BEITR. ARANEOL., 18 (2025) JOERG WUNDERLICH

PAPERS ON TAXONOMY AND EVOLUTION OF FOSSIL AND EXTANT SPIDERS (ARANEIDA)

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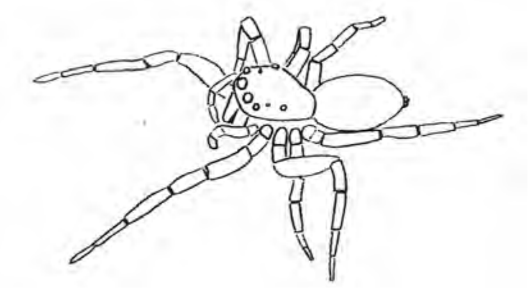

Photos on the front cover:

Photo above: Phoresy and parasitism by arachnids on the same beetle (Elateridae, body length 8 mm). The long arrow points to the phoretic spider, the short arrow points to the two tiny parasitic mites sucking blood from the beetle. - Photo Jonas Damzen. See p. 91f.

Photo below: Lateral aspect of the male archaeoid spider *Planarchaea petersi* n. sp. in 100 million year old Burmese (Kachin) amber, body leg 1.6 mm. Note the long "neck". See p. 53.

Each amber piece is unique, and certain animals preserved in the same piece as syninclusions may tell exciting stories. Four examples of such “frozen behaviour” are treated in this volume. They document cases of phoresy and parasitism in 40 million year-old Eocene Baltic amber (p. 91, 94, photos 20–22) as well as a “dramatic” story of brood care behaviour in Cretaceous amber from Myanmar (p. 96, photos 23–24) which has to be decoded: A female spider with her offspring trapped by a resin during its pretended escape from a resin flood as well a “cocoon” of probable brood care behaviour of a questionable Diplopoda (p. 97, photos 25–26).

Acknowledgement: I thank very much my dear wife Ruthild Schöneich for correcting parts of my manuscripts.

In this vol. 18 of the Beiträge zur Araneologie (Betr. Araneol.) a dozen papers by JOERG WUNDERLICH on extant and fossil spiders and one paper by RUDY JOCQUÉ are united.

The present spider material is stored in the collection of Joerg Wunderlich (CJW) and will most probably be given to the Leibniz Institution Hamburg, Danilo Harms, Museum of Nature (Zoology), and Ulrich Kotthoff, Palaeontolgy of the University of Hamburg.

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BEITR. ARANEOL., 18 (2025: 4–36)

NEW AND RARE SPIDERS (ARANEAE) FROM THE ALGARVE, PORTUGAL

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Abstract: Some species of spiders (Araneae) are described from the SE-Algarve, Portugal: *Micrargpelecopsis* **n. gen**. including *M. ascutata* **n. sp**. and *M. spinosa* **n. sp** (Linyphiidae), *Drassodes balneum* **n. sp.** (Gnaphosidae), *Micaria* ?*triguttata* SIMON 1884 (Gnaphosidae), *Zelotes nigropunctatus* (Gnaphosidae), *Euophrys parvireceptacula* **n. sp**. (Salticidae). Taxonomical notes are given on the the *luctuosus* species-complex of the genus *Aelurillus* SIMON 1884 (Salticidae). Some further spider species are reported/treated from the Algarve: The female of *Silometopus furcatus* WUNDERLICH 2024 (Linyphiidae) is described for the first time, *Emargidromus lusitanica* (KULCZYNSKI 1911) **n. comb**., from *Philodromus* and **n. rank**, from subsp. (Philodromidae) and *Trichothyse furcata* (SIMON 1914) (Gnaphosidae). *Zelotes* (*Civizelotes*) *latapophysis* WUNDERLICH 2024 (Gnaphosidae) is regarded as a younger synonym of *Civizelotes ibericus* SENGLET 2012 (**n. syn**.). - Notes are provided on a questionable stridulatory organ of *Menemerus semilimbatus* (HAHN 1827) (Salticidae), certain spiders adult in the winter season in the Algarve as well as on quite early flowering plants of several families of the same region.

Key words: Agelenidae, Araneae, biogeography, courtship behaviour, cryptic species, endemic species, Erigoninae, flowering plants, forgotten species, Gnaphosidae, hidden species, Linyphiidae, *Micaria*, Philodromidae, Pholcidae, Salticidae, sibling species, Sparassidae, stridulating.

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The type material is still kept in my private collection and will most probably soon be given to the Museum of Nature (Danilo Harms) in Hamburg.

Localities and methods of collection: During the last ca. 15 years I collected spiders of the Algarve, Portugal, mainly around Sao Bras de Alportel and Tavira, e. g. in a house and garden in Mesquite Alta, see Beitr. Araneol. vol. 17 and earlier. At the end of the year 2024 I changed my home to a house 27 km north-east, within a partly fairly "natural" garden of almost 1000 qm in 8950-106 Campeiros, Rue de Campeiros 400-M, 37.248985N 7.531581W, 11 km N Altura, within low hills, not far from the Spanish border, 130 m above see level. Here exist many kinds of flowers, several Olive and Carob trees; specimens of Mantis, Dovetails, Hoopoes and Orioles are occasional visitors. The arachnid fauna of this locality is partly clearly different from the former one, e. g., scorpions live directly near the house in Campeiros; on the other hand the striking Jumping spider *Menemerus semilimbatus* (see below) as well as *Oecobius navus* are common to both gardens on stones and walls. In both – not large! - gardens I saw or collected about 60 species of spiders (almost ca. 1/20 <5%> of the more than 1000 described species in Portugal) of about 32 families (= 2/3 of the 38 families in Portugal).
I collect(ed) by hand, used 15 ground traps at 5 localities and shaked bushes as well as small leaf – rarely needle - trees on my umbrella. Several still not determined juvenile and female specimens in my collection indicate the existence of further undescribed spider species in the Algarve, whose number may be not too low!

Personal notes: (1) In certain regions of the Southern Algarve one do not have to seek for rare or even unknown spider species – one only has to wait in a house or in a fairly natural garden – see above - and spiders will find you! See below, e. g., *Diplocephalus toscanensis* WUNDERLICH 2011, *Micrargpelecopsis spinosa* n. gen. n. sp., *Drassodes balneum* n. sp., *Emargidromus lusitanicus* (KULCZYNSKI 1911), *Pulchellodromus sp.* like *medius* (O. PICKARD-CAMBRIDGE 1872), *Micrommata ligurica* (C. L. KOCH 1845), *Trichothyse furcata* (SIMON 1914) and *Zelotes* (*Civizelotes*) *ibericus* SENGLET 2012.
(2) Here – in the seclusion of the Algarve – one may spend the last time of his life and may reflect the fourth humiliation of mankind: The inhumanity of humans.

