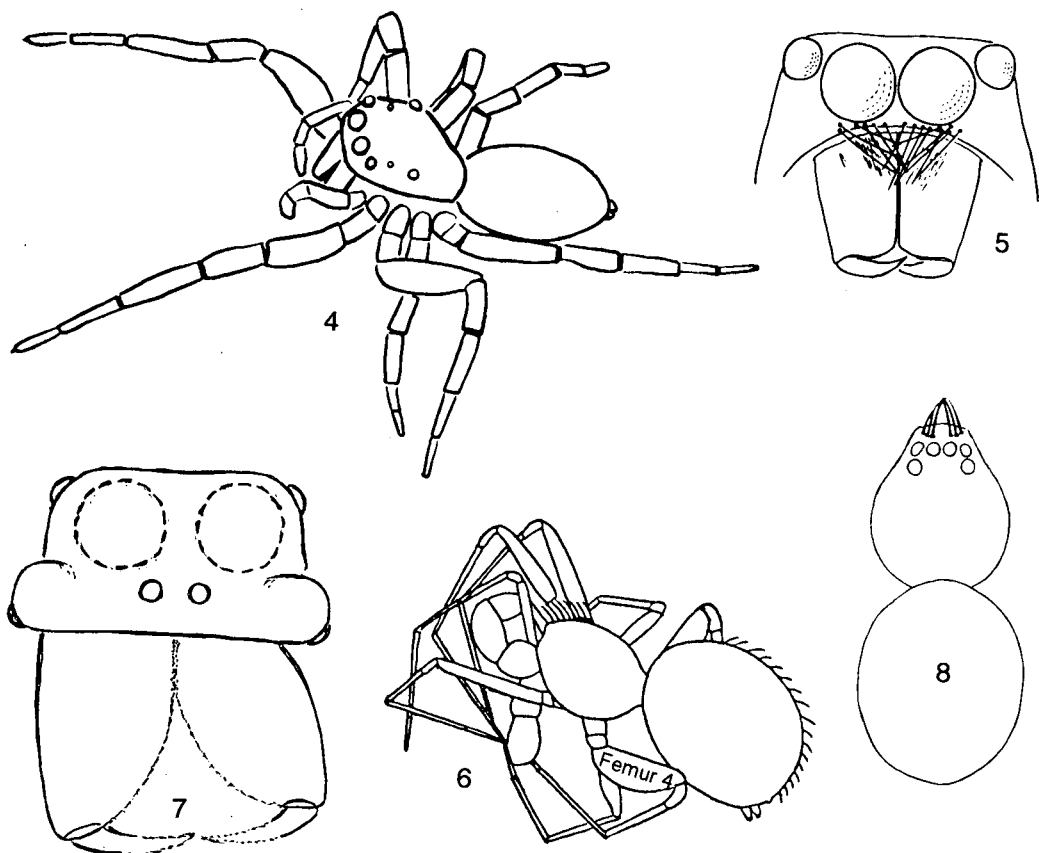


Drawings by M. ROBERTS
(modified)



Figs. 2a-b: Tarsus and metatarsus of two spiders, a member of the family Theridiidae (a) and a member of the family Salticidae (b), lateral aspect; with normal hairs, trichobothria, bristles, scopula, claw tuft and tarsal claws (the paired claws are hidden in fig. b). (Die letzten beiden Fußglieder zweier Spinnen, einer Kugelspinne (a) und einer Springspinne (b) von der Seite; mit normalen Haaren, Becherhaaren, Borsten/Stacheln, Haarbürste, Haarbüschel unter den Krallen und Fußkrallen (die paarigen Krallen in Abb. b sind verdeckt)).

Fig. 3) Ventral aspect of the left σ -pedipalpus of a subadult fossil Linyphiid spider (*Eolabulla*). (Pedipalpus eines fossilen Baldachinspinnen-Männchens kurz vor der Häutung zur Geschlechtsreife von unten).



Figs. 4-5: Fossil members of the family Salticidae in amber. Note the very large anterior median eyes and the unusually long eye field. (Fossile Springspinnen im Bernstein. Man beachte die sehr großen vorderen Mittelaugen und das ungewöhnlich lange Augen-Feld. 4) Dorsal-left aspect of the body. (Körper von oben-links). 5) Frontal aspect of the prosoma. (Vorderkörper von vorn).

Fig. 6) Male member of the genus Orchestina (Oonopidae), taken from PETRUNKEVITCH (1958), body length ca. 1.15mm. Note the thick femur of the left posterior leg. (Männliche Zwerg-Sechsaugenspinne der Gattung Orchestina, Körper-Länge etwa 1.15mm. Man beachte den dicken Schenkel (Femur) des hinteren linken Beins).

Fig. 7) Anterior aspect of a fossil member of the family Deinopidae. Note the unusually large posterior median eyes. (Frontal-Ansicht einer Käscherspinne. Man beachte die ungewöhnlich großen hinteren Mittelaugen).

Fig. 8) Dorsal aspect of a member of the genus Orchestina (Oonopidae), ca. 1.15mm long. (Körper einer Zwerg-Sechsaugenspinne der Gattung Orchestina von oben, Körper-Länge etwa 1.15mm).

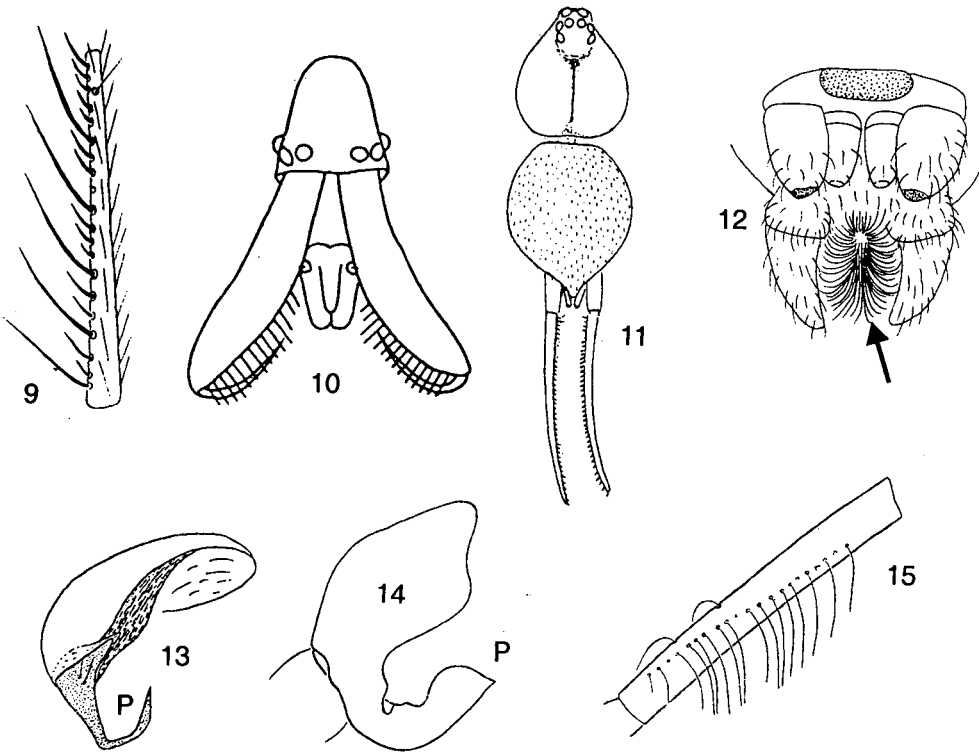


Fig. 9) Typical anterior metatarsal spination of a member of the family Mimetidae. (Typische Beborstung des vorderen Metatarsus einer Spinnenfresser-Spinne).

Fig. 10) Anterior aspect of the prosoma of an Archaea sp. (Archaeidae). Note the long cheliceral bristles ("peg teeth"). (Vorder-Ansicht einer Urspinne der Gattung Archaea. Man beachte die langen Borsten der Kiefer).

Fig. 11) Dorsal aspect of the body of a fossil member of the family Hersiliidae. Note the very long posterior spinnerets. (Körper einer fossilen Kreiselspinne von oben. Man beachte die sehr langen hinteren Spinnwarzen).

Fig. 12) Ventral aspect of the spinnerets and the hairy anal tubercle (arrow) of an extant member of the Oecobiidae: Oecobiini. Taken from DIPPENAAR-SCHOEMAN & JOCQUE (1997). (Spinnwarzen und haariger After-Deckel einer heutigen Scheibennetz-Spinne von unten).

Figs. 13-14: Cymbia with paracymbia (P) of two members of the superfamily Ara-neoidea, of a member of the Linyphiidae and a member of the Nesticidae (14). (Cymbia und Paracymbia (P) zweier Vertreter der Radnetzspinnen-Verwandten, einer Baldachinspinne und einer Höhlenspinne (14)).

Fig. 15) Femoral trichobothria of a member of the family Uloboridae. (Becherhaare auf dem Schenkel einer Kräusel-Radnetzspinne).