Notes on some plants flowering surprisingly already in the winter season 2022–2025 in the Algarve

Besides certain spider species like *Diplocephalus toscanensis* WUNDERLICH 2022 and *Micrommata ligurica* (C. L. KOCH 1845) which I collected during the winter season (see below), I observed between the years 2022 and 2025 several plants starting flowering distinctly earlier within the year than usually published from March or even April:

Borago officinalis: Near Sao Bras de Alportel, Mesquita Alta, 25. XII. 2022,
Campanula sp. indet., 35 cm high, slender leafs, rare: 11 km N Altura, near Campeiros, 25. I. 2025,
Cistus ladanifer: 11 km N. Altura, near Campeiros, 25. XII. 2024,
Cistus ?monspeliensis: 11 km N Altura, near Campeiros, 25. XII. 2024,
Dipcadi serotinum: 11 km N. Altura, near Campeiros, on a small road, 22. II. 2025,
Erica arborea: Near Sao Bras de Alportel, Fonte Ferrea, 19. XII. 2022,
Lupinus albus: 11 km N Altura, near Campeiros, frequent, 26. XII. 2024,

Lupinus luteus: 11 km N Altura, near Campeiros, 9. I. 2025,
Linum ?coloratum: 11 km N Altura, near Campeiros, 13. I. 2025,
Lavandula dentata: 11 km N Altura, near Campeiros, 25. I. 2025,
Nerium oleander: 11 km N Altura, Campeiros, in a garden, 27. XII. 2024,
Ophrys fusca (or iricolor?): Near Qurenca, not rare 22. I. 2023,
Tulipa sylvestris: 5 km E Sao Bras de Alportel, east end of Mesquita Alta, frequent in an mixed open forest, 26. II. 2023,
Ulex parviflorus: 4 km E Sao Bras de Alportel, Mesquite Alta, frequent, 11. I. 2023.

Is the early flowering the result of the warming of the Earth?

NEW DESCRIPTIONS OF SPIDERS (ARANEAE) OF THE ALGARVE AND NOTES ON ALREADY KNOWN SPECIES

Note: The new genus *Micrargpelecopsis* is an explicit example for hidden endemic taxa of the Algarve.

Family PHOLCIDAE

Spermophora senoculata (DUGES 1836)

Material; Portugal, SE Algarve, Campeiros (see above), on a wall in our house, a male few cm away from an egg-bearing female in its capture web, body length 1.6 mm, together with its prey, a female of *Pelecopsis bucephala* (O: PICKARD-CAMBRIDGE 1875) (Linyphiidae), body length 1.7 mm, JW leg. 20. V. 2025, CJW.

Note: In the present area I collected *Spermophora senoculata* only a single time and only in the house. I collected *Pelecopsis bucephala* frequently by hand in the house as well as by traps in the garden

Family LINYPHIIDAE, subfamily ERIGONINAE

Diplocephalus toscanensis WUNDERLICH 2011

Material: Portugal, SE-Algarve, 11 km N Altura, Campeiros, in a house and in a garden (see above) on bushes and trees, ♂♀ JW leg. 25. XII. 2024, CJW.

Distribution: Italy, Portugal.

Micrargpelecopsis **n. gen.**

Etymology: The name combines the names of the linyphiid genera *Micrargus* and *Pelecopsis* whose characters both are similar in some respect to the new genus.

The gender of the name is feminine.

Type species: *Micrargpelecopsis ascutata* n. sp. Further species: *Micrargpelecopsis spinosa* n. sp.

Diagnostic charaters: Prosomal punctations (figs. 1-2), lateral pits of the ♂-prosoma which bears a lobus (figs. 1-2) as well as a scutum of the ♀♂-opisthosoma absent (in *M. spinosa* the ♂-opisthosoma is dorsally weakly leathery), posterior/anterior margins of the fang furrow with 3/4 teeth, sequence of the dorsal tibial bristles 2/2/1/1, bristles quite short on I-II in the male sex, metatarsal IV trichobothrium absent, its position on I in 0.4; body length 1.5-1.6, prosoma: Length 0.6-0.7 mm, colour of prosoma and legs yellowish to medium brown. ♂-pedipalpus (e. g. figs. 3-5): Tibia with a single dorsal-apical apophysis and a larger and bent embolus; ♀: epigyne/vulva (figs. 7-9) with a distinct scape and a pair of large depressions/ pits.

Relationships: Chaetotaxy and trichobothriotaxy are quite similar to the erigonine genera *Micrargus* DAHL 1886 and *Pelecopsis* SIMON 1864. The male cephalic lobe and the structures of the male pedipalpus are quite similar to the apparently most related genus *Pelecopsis* SIMON 1864 but in contrast to *Pelecopsis* punctations of the prosoma, a dorsal scutum of the opisthosoma, lateral pits of the ♂-lobe as well as a scape of the epigyne are absent. In *Micrargus* exist a scape and large pits of the epigyne as in *Macrargpelecopsis* but a cephalic lobe of the ♂-prosoma is absent and lateral pits exist, the embolus is curled distally and bears a long and bristle-shaped basal apophysis.

Distribution: Portugal, hills of the SE-Algarve.

Micrargpelecopsis ascutata n. gen. n. sp. (figs. 1-9)

Etymology: The name of the species refers ot the soft opisthosoma – without a scutum (lat. = shield) - in both sexes.

Material: Portugal, SE-Algarve, 7 km N of Altura (only 3 km S of Campeiros, the locus typicus of *Micrargpelecopsis spinosa* n. sp.), ground traps in a sunny and stony habitat, 1♂ 10 ♀ JW leg. in III-IV 2025; holotype ♂ R347/CJW, 10♀ paratypes R348/CJW. - Note: The left pedipalpus of the holotype and an epigyne are kept separately.

Diagnostic characters: ♂: Cephalic lobe (fig. 1-2) erect, pedipalpal tibial apophysis long, strongly sclerotized and in a medium position, bulbus as in figs. 4-5, embolus in the median part quite thick. Epigyne (figs. 7-8; see fig. 9) with a pair of large depressions/openings whose margin is strongly sclerotized, and anteriorly with a strongly protruding scape which seemingly possesses a tiny opening. Vulva (fig. 9) with quite dark/strongly sclerotized? ducts and a pair of thin-walled and almost globular receptacula seminis.

Description:
Measurements (in mm): ♂: Body length 1.5; prosoma: Length 0.6, width 0.48; opisthosoma: Length 0.8, width 0.5; leg I: Femur 0.55, patella 0.16, tibia 0.44, metatarsus 0.38, tarsus 0.3; tibia II 0.4, tibia III 0.3, tibia IV 0.45. - ♀: Body length 1.5-1.6; prosoma: Length 0.6, width 0.5; opisthosoma: Length 1.0-1.1, width 0.65; leg I: Femur 0.55, patella 0.17, tibia 0.4, metatarsus 0.37, tarsus 0.32; tibia II 0.4, tibia III 0.3, tibia IV 0.47.
Colour: Prosoma and legs yellowish to light and medium brown, the cephalic part may be slightly to fairly darkened, opisthosoma light to dark grey brown.
Prosoma (figs. 1-2) distinctly longer than wide, almost smooth, not punctuated, 8 fairly small eyes, posterior row strongly procurved, cephalic part in the ♀ slightly convex, in the ♂ bearing a hairy erect lobe without lateral pits but with a low basal-posterior depression, clypeus long, chelicerae robust, lateral files widely spaced, fangs long, posterior margin of the fang furrow bearing 3 small teeth, anterior margin with 3 larger teeth and 1 small retrolateral tooth, labium wider than long, sternum almost as wide as long, spacing coxae IX by ca. half of their diameter. - Legs slender, fairly long. I and IV ca. equal in length, hairs short, sequence of the dorsal tibial bristles 2/2/1/1, length 1 1/2 – 2 (on IV) diameter of the tibia in the ♀ but only 2/3 diameter on tibia I-II and only ca. 1 diameter on IV in the ♂. Metatarsal trichobothrium absent on IV, its position on I in 0.4. - Opisthosoma oval, hairs and spinnerets short. - ♂-pedipalpus (figs. 3-6) with short patella and tibia, tibia apophysis long, strongly sclerotized and in a medium position bulbus as in figs, 4-5, embolus thick. - Epigyne/vulva: Figs. 7-9