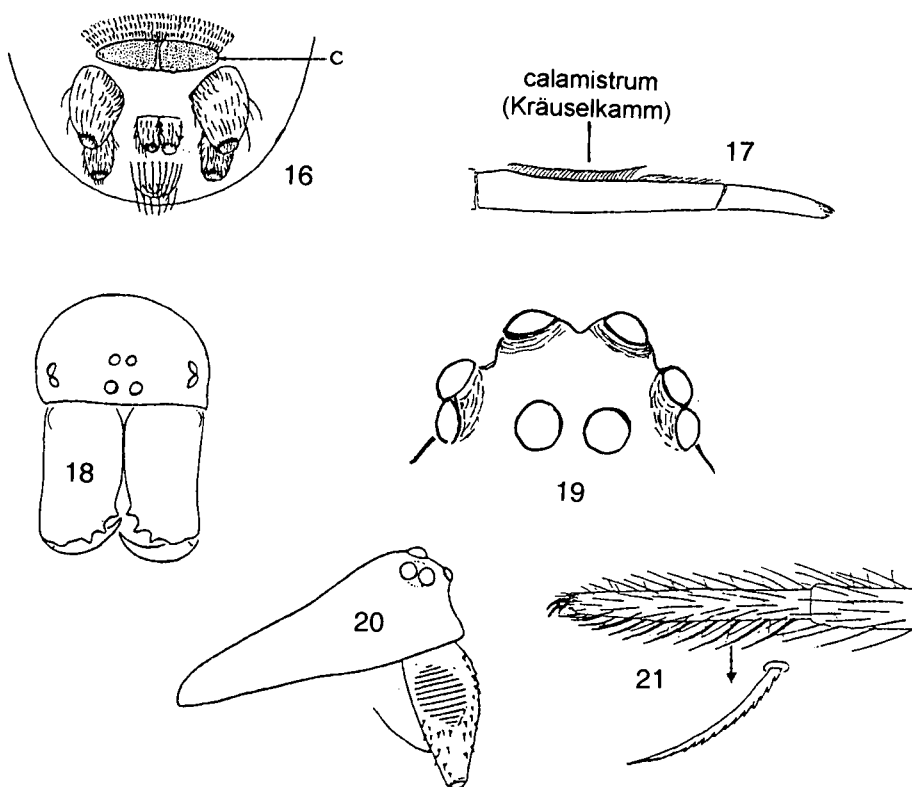


Fig. 16) Spinnerets and cribellum (C) of a member of the Dictynidae: Dictyninae, ventral aspect. (Spinnwarzen und Spinnsieb (C) einer Eigentlichen Kräuselspinne von unten).

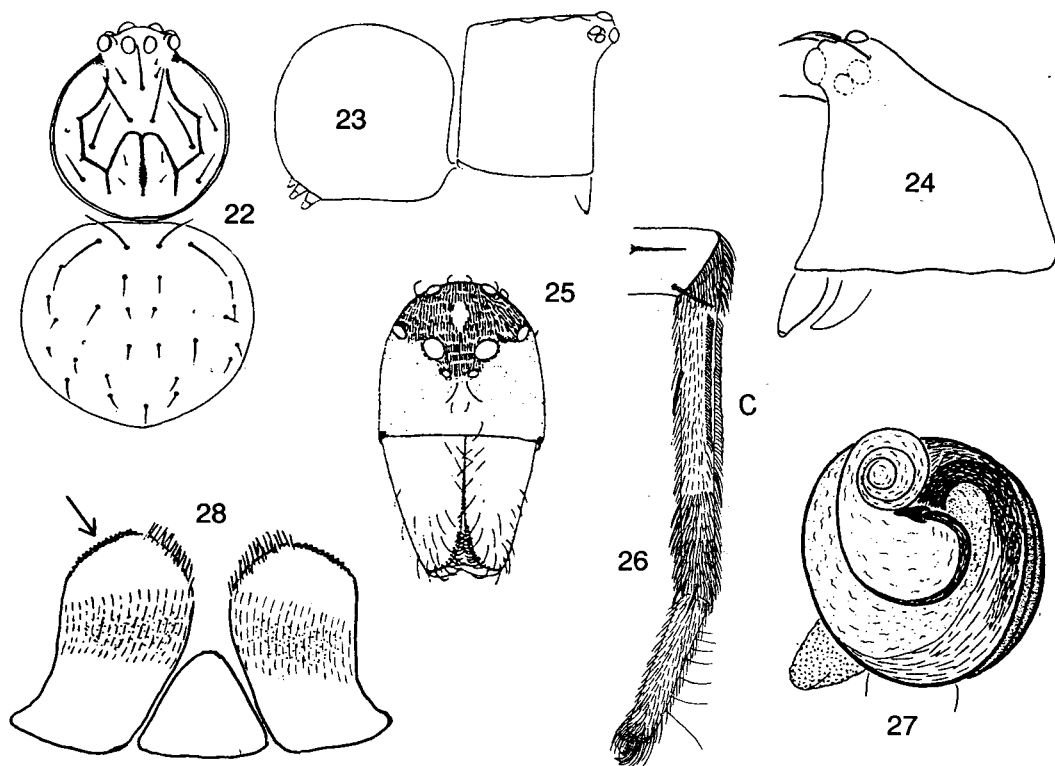
Fig. 17) Tarsus and metatarsus with the calamistrum of a member of the Dictynidae: Dictyninae. (Die letzten beiden Fußglieder mit dem Kräuselkamm einer Eigentlichen Kräuselspinne).

Fig. 18) Typical eye position of a member of the family Araneidae, anterior aspect. (Typische Position der Augen einer Radnetzspinne von vorn).

Fig. 19) Typical eye position of a member of the family Zygiellidae, dorsal aspect. (Typische Position der Augen einer Sektorspinne von oben).

Fig. 20) Lateral cheliceral stridulatory files of a member of the family Linyphiidae. (Seitliche Schriill-Rillen auf den Kiefern einer Baldachinspinne).

Fig. 21) Posterior tarsus of a member of the Theridiidae: Theridiinae with the ventral bent and serrated strong hairs. Taken from DIPPENAAR-SCHOEMAN & JOCQUE (1997). (Hinteres Fußglied eines Vertreters der Eigentlichen Kugelspinnen mit den starken unteren, gebogenen und sägerandigen starken Haaren).



Figs. 22-23) Dorsal and lateral aspect of the body of a fossil Theridiid spider, *Dipoenalasa* sp. Note the distinct furrows on the prosoma. (Ansicht des Körpers einer fossilen Kugelspinne der Gattung *Dipoenalasa* von oben und von der Seite. Man beachte die ausgeprägten Furchen auf dem Vorderkörper).

Fig. 24) Lateral aspect of the prosoma of a fossil Theridiid spider, *Dipoenalasa* sp. (Vorderkörper einer fossilen Kugelspinne der Gattung *Dipoenalasa* von der Seite).

Fig. 25) Frontal aspect of the prosoma of a member of the family Oxyopidae. Note the special eye position and the long clypeus. (Vorderkörper einer Scharfaugenspinne von vorn. Man beachte die besondere Position der Augen und den langen **Clypeus** - dem Abstand zwischen dem Feld der Augen und dem vorderen/unteren Rand des Vorderkörpers).

Fig. 26) Posterior tarsus and metatarsus with the calamistrum in two rows (C) of an extant member of the Amaurobiidae: Amaurobiinae. Taken from WIEHLE (1953). (Die letzten beiden Fußglieder des hinteren Beins mit dem zweireihigen Kräuselkamm des Metatarsus (C) einer Eigentlichen Kräuselspinne).

Fig. 27) Ventral aspect of the right bulbus of the σ -pedipalpus of *Acrometa* sp. (Synotaxidae). (Rechter σ -Pedipalpus einer Kugel-Höhlenspinne der Gattung *Acrometa* von unten).

Fig. 28) **Gnathocoxal depression** and **serrula**: a row of tiny teeth along anterior margin of the gnathocoxa, arrow, frequently only visible as a dark line. (**Depression** und "sägeartiger Rand" (**Serrula**) der Gnathocoxen: Eine Reihe winziger Zähnen (Pfeil), die oft lediglich als dunkler Rand sichtbar ist).

Selected characters and the distribution of spider families and selected subfamilies of the infraorder Araneomorpha (families are listed in alphabetic order within particular groups):

See the remarks below.

+ = present, - and absent characters, characters in brackets are rarely present.

* = extinct taxa.

taxa in Baltic amber are underlined.

Note: A claw tuft is usually absent in three-clawed spiders, but usually present in two-clawed spiders.

Body size in mm. Tiny spiders are <1.5mm long, small spiders 1.5-5mm, spiders of medium length are usually 5-10mm long, large spiders are usually >10mm long.

Distribution: A = Australian Region, AF = Africa, As = Americas, C = cosmopolitan, E = Europe, E = fossil in Baltic amber, H = holarctic, M = Mediterranean Region, Mad = Madagascar, NA = North America, NH = Northern Hemisphere, NT = neotropical, O = Oriental, P = Palaearctic, PS = pansubtropical, PT = pantropical, SA = South America, SAF = South Africa, SH = Southern Hemisphere, T = tropical, WS = widely spread.