Relationships: In *M. spinosa* n. sp. the cephalic lobe of the ♂-prosoma bears small bristles, too, but it is a bit longer and directed fairly posteriorly, the ♂-opisthosoma is dorsally slightly leathery, the ♂-pedipalpal tibial apophysis is shorter, less sclerotized and its position is more prolaterally, the embolus is thinner. ♀: I did not find differences of epigyne and vulva of *spinosa* and *ascutata*.

Distribution: Portugal, SE-Algarve.

***Micrargpelecopsis spinosa* n. gen. n. sp.** (figs. 10-13)

Etymology: The name of the species refers to the small bristles on the cephalic lobe, from spina (lat.) = bristle.

Material: Portugal, SE-Algarve, Campeiros (see above), 11 km N of Altura, in the garden of our house, in ground traps, 1♂1♀ JW leg. in III-IV 2025; ♂ holotype R349/CJW, paratype ♀ R350/CJW. - Note: The left pedipalpus of the holotype and the epigyne are kept separately, the ♀-opisthosoma is loose.

Diagnostic characters: ♂: Cephalic lobe (figs. 10-11) directed backwards, pedipalpal tibial apophysis (fig. 12) strongly sclerotized at its pointed tip, in a more prolateral position, bulbus as in fig. 13, embolus only fairly thick ♀: Epigyne/vulva as in *M. ascutata*, figs. 7-9, see above.

Description:
Measurements (in mm): ♂: Body length 1.5; prosoma: Length 0.65, width 0.5; opisthosoma: Length 0.8, width 0.6; leg I: Femur 0.55, patella 0.17, tibia 0.43, metatarsus 0.38, tarsus 0.32; tibia II 0.38, tibia III 0.28, tibia IV 0.5. - ♀: Body length 1.6; prosoma: Length 0.7, width 0.52; opisthosoma: Length 1.12, width 0.7; leg I: Femur 0.55, patella 0.18, tibia 0.46, metatarsus 0.4, tarsus 0.3; tibia II 0.38, tibia III 0.32, tibia IV 0.57.
Colour similar to *ascutata*, cephalic part fairly darkened.
Remaining characters as in *ascutata* n. sp., except the ♂-prosoma (figs. 10-11) which lobe is directed posteriorly and the ♂-pedipalpus (figs. 12-13) in which only the pointed tip of the tibia apophysis is strongly sclerotized and the embolus is only fairly thick.

Relationships: See above the closely related *M. ascutata* n. sp.

Distribution: Portugal, SE-Algarve.

Silometopus furcatus WUNDERLICH 2024 (fig. 14)

2024 *Silometopus furcatus* WUNDERLICH, Beitr. Araneol., 17: 24, figs. 47-52 (♂).

Material: Portugal, Algarve, near Sao Bras de Alportel, few km away from the type locality, no exact locality, 1♀ JW leg. in Spring of 2022, R346/CJW. - Notes: (1)The opisthosoma of the spider is loose, some leg articles are lost. (2) In spite of certain differences of both sexes (see below) I regard the present female – with little hesitation - as a member of *S. furcatus* which female sex was unknown. The female will be kept in the Zool. Mus. Univ. Hamburg.

First description of the female:
Measurements (in mm): Body length 1.5; prosoma: Length 0.68, width 0.52; opisthosoma: Length 1.0, width 0.9; leg I: Femur 0.5, patella 0.18, tibia 0.4, metatarsus 0.35, tarsus 0.23; tibia II 0.35, tibia III 0.24, tibia IV 0.42.

Several general characters as in the male but cephalic part only slightly convex, posterior eye row slightly procurved, and position of the metatarsal III trichobothrium in 0.62 but not in 0.33 as – apparently incorrectly - noted in the male holotype. All tibiae with a single dorsal tibial bristle in the basal third which is a bit longer than the tibial diameter (sexual dimorphism). Epigyne/vulva (fig. 14) with a longitudinal medial split (cleave) (similar to certain species of the genus *Diplocephalus* whose body colour is dark brown), and widely spaced thin-walled receptcula seminis in a transverse and a more anterior position.

Relationships: The epigyne is similar to *S. curvatus* (O. PICKARD-CAMBRIDGE 1872) which is not known from the Iberian Peninsula. In *curvatus* a similar but longer medial epigynal split exists, the position of the receptacula seminis is more posteriorly, the shape more longitudinally. See also the original description, the morphological relationships of the male.

Distribution: Portugal, Algarve.

Family AGELENIDAE

Eratigena feminea (SIMON 1870)

Material: Portugal, SE-Algarve, 11 km N Altura, Campeiros, 37.248985 N 7. 531581 W, in a house and in the garden, several males JW leg. 23. - 26. I. 2025, CJW.

Distribution: Western Mediterranean.

Family LIOCRANIDAE

Mesiotelus grancanariensis WUNDERLICH 2011

Material: Portugal, SE-Algarve, 11 km N of Altura, Campeiros, in a garden (see above), below a stone, 1♀ JW leg. 21. IV. 2025, CJW.

Distribution: Canary Islands, Madeira, Iberian Peninsula.

Family GNAPHOSIDAE

Drassodes WESTRING 1851

Certain species of the genus *Drassodes* SIMON 1871 are examples for those species of the RTA-clade in which a retrolateral tibial apophysis is quite small – e. g. in the small (body length ♂ only 4.6-5.2 mm) *lacertosus* (O. PICKARD-CAMBRIDGE 1872), *thaleri* HERVE 2009 and *chubyndensis* ESYUNIN & TUNEVA 2002 (♂ ca. 7-10 mm long) – or it is completely absent (only a sclerotized retro-apical margin may exist, fig. 15): see the key below. In the quite small (body length ♂ only 3 mm) *Drassode myolans* CHATZAKI 2012 from Greece a quite unusual and large kind of the RTA exits.

Here I provide a provisorical key to the European males near *luteomicans* and describe a new species from Portugal.

Key to males of the European species of *Drassodes* in which a retrolateral tibial apophysis is absent:

Notes: To my knowledge most important regarding the identification of the species are origin, length and shape of the embolus, its connection to the sperm duct as well as the shape of the sperm duct in ventral and retrolateral aspect. Less important are the intraspecific variable number of leg bristles and the usually quite uniform number and position of teeth of the fang margin.
D. serratichelis of this key is absent on the Iberian Peninsula; *D. luteomicans* has not been reported from the Iberian Peninsula, see below.