- (1) "ARCHAIC" FAMILIES: Three tarsal claws, usually two pairs of lungs (only one pair in the Austrochilinae), most often cribellate (some Gradungulidae are ecribellate); diaxial or semidiaxial fangs, tarsal trichobothria absent, usually only 1 metatarsal trichobothrium (several in some Hypochilidae), cheliceral stridulatory files are present in the Austrochilidae and Gradungulidae, usually "simple" genitalia with the cymbium short and/or outstanding from the bulbus, most often very long ♂-pedipalpus, no epigyne. Three families in probably three superfamilies.

Taxon	usual body size	number of eyes	capture web	special characters	distrib- ution
Austrochilidae.....	medium	8	+/-	horizontal capture web	SA, A
Gradungulidae.....	medium	8	+	very long proclaws I-II	A
Hypochilidae.....	medium	8	+	calamistrum in two rows, gnathocoxal serrula in several rows	NA, China

- (2) DYSDEROIDEA: Usually three tarsal claws, but the unpaired claw is absent in the Dysderidae: Dysderinae, Loxoscelidae, Oonopidae, Orsolobidae and Sicariidae. Most often the anterior median eyes are absent or reduced, tarsal trichobothria absent with the exception of the Caponiidae, only 1 metatarsal trichobothrium, usually simple ♂-genitalia with the cymbium short and/or outstanding from the large bulbus, no epigyne; only the family Filistatidae is cribellate.

Taxon	body size	number of eyes	unpaired tarsal claw	special characters	distribution
Caponiidae.....	small	2,4,6,8	+	tarsal trichobothria, no leg bristles	As, TAF
Drymusidae.....	med.-large	6	+	long leg III, very short cymbium	As, TAF
Dysderidae.....	small-large	6	+/-	patellae distinctly longer than the tarsi	P, mainly M (few C, introduced)
Filistatidae.....	small-large	8	+	cribellate; patella-tibia autotomy	C
Leptonetidae	tiny-small	6	+	tibial glands, long fangs, patella-tibia autotomy	NH
Loxoscelidae.....	small-large	6	-	flattened body, long leg III	PT, PS
Ochyroceratidae..	tiny-small	6	+	long anterior spinnerets, few or no leg bristles	PT
Oonopidae.....	tiny-small	6(4,8)	-	(opisthos. frequently armoured)	C
Orsolobidae.....	tiny-small	6	-	raised tarsal organ	SH
Periegopidae.....	medium	6	+	widely spaced eye diads	A
Pholcidae.....	tiny-large	8,6(2)	+	no leg bristles, modified σ -chel.	C
Plectreuridae...	small-medium	6,8	+	chelicerae fused and laminate, cheliceral stridulatory files	H
Scytodidae.....	small-medium	6	+	no leg bristles, reduced 3. claw	C
Segestriidae.....	small-large	6	+	leg III directed forwards	C
Sicariidae.....	medium-large	6	-	short clypeus, thick spines, long leg III, chelic. stridulat. files	TAF, NT
Telemidae.....	tiny-small	6	+	only 1 tibial bristle, tibial glands, opisthosomal sclerite, no lungs	WS
Tetrablemmidae..	tiny-medium	4,6(2,1)	+	armoured opisthosoma, no leg bristles	PT

(3) ERESOIDEA: Caput large and raised (graded) (flat in the Eresidae: Penestominae and Palpimanidae: Stenochilinae), wide eye field, cheliceral stridulatory files (except in the Eresidae), no leg bristles (except in the Eresidae, in which ventral leg bristles occur and which is the only cribellate family, and in the Huttoniidae on legs III-IV); tarsal trichobothria absent, only 1 metatarsal trichobothrium present, small pedipalpus in both sexes.

Taxon	body size	special characters	distribution
Archaeidae.....	small	long chelicerae, foramen, labral humps	SH
Archaeinae.....	small	femoral hump, sclerot. ring around spinnerets	
Eresidae.....	medium-large	entelegyne, only one pair of rec. sem.	WS
Huttoniidae.....	medium	caput low, bristles on leg III-IV	A
*Lagonomegopidae...	small?	special eye position	Asia
Palpimanidae.....	small-medium	very strong leg I, short tarsi & metat.	C
*Spatiatoridae.....	medium	long prosoma	E

- (4) OECOBIOIDEA : Prosoma wide and nearly circle-shaped, with a narrow eye field, legs usually mediograde, tarsal trichobothria absent, only 1 metatarsal trichobothrium present or several in the Hersiliidae, cribellate are the Lebanoecobiinae and the Oecobiinae: Oecobiini; large anal tubercle, long apical article of the posterior spinnerets, usually with apical cymbial bristles (absent in the extinct Mizaliinae); a patella-tibia autotomy is present at least in the Hersiliidae and the Oecobiini.

Taxon	body size	special characters	distribution
<u>Oecobiidae</u>	tiny-large	special hairs of the large anal tubercle	C
* <u>Lebanoecobiinae</u>	small	cribellate, simple bulbus	Lebanon
* <u>Mizaliinae</u>	medium	large/wide colulus, simple bulbus	<u>E</u>
Oecobiinae.....	tiny-large	complicated bulbus structures	C
<u>Hersiliidae</u>	medium-large	very long posterior spinnerets, several metatarsal trichobothria	C

- (5) ARANEOIDEA s. l.: Presence of a retrobasal paracymbium (lost in the Theridiidae and very few Linyphiidae as *Ceratinopsis*), rosette-shaped position of the spinnerets, tarsal trichobothrium absent, only 1 metatarsal trichobothrium present. Basically with orb web, it may be strongly modified or even absent. Tarsal claw tufts, scopulae as well as paired ventral tibial I-II bristles close to the article are absent. A sclerotized epigyne is present and bears frequently a scapus. Cribellate are only the Deinopidae and the Uloboridae. Basically 8 eyes; 6 eyes are present in some Theridiidae and Uloboridae as well as in numerous Anapidae s. l. - The most diverse superfamily, 17 families; only the tiny Anapidae: Symphytognathinae and the medium-sized Jurassic Juraraneidae (not preserved in amber) are not reported from Baltic amber.

Taxon	body size	special characters	distribution
<u>Anapidae</u>	tiny-small	dwarfism, long tarsi, no femoral bristles, lungs, paracymbium and and ♀-pedipalpus reduced	C
<u>Anapinae</u>	tiny-small	opisthosomal scuta, prosomal wrinkles, apophyses of the ♂-pedipalpus	C
<u>Comarominae</u>	tiny-small	opisthosomal scuta, only 1 tibial bristle	H
<u>Mysmeninae</u>	tiny-small	femoral organ, denticles in the cheliceral furrow	C
<u>Synphrinae</u>	tiny-small	1 promarginal cheliceral tooth, special base of the tibial trichobothria,	NH
Symphytognathinae....	tiny	more or less fused chelicerae, loss of ant. med. eyes & colulus	PT
<u>Araneidae</u>	tiny-large	opisthosomal scutum in the male, short clypeus, wide eye field	C

<u>Araneinae</u>	tiny-large	short clypeus, usually stout leg spines, (gnatho)coxal spur, twisted bulbous embolus + seam guided by the cymbium	C
* <u>Miraraneinae</u>	small	no epigynal scapus, embolus guided by a long conductor	E
<u>Nephilinae</u>	tiny-large	paracymbium bipartite, cymbium partly guiding the long embolus	PT
* <u>Baltsuccinidae</u>	small	advanced position of the tracheal spiracle, opisthosoma usually elongated	E
<u>Cyatholipidae</u>	tiny-small	cribellate, huge posterior median eyes	E, SH
<u>Deinopidae</u>	medium-large	stout leg spines	E, PT
* <u>Juraraneidae</u>	medium	cheliceral stridulat. files, free paracymbium, patella-tibia leg autotomy	Asia
<u>Linyphiidae</u>	tiny-large	"mimetid leg bristles" except in Oarci-ni- σ , frequently cheliceral "peg teeth"	C
<u>Mimetidae</u>	small-medium	denticles in the cheliceral furrow	C
<u>Nesticidae</u>	small-medium	cheliceral stridul. files, cymbial denticulate process, patella-tibia autotomy	H
<u>Pimoidae</u>	small-medium	eye field wide, two tegular apophyses	E
* <u>Protheridiidae</u>	small	paracymbium excavate, denticulate bulbous apophysis	E, A, As
<u>Synotaxidae</u>	tiny-medium	twisted embolus + conductor	C
<u>Tetragnathidae</u>	small-large	tibial apophysis of the σ -pedipalpus, usually cymbial outgrowth	E, ST-T
<u>Diphyinae</u>	small-medium	femoral trichobothria, large chelicerae	C
Tetragnathinae...	small-large	no retrobasal but retrodistal or intern paracymbium, frequently tarsus IV with comb	C
<u>Theridiidae</u>	tiny-large	sternal glands, several long bristles and trichobothria on tibia III/IV	C
<u>Theridiosomatidae</u>	tiny-medium	cribellate, femoral trichobothria	C
<u>Uloboridae</u>	small-large	paracymbium more or less free and movable; open hub	NH
<u>Zygiellidae</u>	small-medium		

(6) RTA-CLADE: Usually with several tarsal and metatarsal trichobothria (reduced or absent in some Dictynidae; tarsal trichobothria are absent in some Dictyninae, the Amaurobiidae: Phyxelinae, the Nicodamidae and the Titanoecidae), a sclerotized epigyne is present. RTA: A retrolateral tibial apophysis is usually present (absent in the Lycosidae, Nicodamidae and Psechridae; also present in some members of the Araneoidea as most Linyphiidae: Erigoninae). The superfamily subdivision of this clade is unclear.

(6a) "TRIONYCHA": Unpaired tarsal claw usually present (reduced or absent e.g. in several Miturgidae, Zoropsidae and very few Zodariidae), claw tuft usually absent. Cribellates are frequent (cribellate members occurs within 10 families): Probably most Amaurobiidae s.l. (e.g. the Amaurobiinae), some Desidae, most Dictynidae: Dictyninae, Miturgidae, Nicodamidae: Megadictyninae, Psechridae,

some Stiphidiidae, Tengellidae, Titanoecidae and most Zoropsidae s. l. (except Machadoniini). - Most spiders build capture webs or tubes; hunters are Cycloctenidae, Chummidae, most Lycosidae, Oxyopidae, most Pisauridae, Senoculidae and Zodariidae.

Taxon	body size	special characters	distribution
<u>Agelenidae</u>	small-large	wide and +/- divided colulus	C
<u>Ageleninae</u>	small-large	one row of tarsal trichobothria	C
<u>Amaurobiidae</u>	small-large	most often cribellate & with additional dorsal tibial apophyses of the ♂-pedipalpus	C
<u>Amaurobiinae</u>	small-large	calamistrum + pseudocalamistrum	H, NT
Chummidae.....	small	opisthosoma with scutum and anterior bristles	SAF
Cycloctenidae.....	small	3 eye rows, mostly flat body & legs laterigrade	A
Desidae.....	small-large	very large and porrect chelicerae	C
<u>Dictynidae</u> s. l.	tiny-medium	reductions of body size & tarsal trichobothria	C
<u>Copaldictyninae</u>	small	cribellate, chelic. files, "paratibia", cymbial "horn"	M
<u>Cryphoecinae</u>	small-medium	ecribellate, strongly sclerot. ♀ genital area	C?
<u>Dictyninae</u>	tiny-medium	basically cribellate, large/modified ♂-chelicerae, long conductor	C
<u>Hahniinae</u>	tiny-medium	ecribellate, usually transverse row of spinnerets, (stridulatory organ)	C
<u>Mizagallinae</u>	small	ecribellate, tuberculate chelicerae, embolic seam	WS
* <u>Ephalmatoridae</u>	small	wide conductor in a circular position	E
Halidae.....	small	3 eye rows, thorax higher than the caput	Mad
* <u>Insecutoridae</u>	medium	single row of tarsal trichobothria, no colulus	E
Lycosidae.....	small-large	special eye position in three rows, no tibial apophysis of the ♂-pedipalpus, ♀ carries egg sac at the spinnerets	C
Miturgidae.....	?	no fovea?	T?
Neolanidae.....	medium	cribellate, leg scopulae present	A
Nicodamidae.....	small-large	cribellate or ecribellate, no tarsal trichobothria, no RTA but dorsal tibial apophysis	A SE Asia
<u>Oxyopidae</u>	small-large	prosoma very high, eye position nearly in a circle	C
<u>Pisauridae</u>	small-large	? - opisthosoma widened in the middle, tapering posteriorly, the female carries its egg sac with the chelicerae	C
Psechridae.....	(med.-)large	cribellate, calamistrum in a field or rows, no RTA	A, Asia
Senoculidae.....	(medium-)large	strongly recurved anterior eye row	M-, SA
Stiphidiidae.....	medium-large	? - frequently ♂ with a stridulatory organ between pedicel/prosoma and opisthosoma	A
Tengellidae.....	large	cribellate, tarsi with scopula	As
Titanoecidae.....	small-large	reduced tarsal trichobothria, parallel gnathocoxae, long calamistrum,	mainly NH
<u>Trechaleidae</u>	small-large	female carries egg sac at the spinnerets, ♂-pedipalpus with ventral hump or apophysis on the tibia	WS
<u>Zodariidae</u>	small-large	no gnathocoxa serrula, usually stout fangs (8 or 6 eyes, an unpaired tarsal claw may be absent)	C
<u>Zodariinae</u>	small-large	hairy femoral gland? Opisthosomal scutum, ring around spinnerets	C

<u>Zoropsidae</u> s.l.	small-large	usually cribellate (except Machadoniini and probably Eoprychiini), σ -tibial suture present except in Acanthocheini, retrobasal paracymbium	M,PT
? <u>Acanthocheini</u>	medium-large	no tibial suture	T, mainly SH
* <u>Eomatachiini</u>	small-medium	claw tufts absent, unpaired tarsal claw present	E
* <u>Eoprychiini</u>	medium	depressed prosoma	E
<u>Machadoniini</u>	medium-large	ecribellate, claw tufts absent, unpaired claw present or absent	AF, O
<u>Udubiini</u>	large	?	Mad
<u>Zoropsini</u>	medium-large	no tibial break/autotomy	P

(6b) "DIONYCHA": Unpaired tarsal claw absent, claw tuft most often present. Ecribellate without exception. Usually hunters, some Salticidae build capture webs.

Taxon	body size	special characters	distribution
<u>Ammoxenidae</u>	tiny-large	chelicerae modified for digging	SAF
<u>Anyphaenidae</u>	small-large	tracheal spiracle in an anterior position	C
<u>Borboropactidae</u>	small-large	"tarsal pit organ", powerful leg I	E, TAF, Asia
* <u>Succiniraptorinae</u>	small	fangs short, clypeus long	E
<u>Cithaeronidae</u>	small-medium	pseudosegmented tarsi, irregular posterior median eyes, subdistal sclerotized ring around posterior spinnerets	SE, Asia, AF
<u>Clubionidae</u>	small-large	pale, weakly sclerotized, mostly wide eye field	C
<u>Corinnidae</u>	small-large	scale-shaped cuticula, frequently with opisthosomal scutum and myrmecomorph	C
<u>Corinninae</u>	small-large	leg I>IV, usually powerful chelicerae	C
<u>Castianeirinae</u>	small-large	leg IV>I, sclerot. trach. openings, long cymbium	WS
<u>Trachelinae</u>	small-medium	leg I>IV, mostly no bristles but cusps of leg I-II	C
<u>Phrurolithinae</u>	small-medium	leg IV>I, gnathocoxal depression, frequently oval posterior median eyes	C
<u>Ctenidae</u>	(medium-)large	three eye rows, concave median apophysis	WS
<u>Gallieniellidae</u>	small-medium	long chelicerae, oval posterior median eyes, small apical article of the anterior spinnerets	A, AF
<u>Gnaphosidae</u>	small-large	oval post. median eyes, depressed gnathocoxae, anterior spinnerets cylindrical, parallel and usually widely spaced	C
<u>Liocranidae</u>	small-large	?	C
<u>Philodromidae</u>	small-large	legs laterigrade, body flat, rec. post. eye row	C
<u>Salticidae</u>	small-large	eyes in 3 rows on a case-shaped high prosoma with extremely large anterior median eyes which are directed forwards	C
<u>Cocalodinae</u>	small-large	large posterior median eyes, median apophysis present, usually numerous retrotromarginal cheliceral teeth, large ventral tibial apophysis of the σ -pedipalpus	WS, E
<u>Lyssomaninae</u>	small-large	4 eye rows, elongate chelicerae & cymbium	PT
<u>Euophryinae</u>	small-large	?	C
<u>Salticinae</u>	small-large	loss of the distal haematodocha	C
<u>Selenopidae</u>	medium-large	legs laterigrade, body flat, anterior position	PT

	of the posterior median eyes	
Sparassidae.....	small-very large trilobate dorsal-apical metatarsal mem- brane, legs usually laterigrade	C
<u>Thomisidae</u>	small-large laterigrade legs with long legs I-II, usually large lateral and small median eyes, ♂ pedipalpal tibia with ventral apophysis	C
<u>Stephanopinae</u> ..	small-large several cheliceral teeth, claw tufts mainly T,E	
Thomisinae.....	small-large no claw tufts, 0-1 chelic. tooth, ♂: Tutaculum	C
<u>Trochanteriidae</u>	small-large legs laterigrade, body flat, chelicerae long and protruding, eye field wide, usually posterior median eyes reduced and re- troventral tibial I-II bristles absent, occasionally long trochanter IV	T

General remarks on the list above:

(1) The limits, subfamilial divisions and - partly - the relationships of several families are yet unsolved, mainly of the Agelenidae (?= Insecutoridae, incl. Cryphoecinae?), Amaurobiidae, Clubionidae, Ctenidae, Desidae (incl. *Toxops*?), Dictynidae, Gnaphosidae, Miturgidae, Zodariidae and Zoropsidae ("my" tribus may be regarded as subfamilies); see the papers on these families (except the Ctenidae) in these volumes. The numbers - and the names - of the superfamilies of the classical "Trionycha" and "Dionycha" are also unclear.