1 Body length 2.7-4.2 mm. Embolus short, almost straight, close to the median apophysis. - Sardinia and East Europe .... serratichelis (ROEWER 1928)

- Body length usually > 5 mm. Structures, shape and position of the embolus different or similar 2

2(1) Embolus long, originating in the middle of the bulbus, continuously and distinctly bent in its whole length. - Widely spread in S-Europe .... lutescens (C. L. KOCH 1839

- Embolus (figs. 16, 19) shorter, originating more in the distal half of the bulbus and less bent 3

3(2) Pedipalpus (figs. 15-17): Sperm duct entering the embolus distinctly S-shape curved and more prolaterally, embolus only slightly bent, median apophysis smaller. Cymbium and bulbus fairly compact. In dunes and in different habitats. - Iberian Peninsula .... _arenosus_ WUNDERLICH 2023

- Pedipalpus (figs. 6-17): Sperm duct entering the embolus more retrolaterally, embolus fairly bent, median apophysis larger. (Shape of cymbium and bulbus variable) 4

4(3) Pedipalpus (figs. 15-17): Cymbium quite long and slender, the distal part about as long as the bulbus which is ca. twice as long as wide, embolus longer, ca. 0.18 mm long, widely spaced from the median apophysis. Tubes of the sperm duct in the basal part of the bulbus distinctly spaced from each other and distinctly spaced from the basal margin of the bulbus. berian Peninsula: Portugal .... _balneum_ **n. sp**.

- Bulbus ca 1.5 times longer than the distal part of the compact cymbium, embolus shorter, closer to the median apophysis. Tubes of the sperm duct in the basal part of the bulbus close together (partly touching) and reaching the basal margin of the bulbus. - France, S-Europe; probably (still?) not known from the Iberian Peninsula ..... _luteomicans_ SIMON 1878

Drassodes balneum **n. sp**. (figs. 15-18)

Etymology: The name of the species refers to the place where the spiders were collected, the bath tub in our house in Campeiros; based on balneum (lat.) = bath tub.

Material: Portugal, Algarve, Campeiros, 11 km N of Altura, 37.248985 N 7.531581 W, holotype (♂), R342/CJW and 1♀ paratype, R343/CJW, JW leg. 20. I. 2025 in the bath tub of our house. The left leg II and both legs IV of the holotype are lost beyond the coxa, the left pedipalpus is loose; the epigyne got lost after its preparation, the opisthosoma of the female spider is loose, its right leg IV is lost beyond the coxa by autotomy. The spiders apparently invaded the house from the garden around the house.

Diagnostic characters: ♂-pedipalpus (figs. .15-17) RTA absent, cymbium and bulbus long and slender, distal part of the cymbium about as long as the bulbus which is twice as long as wide, median apophysis large and widely spaced from the embolus wich is fairly bent, sperm duct entering the embolus more retrolaterally (*). ♀: Epigyne as in fig. 17.

(*) 2♂ from Central Spain possess – according photos kindly send by A. GROMOV via e-mail – a long distal cymbial part as in _arenosus_ but the sperm duct is apparently more away from the basal margin of the bulbus and enters probably the embolus more from basally.

Description:
Measurements (in mm): ♂: Body length 8.5; prosoma: Length 4.3, width 2.9; opisthosoma: Length 5.0, width 1.9; leg I: Femur 3.6, patella 2.0, tibia 4.0, metatarsus 3.2, tarsus 2.0; tibia II 3.0, tibia III 2.3, tibia IV unknown; pedipalpus: Patella 0.75, tibia 1.1, cymbium: Length 1.1, width 0.35, bulbus: Length 0.53, width 0.25, embolus 0.18. - ♀: Body length 9.0; prosoma: Length 3.55, width 2.6; opisthosoma: Length 5.55, width 3.3; leg I: Femur 3.0, patella 1.5, tibia 2.5, metatarsus 2.0, tarsus 1.6; tibia II 2.3, tibia III 1.6, tibia IV 2.8.
Colour: Prosoma and legs light grey brown, chelicerae darkened, legs I-II beyond the femora darkened.
Prosoma 1.48 times longer than wide, bearing short hairs, thoracic fissure long, 8 eyes in two rather wide rows, posterior row slightly to fairly procurved, posterior median eyes oval, spaced by almost their diameter, fangs long, posterior margin of the fang furrow with 2 tiny widely spaced teeth, anterior margin with 3 large teeth, the median one largest. - Legs fairly long, order IV/I/II/III, hairs fairly short; bristles: Femur I dorsally 1/1 and 1 prolaterally in the distal half, II additionally with a prolateral one near the middle, patellae none, tibiae I-II with a prolateral bristle in the distal half, metatarsi I-II with 1-2 ventral bristles in the basal half, femora, tibiae and metatarsi III-IV with numerous bristles. All tarsi and metatarsi I-II bear a well developed scopula. - Opisthosoma distinctly longer than wide (see above), dorsally covered with short hairs, anteriorly with long hairs. - ♂-pedipalpus (figs. 15-17 see above) with slender articles, tibial apophysis absent but a wide sclerotized apical margin exists, median apophysis large, distinctly spaced from the embolus. - Epigyne as in fig. 18.

Relationships: According the structures of the bulbus *D. arenosus* WUNDERLICH 2023 (figs. 19-20), also described from the Algarve (Portugal), and *D. luteomicans* SIMON 1878 (complete distribution unsure) are closely related, see the key above.
Notes: Regarding *D. arenosus* and *D. balneum* the key of the WSC of the European species may lead to *Drassodes luteomicans* SIMON 1878 which was based on the female sex from Corsica (not from the mainland of France). The species is widely spread in S-Europe and is also reported from France, Spain and N-Africa by different authors, see the WSC. The determinations have to check. In my opinion the specimens reported as *luteomicans* by several authors represent partly different strongly related similar species. According to the figs. provided by BARRIENTOS et al. (2022: 36, figs. 5A-D) and (2023) under *D. luteomicans*, spiders from Spain, I am not quite sure about the correct determination; in my opinion the spiders are most likely members of *D. arenosus*. - According mainly to the more compact cymbium and bulbus, the more retrolateral connection of sperm duct and embolus as well as the position of the sperm duct in the basal half of the bulbus *D. luteomicans*: PANTINI et al. (2013) from Italy has, in my opinion, probably been correctly determined but the holotype of *luteomicans* has to check. See the key above.

In each of the three species in question different characters – like the shape of cymbium and bulbus as well as the introducing position of the sperm duct to the embolus – are linked with each other and point to the existence of different species.

Distribution: The Iberian Peninsula.

Micaria WESTRING 1851

See, e. g., BOSMANS & BLICK (2009), MUSTER & MICHALIK (2020) and WUNDERLICH (1980). The enormous diversity like of colour and morphology in Chinese species has recently been reported by LIU & ZHANG (2025).

The myrmecomorphic genus *Micaria* is diagnosed by a special character of the spinnerets and by the existence of special hairs of body and legs. Most members of this more or less ant-shaped spiders possess furthermore an inclination of the opisthosoma and apparently pseudo-segmented (flexible) tarsi; both characters are absent, e. g., in the species treated below, *M*. ?*triguttata*. In the *diversa* species-group in the sense of LIU & ZHANG exists a remarkable sexual-dimorphism:Tibia and metatarsus I-II of females bear long paired ventral bristles (fig. 22) in contrast to the male sex in which only few weak bristles may exist.