(2) Only few subfamilies are listed, mainly those which are known in Baltic or Dominican amber.

(3) Acanthoectenidae: See Zoropsidae, Amphinectidae: See Amaurobiidae, Aphantochilidae: See Thomisidae, Argyronetidae: See Agelenidae, Arthrodictynidae: See Dictynidae, Cryptothelidae: See Zodariidae s. l., Cybaeidae: See Agelenidae, Diguettidae: See Plectreuridae, Dolomedidae: See Pisauridae, Hadrotarsidae: See Theridiidae, Hahniidae: See Dictynidae s. l., Holarchaeidae: See Mimetidae, Homalonychidae: See Zodariidae s. l., Inceptoridae: See WUNDERLICH (1986: 25), Lamponidae: See Gnaphosidae, Mecysmaucheniidae: See Archaeidae, Malkariidae: See Mimetidae, Micropholcommatidae: See Anapidae, Miturgidae: See Clubionidae, Mysmenidae: See Anapidae, Pararchaeidae: See Mimetidae, Phyxelidae ?= Amaurobiidae, Platoridae: See Trochanteriidae, Prodidomidae: See Gnaphosidae, Symphytognathidae: See Anapidae.

(4) The following families are not - or only marginally - treated in these volumes: Ammoxenidae, Bradystichidae, Chummiidae, Cithaeronidae, Cycloctenidae, Desidae (most probably not monophyletic), Gallieniellidae, Lycosidae, Miturgidae (incl. Tengellinae?), Neolanidae, Nicodamidae, Psechridae, Selenopidae (see the paper on spiders in copal from Madagascar), Senoculidae, Stiphidiidae, Tengellidae, Titanocidae Toxopidae s. str. and Zoridae (see Liocranidae).

Remarks on selected special characters (see also above):

(1) Members of some families possess quite variable characters, e.g. 8 or only 6 eyes may be present, an unpaired tarsal claw or a cribellum may be present or absent. Such families can be found in different positions in the keys.

(2) Eyes. Most spiders have 8 eyes, some possess 6 eyes (e.g. most Dysderoidea, some Mygalomorpha and Uloboridae, numerous Anapidae), members of the Tetrablemmidae may have 4 or 2 eyes or even - one species - only a single eye; numerous cave dwelling spiders are eyeless. In some families - e.g. Deinopidae, Oxyopidae, Lycosidae and Salticidae - the eye position is characteristic and unique; within other families - e.g. the Pholcidae and Uloboridae - the number and the position of the eyes is quite variable. The position of the posterior eye row may be straight (fig. 1b) or anteriorly concave (= procurved) or anteriorly convex (= re-curved) (fig. 4).

(3) The fovea is a more or less deep depression of the prosoma which occur in numerous spiders; in other spiders a "thoracal fissure" or ridge is present, in few spider taxa none of these structures is present.

(4) The mouth parts (fig. 1a). Most striking are the two-jointed chelicerae; its basal article may be protruding - e.g. in the Mesothela, Mygalomorpha, some Clubionidae and Corinnidae - or strongly enlarged and diverging -, e.g. in numerous Tetragnathidae and most Archaeidae (fig. 10). In some taxa the basal cheliceral articles are fused together, e.g. in several members of the Dysderoidea, the Symphytognathinae of the Anapidae s. l. and the Mimetidae: Mimetini.

Retrolateral (outer) cheliceral stridulating files (photo 261, fig. 20) are present - although hard to observe in most fossil spiders -, e.g. in the Archaeidae, several Dysderoidea, some Hahniidae, the Linyphiidae, some Mimetidae (prolateral files in *Pararchaea*), the Palpimanidae, Pimoidae, Spatiatoridae and rarely in some other families as Araneidae and Tetragnathidae; see the paper on the family Linyphiidae in these volumes. Such files are very rare in the RTA-clade.

The fangs may be stout, e.g. in the Segestriinae: Ariadninae and in most Zodariidae, long e.g. in the Tetragnathinae. In the Mesothelae and Mygalomorpha - see the paper on this infraorder in this volume - the position of the fangs is nearly parallel, in the Araneomorpha the fangs are working - nippers-shaped - against each other (less distinct e.g. in the Dysderidae) and are crossed in the resting position. On the ventral side the labium is situated in front of the sternum between and at the base of the gnathocoxae. In most spiders the gnathocoxae anteriorly bear a "serrated" margin which consists of tiny teeth, the gnathocoxal serrula (arrow in fig. 28). In some taxa - e.g. in some Prodidominae (Gnaphosidae) and Trochanteriidae as well as in all Zodariidae - such a serrula is absent; this is considered an important taxonomical character. A further - inner and mostly hidden - structure of the mouth parts is the labrum which can be observed in some fossil Archaeidae in the frontal aspect. An anterior labral outgrowths is present e.g. in the Anapidae: Anapinae and Comarominae.

(5) The (pairs of) legs are designated in its order (sequence): I-II-III-IV.

(6) The leg position. In most spiders the legs I-II are directed forward and legs III-IV are directed backwards (in numerous fossil spiders exist an unnatural leg position!). This position is called prograde, and leg I is usually longer than II in these spiders. - Members of the family Segestriidae have a unique position: Legs I-III are directed foreward, only leg IV is directed backwards (photo 15). - In several families

- e.g. the Philodromidae, Selenopidae, Sicariidae, most Sparassidae, Thomisidae and Trochanteriidae - the legs are directed sideways (laterigrade), the powerful legs I and II are curved sideways in a concave position, frequently in a "sit-and-wait" position (photos 400, 436-437, 390-394). In these spiders the body is flattened and leg I is usually shorter than II. - In some spiders the leg position is more or less intermediate between these two positions - prograde and laterigrade -, usually leg I or IV is the longest and the patella III-IV is directed backward. I call this position "mediograde" according to an suggestion of P. JÄGER (SMF). Such a position is present e.g. in some members of the Scytodidae, some Sparassidae as *Micrommata* LATREILLE 1804, some Mimetidae as *Praeoarces* n. gen., most Oecobioidae, some Araneidae and some fossil Synotaxidae as *Acrometa* PETRUNKEVITCH 1942 (photos 36, 94, 217, 219).

(7) The tarsus (fig. 2) - as the eyes, the spinnerets and the genital organs, too, see above - has a special taxonomical value. There may be three claws - one pair and a single small unpaired ("third") claw between the paired claws - which are usually freely observable. Other spiders have only a pair of tarsal claws; in these spiders usually an additional brush of hairs is present under the claws: A "true claw tuft" of flattened/spatulate hairs (photos 427-428) or a "false claw tuft" of thin hairs. A tarsal scopula (photo 389) may be present which consists of spatulate hairs, a "pseudoscopula" consists of more or less dense thin hairs. (Also the metatarsus and distal parts of the tibia may bear a scopula or pseudoscopula).

(8) Leg autotomy. In some families - e.g. the Agelenidae - leg autotomy is extremely rare; in most spider families a break may occur between the coxa and the trochanter - photo 14, see the chapter on the leg autotomy in this volume -, and in numerous fossil spiders one or several loose legs are placed near the spider in the fossil resin. In fewer families - e.g. in about 40% of the fossil Linyphiidae as well as in the rare Pimoidae and in the rare Leptonetidae - such a break frequently occurs between patella and tibia and may be helpful in the determination of a member of these families, photo 674. A unique case is the breaking at a suture near the base of the tibia in the males (!) of fossil Zoropsidae, e.g. in the genus *Eomatachia* PETRUNKEVITCH (photo 318), whose members are not rare in Baltic amber (in the extant Zoropsini a tibial suture is present but no break occurs in this position), see the paper on this family.

(9) Spinnerets, cribellum and calamistrum. Most spiders possess three pairs of spinnerets - called anterior (-lateral), median and posterior spinnerets; the median ones being the smallest and hidden in most fossils. The "archaic" Mesothelae have four pairs of spinnerets in an advanced position. Members of the Zodariidae have three, two or even only one (the anterior) pair, and also in some Mygalomorpha the number of spinneret pairs is reduced. In some Mygalomorpha, the Hersiliidae (fig. 11) and the Agelenidae (e.g.) the posterior spinnerets are strongly elongated and may bear medial spinules (spigots, spinning tubes). - Cribellum and calamistrum are present in many families - see the tab. above -, and may be reduced especially in the male sex of certain families, e.g. the Dictynidae, see the paper on this family in these volumes. The cribellum (photos 285, 305, fig. 16) looks similar to a wide sieve and is situated in front of the spinnerets; it may be divided. Unfortunately in the fossil spiders the cribellum is frequently hidden by a white emulsion or because

of its special resting position. In numerous spiders the cribellum is replaced by a lobe, the colulus (fig. 1a), which is usually pointed lobe, but may be slightly divided (in the Agelenidae) or may be a wide lobe (in the genus *Mizalia* KOCH & BERENDT 1854 (Oecobiidae)). In several families the colulus is strongly reduced, replaced by a pair of hairs or is completely lost; in the family Theridiidae we find all the three stages. If the anterior spinnerets are slender and close together a cribellum is always absent. - The calamistrum (photo 557, fig. 17) is usually a single row of short and bent hairs retrodorsally on the metatarsus IV, there are rarely two rows (e.g. in the Amaurobiinae) (fig. 26) or a field/indistinct row of hairs (Psecridae). Usually the margin of the metatarsus which bears the calamistrum is compressed; in the Uloboridae the metatarsus IV is distinctly concave along the calamistrum.