The frequently species-specific colouration of body and legs may partly rubbed of and may mislead determinations.

Certain species of *Micaria*, probably sibling species, are good examples "hidden" or "cryptic" species, and also for "forgotten" species, which are quite similar and hard to discriminate and were erroneously synonymized. An example is *Micaria micans* which has been synonymized by most previous authors with *pulicaria*. *M. micans* was recently revived by MUSTER & MICHALIK (2020) with the help of several methods; corresponding differences were found, e. g., in genetics, (genital)morphology, ecology and biogeography. A striking differentiating character refers to the pattern (longitudinal bands) of colour (pigmentation) and special hairs on femur IV in both sexes which exists in *micans* - and quite similar in the questionable *triguttata* (see below, fig. 23) - but are absent in *pulicaria* in which the hairs and pigmentation of femur IV are like on femora I-III. This difference of the two species in question has already been recognized by BÖSENBERG (1902); WUNDERLICH (1980) regarded this difference erroneously as a kind of intraspecific variability of *pulicaria*. *Micaria pulicaria* is probably not a "sampling species" of more than two species; phylogenomic data are still discussed.

I found this remarkable and striking character of femur IV also in a questionable female of *M. triguttata* (fig. 23). It may exist even in certain other species of *Micaria* but an investigation is outstanding. In certain species of *Micaria* in China, see LIU & ZHANG (2025), exist also longitudinal bands of hairs and pigmentation on femur IV, e. g., in *lenzi* BÖENBERG 1899, but these structures are different: In *lenzi* exists a *light* band between dark bands similar to *M. xizang* LIU & ZHANG 2025: Fig. 42 C. In *M. fulgens* (WALCKENAER 1802) femur IV bears dorsally a dark longitudinal band but light lateral bands are *absent*.

Micaria ?***triguttata*** SIMON 1884 (figs. 21-25)

Material: Portugal, E-Algarve, 7 km N Altura, 3 km S Campeiros (see above), open stony locality, 1♀ JW leg. 8. II. 2025, R354/CJW. - Note: The opisthosoma and the right leg II are loose, the epigyne is kept separately, the right leg III is lost.

Diagnosis (♀): Legs I-II bear a quite high number of strong paired ventral bristles (fig. 22): Tibia I proventral 9, retroventral 7, metatarsus I 8 pairs; tarsus I as long as metatarsus I;

femur IV bearing dorsally a longitudinal band of dark hairs on a dark ground between bands of yellowish hairs (fig. 23); white hairs: See below; epigyne/vulva (figs. 24-25) with a wide hood (transverse fold) reaching laterally far posteriorly.

Description:
Measurements (in mm): Body length 3.9; prosoma: Length 1.45, width 1.0; opisthosoma: Length 2.5, width 1.3; leg I: Femur 1.0, patella 0.45, tibia 0.65, metatarsus 0.6, tarsus 0.6; tibia II 0.6, tibia III 0.55, tibia IV 0.93.
Colour (most white hairs are rubbed off): Prosoma dorsally and ventrally black; pedipalpus: Femur black, remaining articles yellowish, legs mainly black but coxae III-IV partly yellow, patella, tibia, metatarsus and tarsus I-II yellowish, metatarsus and tarsus III-IV dark grey, femur IV (fig. 23) dorsally with a longitudinal band of dark hairs on a dark pigmented ground between yellowish hairs. Opisthosoma mainly black ventrally medium grey, dorsally in the anterior as well as in the posterior half each with a small spot of white hairs, laterally with larger oblique bands of white hairs, white hairs exist also above spinnerets.
Prosoma (fig. 21) 1.45 times longer than wide, quite fine punctuated, posterior eye row slightly procurved, posterior median eyes oval, spaced by almost 3 of their largest diameters. - Legs slender, order IV/I/II/III, tarsus I as long as metatarsus I, tarsi not pseudo-segmented (flexible), femur IV see above, femur III without dorsal bands, bristles (some are rubbed off): Femur I 2 prolaterally in the distal half and a dorsal bristle in the basal half, femur IV with 1/1 dorsal bristles, tibia and metatarsus I-II: See above, legs III-IV with numerous bristles. - Opisthosoma 1.9 times longer than wide, without inclination. - Epigyne/vulva (figs. 24-25) with a wide hood which reaches laterally to the middle of the kidney-shaped (primary) receptacula seminis, copulatory ducts long.

Relationship: A member of the *Micaria dives*-group in the sense of LIU & ZHANG 2025. *M. triguttata* SIMON 1884 may be most related but in – actually conspecific? females of *triguttata* the body length is – according to the “Spiders of Europe” - only 2.6-3.25 mm, tibia I-II – according to WUNDERLICH (1980) – bear only 5-6 pairs of ventral bristles, and the epigynal hood is laterally shorter, see WUNDERLICH (1980: Fig. 47b). - I do not know a sure female of *M. triguttata*. *Triguttata* has been described from Spain: Miranda de Ebro, the locus typicus, based on the male sex and juveniles but no female, see WUNDERLICH (1980: 270). The variability of ventral bristles of tibia and metatarsus I-II in the female sex and the existence of dorsal bands of femur IV (it never has been studied) remains still unknown to me, and so the conspecifity of the present female with *triguttata* remains unsure; i do not want to exclude that it may me the member of an unnamed – cryptic - species. - In females of *M. corvina* SIMON 1878 from N-Africa – according to A. GROMOV (e-mail in IV 2025) - tibia I-II bear only less than 5 pairs of ventral bristles and the ventral opisthosomal colour is light.

Distribution: SE Portugal.

Trichothyse furcata (SIMON 1914) (under *Poecilochroa*)

Material: Portugal, SE-Algarve, 11 km N Altura, Campeiros (see above), at a door of our house to the garden, 1♂ JW leg. 16. VI. 2025, R357/CJW.

The genus *Trichothyse* TUCKER 1923 is very close to *Poecilochroa* WESTRING 1874, see SANKARAN et al. (2025) who transferred the present and some other species from *Poecilochroa*; it is distributed in Africa and the southern Palaearctic, three species are known from the Iberian Peninsula. The males can best be identified by the shape of the furcate pedipapal tibial apophysis; in contrast the structures of their bulbi may be very similar.
I identified the present male by the photos provided by OGER. The figs. of *furcata* given by DI FRANCO (2001, figs. 3-4) (under *Poecilochroa*) seem to me a bit different to the present male: The branches of the tibial apophysis and the embolus are slightly smaller and the sclerites of the bulbus are also shown a bit different.

Distribution: Spain, France, Italy, Greece; new to the fauna of Portugal.

<ins>*Zelotes* (*Civizelotes*) *latapophysis* WUNDERLICH 2024 = *Civizelotes ibericus* SENGLET 2012 (**n. syn.**)</ins>

<ins>New material</ins>: S-Portugal, Campeiros, in a house, locus typicus, 1♂ JW leg. 10. IV. 2024, CJW.