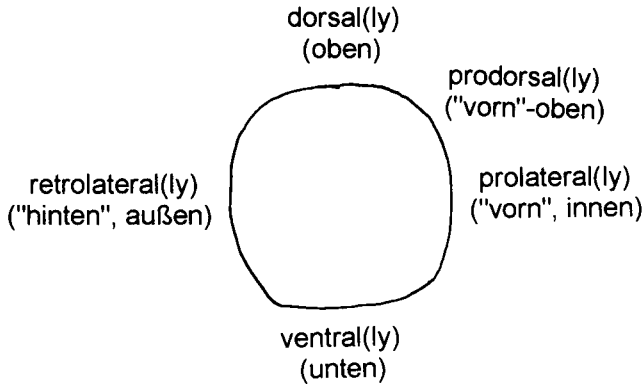
(10) Spines, bristles, hairs and trichobothria (figs. 2a, b) and **terms of the position** in spiders (see the figs. below):

Anterior = in front (in German: vorn),
 apical = at the tip (am Ende),
 basal = at or near (proximal) the base (am Grunde, nahe dem Grunde),
 distal = away from a structure of the middle (jenseits einer Struktur oder der Mitte),
 dorsal = the upper surface (oben),
 frontal = see anterior (frontal view),
 lateral = at the side (seitlich),
 medial, median = (in the) middle (in der Mitte, mittlere Position),
 posterior = (situated) behind (hinten),
 pro- : See anterior,
 procurved = the outer edges - e.g. of an eye row - are in front of the central part;
 see recurved (außen nach vorn gebogen, vorn konkav; siehe recurved),
 prolateral = situated at the anterior side (seitlich-vorn),
 retro- : See posterior,
 recurved = the outer edges - e.g. of an eye row - are behind the central part; see
 procurved (außen nach hinten gebogen, vorn konvex; siehe procurved),
 retrolateral = situated at the posterior side (seitlich-hinten),
 ventral = the under surface (unten), side of the venter (Bauchseite).

Several, one or none of the distal five leg articles - femur, patella, tibia, metatarsus and tarsus - may bear bristles. Tarsal bristles are rare and present ventrally-distally e.g. in the Filistatidae, Oecobiidae and some Uloboridae and Mygalomorpha. Slender "macrosetae" are called bristles, stout "macrosetae" - as in the Ctenizidae and in most Thomisidae - are called spines, but due to transitions the limit between both is not clear.

Trichobothria occur at least on the tibia and the metatarsus, rarely on the femora, (Uloboridae and several Tetragnathidae). They are most frequent on tarsi and metatarsi in members of the Mygalomorpha and of the RTA-clade (reduced or even absent in the Nicodamidae, Titanoecidae and some Dictynidae), see the paper on the superfamily Araneoidea. Within the superfamilies Dysderoidea (except the Caponiidae), Eresoidea, Oecobioidae and Araneoidea tarsal trichobothria are absent, and usually only a single metatarsal trichobothrium is present (usually two in the Hersiliidae). Most trichobothria are situated in a dorsal position and possess an enlarged base (fig. 2) in contrast to normal hairs. They are thin, usually long, and

most often bent backwards (to the base of the leg article); normal hairs are shorter and straight, with a tiny base. In several families - distinct e.g. in the family Agele-
nidae - the long tarsal trichobothria are increasing in length along the tarsus.



Cross-cut through a right femur, seen from the tip, to show the terms of different positions

(11) The tracheal spiracle is a slit-like opening of one of the respiratory systems on the ventral side of the opisthosoma; it may be paired. (The second respiratory system is the lung system). In most spiders it is situated closely in front of the spinnerets, but in several taxa - e.g. in *Argyroneta*, the Anyphaenidae, Cyatholipidae, most Hahniinae (photo 297) and *Pachygnatha* - it is situated far in front of the spinnerets and may be very wide (photo 209); in tiny spiders as Anapidae it may be strongly reduced or even absent. In most fossil spiders the tracheal spiracle is hard to recognize and most often covered/hidden by a white emulsion.

Suborders and infraorders of the order ARANEAE:

1. suborder Mesothelae
(German name: Gegliederte Spinnen)

2. suborder Opisthothelae
(German name: Ungegliederte Spinnen)

a) infraorder Mygalomorpha (= Orthognatha)
(German name: Längskieferspinnen)

b) infraorder Araneomorpha (= Labidognatha)
(German name: Querkieferspinnen)

Key to the families of the Mygalomorpha: See the paper on this infraorder in this volume.

Infraorder Araneomorpha:

Body length 0.6-1.5mm.**key 1**

- body length >1.5mm.**key 2**

Remarks: (1) Key 2 includes most members of the **RTA-clade** ("Dionycha" + "Trio-nycha"), but few fossil taxa of the RTA-clade - e.g. some members of the Dictynidae s. l. - are smaller than 1.5mm and are included in key 1. - (2) The RTA-clade includes taxa in which usually a retrolateral tibial apophysis is present; exceptions of the RTA-clade are e.g. the Lycosidae, Nicodamidae, Corinnidae: Castianeirinae and (all?) Psechridae in which a retrolateral tibial apophysis is absent. (In the Nico-damidae the retrolateral tibial apophysis probably changed to a mid-dorsal position, in the Lycosidae and Psechridae it has probably been lost; these families are un-known from amber fossils).

	6 eyes	8 eyes
opistho-somal scutum present	<u>tab. A</u> Anapidae, Tetrablem- midae, Oonopidae	<u>tab. B</u> Anapidae, Araneidae, Cyatholipidae, Theridiidae
opistho-somal scutum absent	<u>tab. C</u> Anapidae, Oonopidae, Pholcidae, Telemidae	<u>tab. D</u> Anapidae, Cyatholipidae, Dictynidae, Li- nyphiidae, Sy- notaxidae, The- ridiosomatidae

Key 1 (above): Survey of the families of the superfamily Araneomorpha in Baltic amber, body length 0.6-1.5mm. Anapidae are listed four times in this tab., Cyatholipidae and Oonopidae two times

Tab. A:

1 Leg bristles absent (except for the σ -leg I of some of the extant species). The chelicerae bear large anterior outgrowths in the fossil male, a smaller outgrowth is present in the eye field. Bulbus simple. *Balticoblemma* n. gen., photo 51. Tetrablemmidae

- Leg bristles present. Cheliceral and prosomal outgrowths absent. 2

2(1) Caput higher than the thorax, tarsi usually longer than the metatarsi. Bulbus complicated. The σ -leg I may be modified. Photos 143-179 Anapidae

- Thorax higher than the caput, tarsi distinctly shorter than the metatarsi. Bulbus simple. *Stenoonops*, photo 35 Oonopidae: Gamasomorphinae

Tab. B:

1 Tarsi usually longer than the metatarsi, the σ -leg I is frequently modified (thickened, bent, with spurs or spines), lung covers absent or strongly reduced. Photos 143-179. Anapidae

- Tarsi distinctly shorter than the metatarsi, the σ -leg I is modified in the Cyatholipidae, lung covers not reduced. Males. 2

2(1) Retrobasal paracymbium absent. E.g. *Phoroncidia*. Theridiidae

- Retrobasal paracymbium present. 3

3(2) Leg I modified (tibia bent, metatarsi with spurs), paracymbium divided. E.g. *Succinilipus*. Photos 189-209 Cyatholipidae

- σ : leg I not modified, paracymbium undivided. *Eonephila* (part.), photo 126. Araneidae

Tab. C:

1 Femur IV distinctly thickened (fig. 6); pedipalpus simple, pear-shaped. (Unpaired tarsal claw absent). *Orchestina*, photos 29-34 Oonopidae

- Femur IV not thickened. Unpaired tarsal claw present. 2

2(1) Leg bristles completely absent. (Articles of the σ -pedipalpus thickened similar to *Orchestina*, see no. 1. *Paraspermophora*, photos 52-55 Pholcidae

- The legs bear at least few bristles on the tibiae, articles of the σ -pedipalpus slender 3

3(2) Tarsi usually longer than the metatarsi, cymbium close to the complicated bulbus. The σ -leg I may be modified. Several genera, photos 143-179 Anapidae

- Tarsi distinctly shorter than the metatarsi, cymbium outstanding from the simple bulbus. σ -leg I not modified. Questionable *Telema*, photos 49-50. Telemidae

Tab. D:

1 Tarsi usually longer than the metatarsi. The σ -leg I may be modified, photos 143-179. Anapidae

- Tarsi distinctly shorter than the metatarsi. σ -leg I not modified 2

2(1) Metatarsi with several trichobothria, pedipalpal tibial and/or patellar apophysis present, paracymbium absent. *Eobrommella* and *Eohahnia*, photos 283, 297. Dictynidae

- Only one metatarsal trichobothrium, pedipalpal tibial and patellar apophysis absent, a retrobasal paracymbium is present. 3

3(2) Tibia I with lateral bristle(s) in the distal half. 4

- Tibia I without lateral bristle(s). 5

4(3) Legs long and slender, paracymbium large. Photos 248-263 Linyphiidae

- Legs stout, paracymbium indistinct, bulbus large. Photos 138-142. Theridiosomatidae

5(3) Cymbium usually with large retrolateral bristles (*Spinilipus*), photos 192-200 Cyatholipidae

- Cymbium without such bristles. Photos 223-233. Synotaxidae

Key 2	unpaired tarsal claw absent, claw tufts mostly present (1), cribellum absent, leg scopula present or absent	unpaired tarsal claw present and claw tufts absent (2), cribellum present or absent, leg scopulae very rarely present (2)
no tarsal trichobothria, only 1 metat. trichobothrium	Oonopidae (<i>Orchestina</i>)	<u>tab. E</u> Araneoidea s.l., Dysderoidea s. l. (3), Eresoidea s. l., Oecobioidae

at least 1 tarsal trichobothrium, several metat. trichobothria (5)	<u>tab. F</u> "Dionycha" (4)	<u>tab. G</u> "Trionycha"
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- (1) A claw tuft is absent in numerous Thomisidae (tab. F).
 (2) Occasionally the unpaired tarsal claw is absent and a claw tuft may be present: In the Dysderidae (mainly the Dysderinae), Loxoscelidae, Oonopidae, Orsolobidae, Sicariidae, some Zoropsidae which bear a leg scopula, and few Zodariidae; except the Oonopidae these taxa are not known from Baltic amber; Oonopidae in Baltic amber are usually less than 1.5 mm long (the genus *Orchestina*), see key 1. In the Scytodidae the unpaired tarsal claw is strongly reduced.
 (3) Frequently with only 6 eyes.
 (4) In several families the leg position is laterigrade.
 (5) Both may be absent or indistinct in some Dictynidae (tab. G). (Tarsal trichobothria are absent in the Nicodamidae, Titanoecidae and Amaurobiidae: Phyxelinae, which are not known from Baltic amber).

Key 2 (above): Survey of the families of the infraorder Araneomorpha in Baltic amber, body length >1.5mm

Tab. E:

Remarks: (1) On the keys to the families: See the papers on the four superfamilies in these volumes. (2) On cribellate spiders of this tab.: Not known from Baltic amber are (a) the only cribellate family of the Dysderoidea, the Filistatidae, (b) the only cribellate family of the Eresoidea, the Eresidae (both prefer dry biotopes), and (c) the cribellate Oecobiini of the Oecobiidae. The remaining cribellate families in this tab. are the Deinopidae and the Uloboridae of the superfamily Araneoidea s. l.

1 Leg bristles completely absent in the fossil spiders and cheliceral "peg teeth" present (fig. 10). Eresoidea 2

- Usually at least few leg bristles present, cheliceral "peg teeth" usually absent (present only in the Mimetidae (Araneoidea), see below). If leg bristles are completely absent - in some Dysderoidea, e.g. the Pholcidae - cheliceral "peg teeth" are absent 3

2(1) Dorsal femoral hump present (photos 63-64). Patellae not unusually long. Chelicerae usually strongly elongated and diverging (fig. 10) (weakly diverging in *Baltarchaea*). Archaeidae: Archaeinae

- Dorsal femoral hump absent. Patellae unusually long. Chelicerae not strongly elongated and diverging. *Spatiator*, photos 84-85. Spatiatoridae

- 3(1) Posterior spinnerets very long (fig. 11) or anal tubercle modified, large and hairy (fig. 12). Oecobioidae. 4

- Posterior spinnerets and anal tubercle not modified. 5

- 4(3) Posterior spinnerets unusually long (fig. 11), head region elevated, anal tubercle not modified. Photos 90-92 Hersiliidae

- Posterior spinnerets of a normal size, head region not raised, anal tubercle large and hairy (fig. 12). *Mizalia*, photos 95-97. Oecobiidae: Mizaliinae

- 5(3) Fossil spiders ecribellate (the extant Filistatidae is the only cribellate member of the Dysderoidea). ♂: At least one article of the pedipalpus is usually distinctly thickened (photo 34), cymbium usually short and/or outstanding from the bulbus, not covering the bulbus which is usually simple and has no or very few apophyses; retrobasal paracymbium absent. ♀: A sclerotized epigyne and a scapus are absent. 10 families in Baltic amber. See the key in the paper on this superfamily in this volume. Photos 14-55. Superfamily Dysderoidea

- Ecribellate (most families), but Deinopidae and Uloboridae are cribellate. ♂: Articles of the pedipalpus extremely seldom thickened, cymbium usually large and dorsally covering the bulbus which is complicated (very few exceptions in extant spiders), a retrobasal paracymbium is most often present (figs. 13-14) (absent e.g. in the Deinopidae, Uloboridae, Therididae and most Anapidae). ♀: Epigyne usually present (absent in several members of the Tetragnathidae), frequently with a scapus (e.g. photo 252). (A dorsal scutum of the opisthosoma occurs at least in the males of the fossil Araneidae as well as certain members of the Anapidae (Anapinae, Comarominae) and Cyatholipinae). - Except for the Juraraneidae all the remaining 15 families are present in Baltic amber. Most diverse spider superfamily in Baltic amber: Araneoidea s. l. 6

- 6(5) Special eye position with extremely large posterior median eyes which are directed forward (fig. 7) and the anterior lateral eyes at the margin of the prosoma. Cribellum and calamistrum present, similar to figs. 16-17. Photos 113-115 Deinopidae

- Eye position different. Cribellum and calamistrum present only in the Uloboridae, no. 7 7

- 7(6) Femoral trichobothria present (fig. 15). Cribellum (fig. 16) and calamistrum (fig. 17) present (as in the Deinopidae). Eye field very wide. Photos 98-112... Uloboridae

- Femoral trichobothria, cribellum and calamistrum absent. Eye field more narrow. 8

- 8(7) Tibia and/or metatarsus I-II prolaterally with long bristles and usually short bristles between them, which are more strongly bent (fig. 9). The chelicerae bear

- "peg teeth" (long bristles), which are hard to recognize in most fossils. Photos 242-244. Mimetidae
- No such leg bristles neither cheliceral "peg teeth". 9
- 9(8) Clypeus short, most often shorter than the length of the field of the median eyes. Legs and leg bristles usually stout 10
- Clypeus usually longer than the length of the field of the median eyes, in the Baltsuccinidae and Protheridiidae both are equal in length. Legs and leg bristles most often slender (usually stout in the Theridiosomatidae). 11
- 10(9) Eye field usually very wide, with the median eyes most often distinctly closer to each other than to the lateral eyes (fig. 18), similar to the Protheridiidae. A hardened or scutate opisthosoma usually present, at least in the fossil males. Photos 126-137. Araneidae
- Eye field more narrow, the median eyes usually not distinctly closer to each other than to the lateral eyes (fig. 19). Opisthosomal scutum absent. Photos 123-125. Zygiellidae
- 11(9) Tarsi usually longer than the metatarsi. The tibia I may bear lateral bristles, the anterior median eyes may be reduced or even absent. The male leg I is frequently modified: Thickened, bent, with spurs or spines. A retrobasal paracymbium is reduced or - most often - absent. Photos 143-180 Anapidae
- Tarsi usually shorter than the metatarsi. Tibia I with or without lateral bristles. The male leg I may be modified only in the Cyatholipidae. A retrobasal paracymbium is absent only in the Theridiidae which may be similar to the Anapidae but never possess lateral bristles on tibia I and have (in the fossils very) rarely only 6 eyes. . . 12
- 12(11) Femoral and/or metatarsal and/or lateral tibial bristle present. 13
- Femoral and/or metatarsal and/or lateral tibial bristles absent. 18
- 13(12) Tibia III and/or IV bear several long trochobothria and bristles. Paracymbium small, bulbus usually very large. The sternal pits - which are the best family character - are rarely observable in the fossil spiders. Photos 138-142. Theridiosomatidae
- Tibia III and IV with fewer/shorter bristles and trichobothria. Sternal pits absent. 14
- 14 (13) Chelicerae with lateral stridulatory ridges (files) (fig. 20), which may be hard to recognize or even absent in the fossils. Leg autotomy is present between patella and tibia in about 40% of the fossil spider specimens (photo 674). Cymbium frequently with one or several outgrowth(s), paracymbium sickle-shaped (figs. 13), epigyne with a long scapus in the fossils (photo 252) 15

- Cheliceral stridulatory ridges absent. Leg autotomy between coxa and trochanter. A cymbial outgrowth is present in most of the fossil Tetragnathidae, a long epigynal scapus is absent in the extant - and most probably in the fossil - Tetragnathidae. The females of the fossil spiders are unknown.16