The recently collected male is much better preserved than the holotype and shows well the structures of the bulbus.

Distribution: France, Iberian Peninsula.

***Zelotes nigropunctatus* n. sp.** (figs. 26-28)

<ins>Etymology</ins>: The name of the species refers to the black and wrinkled/punctate prosoma, from nigrum (lat.) = black and punctatus (lat.) = punctate.

<ins>Material</ins>: Portugal, SE-Algarve, ca. 3 km S from the Lake Beliche, southern margin of a dirt road, ca. 80 m, holotype ♀ JW leg. 3. VI. 2025 below a stone; F356/CJW. - <ins>Note</ins>: The opisthosoma is loose, the epigyne is kept separately.

Diagnosis (♀; ♂ unknown): Colour of prosoma and legs mainly black but femur I prolaterally in the basal half with a <ins>striking large yellowish spot of the cuticula</ins>, prosoma finely but distinctly wrinkled and punctate; epigyne/vula (figs. 27-28) distinctly longer than wide, with a weakly sclerotized <ins>pair of lateral fields</ins> (as in the strongly related *Z. alpujarraensis* SENGLET 2011), ducts strongly bent posteriorly and bearing globular structures near their end.

Description (♀):
Measurements (in mm): Body length 7.3; prosoma: Length 2.8, width 2.1; opisthosoma: Length 4.9, width 3.0; leg I : Femur 2.0, patella 1.2, tibia 1.3, metatarsus 1.2, tarsus 0.9; tibia II 1.2, tibia III 0.9, tibiaI V 1.7.

Colour: Prosoma, pedipalpi, legs and spinnerets almost uniformly black, coxae ventrally distinctly and metatarsi slightly lighter, femur I prolaterally in the basal half with a striking large yellowish spot of the cuticula, opisthosoma dorsally dark grey, ventrally medium grey.
Prosoma (fig. 26) 1.3 times longer than wide, anteriorly not strongly narrowed, finelly wrinkled and punctate. hairs short, thoracic fissure long, anterior margin of the fang furrow with 4 teeth, posterior margin with a single tooth near the base of the fang. - Legs only fairly long, order IV/I/II/III, metatarsal III-IV combs, tarsi and metatarsi I-II scopulae and claw tufts well developed, bristles on tibia I-II absent, metatarsus I-II may bear 1 or 1/1 ventral bristles, patella III bears a retrolateral bristle. - Opisthosoma 1.6 times longer than wide, bearing short hairs. - Epigyne/vulva: See the diagnosis.

Relationships: According to the structures of the epigyne – especially the existence of sclerotized lateral fields – *Z. alpujarraensis* SENGLET 2011 from Spain and probably from Iran – see ZAMANI et al. (2022) - is closely related; in *alpujarraensis* the colour of prosoma and legs is dark brown, the opisthosoma is covered with copper-coloured hairs, the receptacula seminis are thick-walled, the epigynal ducts are less spaced from each other, not strongly bent posteriorly and bear no separate globular structures near their ends.

Distribution: Portugal, SE-Algarve.

Family SPARASSIDAE

Micrommata ligurica (C. L. KOCH 1845) (fig. 29)

Material: Portugal, SE-Algarve, 11 km N Altura, Campeiros, 37.248985 N 7. 531581 W, in our house, apparently introduced from the garden, 1 subad. ♂ JW leg. 31. XII. 2024, adult 23. I. 2025, CJW; 1 JW leg. 7. III. 2025, CJW.

Thanks to the recent important revision of the genus *Micrommata* LATREILLE 1804 by JÄGER (2023) I identified the present specimens. The thin sperm duct and even the free embolus of this species (fig. 29) are well observable in the freshly moulted male. The short free part of the embolus has not been figured by JÄGER (figs. 84-85), it is bent, its tip is hidden.

Distribution: Western Mediterranean.

Family PHILODROMIDAE

In our garden of Campeiros (see above), e. g., from an Almond tree and an Apricot tree – I collected in IV-VI 2025 some remarkable philodromid species (CJW): *Philodromus buxi* SIMON 1884, *Pulchellodromus simoni* (MELLO-LEITAO 1929), *P. glaucinus* (SIMON 1870) as well as two further rare species:

Emargidromus WUNDERLICH 2012

Type species: *E. emarginatus* (SCHRANK 1803) (under *Aranea emarginata*), widely distributed in the Holarctis. - Further species: *Emargidromus lusitanicus* (KULCZYNSKI 1911) (from *Philodromus*, **n. comb**. and from subspecies, **n. stat**.) (♀ unknown) and *Emargidromus orientalis* (SCHENKEL 1963) (**n. comb.**, from *Philodromus*) (♂ unknown, China).

Diagnosis: Metatarsus I-II with 2 pairs of ventral bristles besides other bristles but *without apicals*; ♂-pedipalpus (figs. 30-32): Tibia bent in a right angle, apically bearing a wide flat and a short bent apophysis, cymbium and bulbus distinctly longer than wide, median apophysis well developed and pointed, guiding the tip of the embolus; ♀: Epigyne/vulva of *E. emarginatus*: Median septum of the epigyne u-shaped, sperm duct openings posterior-retrolaterally. - Position of the eyes and most other characters quite similar to *Philodromus* THORELL 1869, see also below.

Relationships: In the strongly related genus *Philodromus* THORELL 1869 metatarsus I and II bear apical bristles, the tibia of the ♂-pedipalpus is not or only slightly bent and its apophyses are different; ♀: Median septum of the epigyne not u-shaped, sperm duct openings prolaterally.

Ecology: Species of higher strata of the vegetation.

Distribution: Europe to Japan.

Emargidromus lusitanicus (KULCZYNSKI 1911) **n. comb., n. stat.** (figs. 30-32)

Philodromus emarginatus lusitanica KULCZYNSKI 1911

According to the close relationships to the type species of *Emargidromus* - e. g., absence of apical metatarsal I-II bristles and the structures of the ♂-pedipalpus -, I transfer *lusitanicus* from *Philodromus* to *Emargidromus* (**n. comb**.); based on the structural differences of the tibial apophyses of the pedipalpus and the shape of the tegulum (see below) I regard *lusitanicus* (**n**. **stat**.)and *emarginatus* as separate (sibling) species which both occur in Portugal, so far known without hybridization.

Material: Portugal. The deposition of the type male is unknown to me. - New material: Portugal, SE-Algarve, Campeiros (see above), on the SE exposed outside wall of our house, few meters away from a large leaf tree in the garden of our neighbour, JW leg. 23. IV. 2025, R352/CJW.

Diagnosis (♂; ♀ unknown): Tegulum basal of the median apophysis with a distinct inclination (arrow in fig. 32), apical margin of the retroventral pedipalpal tibial apophysis 0.4 mm wide (fig. 31), retrodorsal pedipalpal tibial apophysis (fig. 30) strongly bent and ventrally distinctly concave (fig. 31).