15(14) Metatarsus I-II with more than 5 bristles or with 2 bristles in the basal half. The cymbium bears a denticulate process, the paracymbium is fused to the cymbium, a needle-shaped apophysis of the bulbus is absent, the scapus of the epigyne possesses lateral folds. Genus *Pimoa*, photo 247. Pimoidae

- Metatarsus I-II (in the fossil spiders in Baltic amber) with 1 bristle only or with 1 bristle in the basal half and 1 bristle in the distal half. A denticulate cymbial process is absent, the paracymbium is a free (movable) sclerite, in the fossil spiders the bulbus bears a needle-shaped long distal apophysis (photo 253), the scapus has no lateral folds, but there may be a ventral fold or dorsal depression (photo 252). Members of the genus *Custodela* are not so rare in Baltic amber. Photos 248-263. Linyphiidae

16(14) ♂-pedipalpus (photos 181-185): Paracymbium divided, with a quite slender branch, embolus very long and curved. Baltsuccinidae

- ♂-pedipalpus different.17

17(16) Pedipalpus, with two tegular apophyses, one of these is denticulate. Photos 186-188. Protheridiidae

- Pedipalpus different, a denticulate tegular apophysis is absent. Some legs articles are usually very hairy. Photos 116-122. Tetragnathidae

18(12) A comb of tarsus IV may be present (fig. 21). A denticulate tegular apophysis is absent in the fossil spiders.19

- No comb of metatarsus IV. A denticulate tegular apophysis is usually present.20

19(18) ♂-pedipalpus: Tibia plate-shaped elongated and with a row of strong hairs near the end, retrobasal paracymbium absent, a retrodistal paracymbium may be present. Representatives e.g. of *Dipoena* (figs. 22-24) and *Clya* (= *Nanomysmena*) are frequent in Baltic amber. Theridiidae

- ♂-pedipalpus (e.g. fig. 14): Tibia not elongated, retrobasal paracymbium present, usually large and complicated. Representatives of e.g. *Eopopino* are not too rare in Baltic amber. Nesticidae

20(18) Opisthosoma usually distinctly extending beyond the spinnerets, an opisthosomal scutum may be present, paracymbium divided, claw of the ♀-pedipalpus absent. The ♂-leg I may be modified (photos 204-205). The characteristic advanced position of the wide fold of the tracheal spiracle (photo 209) is frequently not recognizable in the fossil spiders. Representatives of *Succinilipus* and *Spinilipus* are not so rare. Photos 189-209. Cyatholipidae

- Opisthosoma - in the fossil spiders - not or not distinctly extending beyond the spinnerets, opisthosomal scutum absent, paracymbium variable, claw of the ♀-pedipalpus usually present. ♂-leg I not modified. Position of the narrow tracheal spiracle close to the spinnerets. Photos 210ff. Synotaxidae

Tab. F:

1 Eyes (figs. 4-5) in three rows on a case-shaped high prosoma with extremely large anterior median eyes which are directed forwards. Photos 411-430. . . Salticidae

- Eye position different. 2

2(1) Legs directed sideways (laterigrade) (photos 390, 399): The powerful legs I and II are curved sideways in a concave position in the "sit-and-wait" position. The body is more or less flattened, leg I is usually shorter than leg II 3

- Prograde leg position (e.g. photo 370, but see the unnatural position e.g. in photo 382!): Legs I and II are directed forwards, III and IV backwards. The body is not flattened, leg I is longer than leg II. 4

- In certain members of other families - mainly the Gnaphosidae and Liocranidae, see below, nos. 4 and 7 - the leg position is intermediary, "mediograde".

3(2) Only one (the proventral) row of ventral tibial I-II bristles is present in the fossil spiders, lenses of the posterior median eyes reduced and oval. Especially juveniles of the genus Sosybius are not rare in Baltic amber. Photos 389-394. Trochanteriidae

- Tibia I-II bears paired ventral bristles, lenses of the posterior median eyes circular and usually small. The lateral eyes may be larger than the median ones and situated on humps. Photos 399-410. Thomisidae

- **Not reported** from Baltic amber - but expected in this kind of amber - are the following families in which the leg position is laterigrade, too: (a) In the frequently large Sparassidae (= Heteropodidae), the end of the metatarsi has a trilobate membrane, (b) in the usually large Selenopidae (photo 395) six eyes are present in the wide first row, (c) in the Philodromidae - most extants are larger spiders, too - only one row of tarsal trichobothria is present (in fact in all taxa?).

4(2) Shape of the - usually widely spaced and long - anterior spinnerets cylindrical (photo 388), posterior median eyes oval, gnathocoxae with a distinct depression. Gnaphosidae

- Shape of the anterior spinnerets more or less conical (photo 371) (cylindrical in the males of certain Clubionidae), their bases usually close together, posterior median eyes usually circular, gnathocoxae usually without a depression, but in the fossil Corinnidae - all taxa are members of the subfamily Phrurolithinae, see no. 6 - oval posterior median eyes and gnathocoxal depressions are present. 5

- 5(4) Leg I powerful and distinctly the longest, with the femur thickened prolaterally and bearing tubercles/spines and a depression, tarsi, metatarsi and tibiae depressed dorsally or laterally. Photos 397-398. Borboropactidae: Succiniraptorinae
- Leg I not distinctly the longest, its articles not depressed. 6
- 6(5) The opisthosoma bears a dorsal scutum (photos 370, 376, 385), posterior median eyes usually oval, gnathocoxal depression present. The spiders may be ant-shaped. Photos 366-387. Corinnidae: Phrurolithinae
- Opisthosomal scutum absent, shape of the posterior median eyes circular, gnathocoxal depression absent. Not ant-shaped spiders 7
- 7(6) Euy field very wide (about 4/5 of the width of the head region), posterior eye row straight or procurved in the fossil spiders (fig. 1b). 8
- Eye field more narrow, posterior eye row strongly recurved in the fossil spiders (photo 361). ♂-opisthosoma in most fossil spiders in Baltic amber - the genus *Apostenus* - with striking ventral stridulatory spines (photos 360-365). Liocranidae
- 8(7) Position of the tracheal spiracle one third or more in front of the spinnerets (hard to observe in fossil spiders). Anyphaenidae
- Position of the tracheal spiracle close to the spinnerets. Clubionidae

Tab. G:

- 1 Clypeus very long and prosoma very high and eye position almost in a circle (fig. 25). Photos 338-340 Oxyopiidae
- Clypeus lower, eye position not similar to a circle. 2
- 2(1) Opisthosomal scutum present at least in the fossil males (absent in several extant Zodariidae), e.g. figs. 341, 350 3
- Opisthosomal scutum absent. 5
- 3(2) Pedipalpus with extremely long embolus/conductor. Three species of the genus *Mastigusa*, similar to photo 276. Dictynidae: Cryphoecinae (part., see nos. 8 and 9)
- Pedipalpus different. 4
- 4(3) Gnathocoxae strongly converging above the labium, gnathocoxal serrula absent, fangs stout. Photos 346-355. Zodariidae

- Gnathocoxae not converging, serrula present, fangs of usual length. Photos 341-344. Ephalmatoridae
- 5(2) Cribellum (fig. 16) and calamistrum (figs. 17, 26) present. 6
- Cribellum and calamistrum absent. 9
- 6(5) Calamistrum in a double row (fig. 26). Fossil males are unknown. Amaurobiidae: Amaurobiinae
- Calamistrum in a single row (e.g. fig. 17). 7
- 7(6) Three eye rows, tarsal claw tufts present (similar to fig. 1b). Photos 321-323. Zoropsidae: Eoprychiini
- Two eye rows (fig. 1b), tarsal claw tufts absent (similar to fig. 1a). 8
- 8(7) Tarsal trichobothria in an irregular position. Fossil males: Chelicerae not enlarged, the tibia of the pedipalpus bears 3 or 4 apophyses, which originate in the basal half of the article. Photos 314-320. Zoropsidae: Eomatachiini
- Tarsal trichobothria in a regular row or reduced. Males: Chelicerae frequently enlarged; no such pedipalpal tibial apophyses. The male chelicerae may be enlarged and diverging (e.g. photos 288-289). Dictynidae: Dictyninae (part., see nos. 3, 9)
- 9(5) Body length of the fossil spiders usually less than 3 mm, chelicerae frequently enlarged (e.g. photo 302). Dictynidae (part., see nos. 3 and 8)
- Body length usually more than 3 mm, chelicerae not enlarged. 10
- 10(9) Posterior spinnerets very long, anterior spinnerets usually widely separated, colulus wide and more or less divided. (Incl. all or some taxa of the Cryphoecinae? Photos 270-274). Photos 308-310 Agelenidae
- Posterior spinnerets not (very) long, anterior spinnerets not widely separated, colulus not divided. Most of the rare fossil taxa are identifiable only by the adult male, see the papers on these families in these volumes: Insecutoridae (similar to most Agelenidae the cymbium is strongly elongated in the fossils) (photos 311-313), Pisauridae (the cymbium is fairly elongated in the fossils) (photos 325-334) and Trechaleidae (the cymbium is not elongated in the fossils) (photos 335-336).

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