Description of the present ♂; see also the original description by KULCZYNSKI (in latin):
Measurements (in mm): Body length 3.5; prosoma: Length 2.0, width 1.8; opisthosoma: Length 2.5, width 1.5; leg I: Femur 2.2, patella 1.0, tibia 2.1, metatarsus 2.0, tarsus 1.3; tibia II 2.5, tibia III 1.8, tibia IV 1.8.
Colour dorsally mainly dark brown, ventrally lighter, medium part of the prosoma and sternum yellow, opisthosoma dorsally with several light spots, behind the epigastral furrow light grey, legs mainly dark brown, partly spotted and annulated, coxae and femora ventrally yellowish.
Prosoma 1.1 times longer than wide, 8 small eyes as in *Philodromus*, posterior row straight, fovea absent, clypeus anteriorly with 3 pairs of bristles, anterior margin of the fang furrow with a single larger tooth. - Legs long, order II/I/III-IV, 2 pairs of *ventral* bristles each on tibia and metatarsus I-II, apical bristles existing on the tibiae but not on the metatarsi, claw tufts dense, scopulae on tarsi and metatarsi fairly dense. - Opisthosoma fairly flattened, 1.7 times longer than wide, widest in the posterior half, dorsally bearing 3 pairs of distinct sigillae, ventrally behind the epigastral furrow with numerous quite short spines and short partly thickened hairs. - Pedipalpus (figs. 30-32; see also above): Patella short, tibia bent in a right angle, cymbium and tegulum distinctly longer than wide, tegulum bulging probasally, embolus describing almost half a circle, median part hidden in ventral aspect, its tip guided by the pointed median apophysis which is surrounded by a fleshly structure, sperm duct quite long, curved and narrow.

Relationships: In the strongly related *E. emarginatus* (SCHRANK 1803) (*) a distinct retrolateral inclination of the tegulum ist absent, the retroventral pedipalpal tibial apophysis is shorter – 0.27 mm wide according to KULCZYNSKI (1911: 64) – (0.4 in *lusitanicus*) (**) -, the retrodorsal pedipalpal tibial apophysis is less bent and less concave ventrally (opposite to the retroventral apophysis).

(*) See WUNDERLICH (2012: 48, figs. 11-14, ♂♀). The epigyne posesses an u-shaped sclerotized structure around a pit; the vulva posesses globular receptacula seminis. - The description of the species by SCHRANK (1803: 230) from Germany (Ingolstadt) is very short and unspecific, even the identity of the genus is not sure; furthermore it is based on spiders living *in* houses, but members of true *emarginatus* live actually in higher strata of the vegetation. On the other hand I collected the present male of *E. lusitanicua* on the – *outside* – wall of a house.

(**) Regarding *emarginatus* LOGUNOV & HUSEYNOV (2008: 121) noted: “One of our sample (3♂♂ 1♀) from from Kilyazi <13> contained the males with visible wider tibial apophysis. ... No taxonomic value has been paid to this difference, for no other differences have been found in the copulatory organs both of males and females.”. In my opinion this sample from Azerbaijan has to restudy.

Distribution: Portugal.

Pulchellodromus medius (O. PICKARD-CAMBRIDGE 1872)

Material: Portugal, Algarve, Campeiros (see above), in the garden of our house, beaten from an apricot tree. 1♀, JW leg. 5. V. 2025, R351/CJW. The specimen will be given to the University of Hamburg.

Distribution: The species has been known from Italy to Russia and is new to the fauna of Portugal and the Iberian Peninsula.

Family THOMISIDAE

?***Ebrechtella patellamaculata*** WUNDERLICH 2023 (photo 1)

Material: Portugal, E-Algarve, ca. 3 km E Campairos (see above), below a stone, 1♂ JW leg. 10. VI. 2025, R358/CJW. - Note: The male is complete and in a good condition.

Size, shape and colour – including the small dark spot ventrally on patella I – are as in the holotype. Only the holotype of this species was known up to now; the female and the relationships remain unknown.

Distribution: Portugal, Algarve.

Family SALTICIDAE

Aelurillus SIMON 1884

Aelurillus is a diverse genus around the Mediterranean, see AZARKINA & LOGUNOV (2006), about 35 species are known. Like in numerous other salticid genera a strong sexual colour dimorphism exists and the determination to the species may be difficult, especially for females because of their quite similar and intraspecific variable epigynes and even vulvae. Because of their dorsally hidden embolic division of the non-expanded bulbus the determination of males is difficult, too, and the shape, size and position of the sclerites of the embolic division may be variable. A special difficult group is represented by the species around *A. luctosus* which I call the *luctuosus* species-complex. In the following I provide a key to the males of this group and some notes on *luctuosus*, mainly based on spiders from Portugal.

Key to males of the *luctuosus* species-complex:

1 Clypeus bearing a field of dense white hairs, see AZARKINA & LUGONOV (2006): figs. 13, 15). Algeria, Tunisia .... *basseleti* (LUCAS 1846)

- Clypeus black, without white hairs, see AZARKINA & LUGONOV (2006: figs. 7, 9, 11). Mediterranean 2

2(1) Cephalic part dorsally anteriorly-medially with a stripe of white hairs, see AZARKINA & LUGONOV (2006: figs. 84-85). Algeria, Tunisia .... *monardi* (LUCAS 1846)

- No such stripe. Embolic division see AZARKINA & LUGONOV (2006: figs. 46-56); figs. 33, 36, see below. Widely spread in the Mediterranean. Copulatory structures quite diverse; probably a “sampling species”.. *luctuosus* (LUCAS 1856)

Aelurillus ?luctuosus (LUCAS 1846) (figs. 33-37)

Material: Portugal, SE-Algarve, N Altura, JW leg. in sunny localities on and under stones in III-IV 2025; (1) Campeiros, 37.248985N 7.531581W, and 3 km south of this village, 1♂ (right pedipalpus absent, left pedipalpus dissected), 3♀ (1 epigyne loose) R344/CJW; (2) at the margin of the lake Beliche, 1♂ (right pedipalpus absent, left pedipalpus dissected), 1♀**,** both captured in the same pit fall, R345/CJW. The spiders will be kept in the Zool. Mus. Univ. Hamburg.

Measurements (in mm): Prosomal length/width (1) spiders from Campeiros, ♂ 2.2/1.6, ♀ 3.0-3.3/2.2-2.4; (2) spiders from Beliche ♂ 3.0/2.2, ♀ 3.3/2.3.
Colour and further characters: See AZARKINA & LUGONOV (2006) and the key above.
Embolic division of the present spiders: Figs. 33 and 36, epigyne: Figs. 34 and 37, vulva: Fig. 35.

Relationships and discussion: Shape, size and position of the sclerites of the embolic division and of the female copulatory organs are quite variable in *luctuosus*, see AZARKINA & LUGONOV (2006). In the male from Beliche the long sclerite of the embolic division is thinner and its position is longitudinal in contrast to the male from Campeiros; the posterior sclerotized epigynal plate of the female from the lake Beliche is distinctly larger than in the females from Campeiros. - According to the prosomal colour *luctuosus* differs from the related species by “negative characters”: White hairs of the clypeus are absent in contrast to *basseleti*, and an anterior median prosomal stripe of white hairs is absent in contrast to *monardi* and *basseleti*. Based on the scarce present material I am not sure about the conspecifity of the spiders from Campeiros and Beliche – see the figs. -, and I do not want to exclude that *luctuosus* may be a “sampling species”. Further material and studies are needed for a definitive conclusion.

***Euophrys parvireceptacula* n. sp.** (figs. 38-43)

Etymology: The species is named after its unusually small receptacula seminis, from parvus (lat.) = small.

Material: Portugal, SE-Algarve, (1) ca. 3 km S from the Lake Beliche, southern margin of a dirt road, ca. 80 m, 1♀ holotype, JW leg. 3. VI. 2025 below a stone, R355/CJW. - Note: The opisthosoma is loose, the epigyne is kept separately; (2) quite near to the Lake (Barragem) Beliche, probably not more than 50 m, SW exposed stony slope near the east end of the the large dam wall, pit fall, paratype ♂ JW leg. in V. 2025, R353/CJW. - Note: The left pedipalpus is kept separately, the opisthosoma is almost loose.

Diagnostic characters: Colour of prosoma, pedipalpal articles and most leg articles dark grey (almost black) but tarsi yellow and legs III-IV fairly annulated, only weakly in the female, peltidium, clypeus and chelicerae with remains of white (no orange or red) hairs, a narrow band of white hairs remains ventrally on the clypeus in both sexes, opisthosoma uniformly medium to dark grey, remains of white hairs, spinnerets dark grey; ♀-pedipalpus: Tarsus black, remaining articles partly dark and partly yellow. - ♂-pedipalpus (figs. 38-40): Tibial apophysis quite thin, 0.16mm long, tibia basal of its apophysis 0.2 mm long, tegular disc, embolus and conductor loop large, transverse diameter of the disc 0.25 mm, embolus and conductor close together and close to the disc. - ♀: Epigyne (fig. 41) with a wide and not distinct divided light field as well as well observable receptacula seminis and ducts; vulva (fig. 42) with quite small and thin-walled receptacula seminis in a posterior position which are almost touching and with long ducts. - Larger spiders, body length more than 5 mm.

Description:
Measurements (in mm). ♂: Body length 5.1; prosoma: Length 2.5, width 2.0, height 1.5; opisthosoma: Length 2.8, width 1.7; leg I: Femur 1.8 (diameter 0.75), patella 0.9, tibia 1.3 (diameter 0.58), metatarsus 0.8, tarsus 0.6; tibia II 1.0, tibia III 0.83, tibia IV 1.5; pedipalpus: Femur 0.8, patella 0.3, tibia basal of its apophysis in retrolateral aspect 0.2, tibial apophysis 0.16, cymbium 0.7, transverse diameter of the tegular disc 0.25. - ♀: Body length 5.6; prosoma: Length 2.8, width 2.0, height 1.5; opisthosoma: Length 3.1, width 2.1; leg I: Femur 1.5, patella 1.0, tibia 1.0, metatarsus 0.7, tarsus 0.55; tibia II 0.9, tibia III 0.9, tibia IV 1.3; diameter of a receptaculum seminis 0.07.
Colour: See the diagnosis. Most white hairs are rubbed off. I found no orange or red hairs.
Prosoma (♀ fig. 41) 1.25-1.4 (♀) times longer than wide, hairs of medium length, fovea absent, fang furrow (♀): Anterior margin with two large teeth, posterior margin with a single large tooth. - Legs: Order IV/I/II/III; ♂-femora I-II and tibia I distinctly thickened (see above); bristles: Femora, besides apicals, dorsally 1/1, patellae III-IV with a lateral pair, tibiae and metatarsi I-II besides laterals and apicals ventrally with 2 pairs; scopulae absent, claw tufts well developed. - Opisthosoma 1.48-1.65 (♀) times longer than wide, dorsally with longer normal hairs, ventrally with shorter hairs. - ♂-pedipalpus: See the diagnosis. Femora without bristles or strong hairs, ventral hump of the tibia well developed. - Epigyne/vulva: See the diagnosis.

Relationships: Most members of European *Euophrys* are smaller, their colour of body and legs is different, the retrolateral margin of the pedipalpal tegular disc is more spaced from embolus/ conductor, see x in fig. 40, the receptacula seminis are distinctly larger (compare fig. 43), the ducts of the vulva are different, shorter. In the most related *E. innotata* (SIMON 1868) the tarsi are yellow as in *parvireceptacula* but the ♀-opisthosoma is spotted and the structures of epigyne/vulva are clearly different, the receptacula seminis are much larger, the epigynal ducts are distinctly shorter (♀ from Catalonia, Spain, BOSSELAERS (2018)). - According to the tegular disc, the position of embolus and conductor, epigyne and vulva as well as the large size (body length in the male sex 6 mm) *Euophrys nigritarsis* (SIMON 1868) from France and probably Spain (Balearic Islands) is also related to *parvireceptacula*. *E. nigritarsis* possesses also a large tegular disc but dark tarsi, the embolus is more away from the retrolateral margin of the disc, the position of sperm duct and embolus are a bit different, the receptacula seminis are distinctly larger. Furthermore *nigritarsis* is apparently a species of high mountains, DENIS collected specimens in 2020 – 2910 m; the type locality is in the East Pyrenees. - In *E. terrestris* (SIMON 1871) the colour of body and legs is reported as quite variable, the receptacula seminis are much larger, the epigyne and the ducts of the vulva are different.

Distribution: Portugal, SE-Algarve. Reports of related species out of (high) mountains, like *nigritarsis*, which are reported by several authors, will have to be checked.

Evarcha arcuata (CLERCK 1757)

Material: Portugal, E-Algarve, Campeiros, 11 km N Altura, in a garden, 1♂ JW leg. in III 2025, CJW.

Remark: The tibial apophysis of the present male is clearly pointed as shown in the figs.

given by ZABKA (1997) but not blunt as shown by other authors like BRAENDEGAARD (1966) or LOCKET & MILLIDGE 1951); see WSC, spiders of Europe.

Heliophanus haymozi LOGUNOV 2015

Material: Portugal, E-Algarve, stony habitat near the SE part of the Lake Beliche, 1♂ JW leg. 25. IV. 2025, CJW.

Note: According to LOGUNOV (2015) the colour of the ♂-opisthosoma of the species is ventrally yellow brown and the spinnerets are yellow. In the present specimen the opisthosoma, the spinnerets and also the prosoma are black.

Distribution: Iberian Peninsula.

Menemerus semilimbatus (HAHN 1827) and its questionable stridulatory organ (fig. 44)

Stridulating in spiders possesses various functions, both interspecific – e. g. to threaten potential predators – and intraspecific – e. g. ovoid cannibalism or repellent conspecific males or it is connected with courtship behaviour, to attack partners, or females use stridulation to inform males of receptivity.
The widely distributed Jumping spider *Menemerus semilimbatus* is not rare in the Algarve. In June 2025 I was lucky to observe several males and females of this species on stones in the morning before the heat of the midday at about 11 a. m. during sunshine. (See also observations of the prey capturing behaviour of this species in the Algarve by WUNDERLICH (2023: 8)). Members of both sexes were moving their pedipalpi rapidly and continuously up and down without recognizing another conspecific specimen nor another arthropod nor me. What is the meaning of this striking behaviour?
Remarkably in *semilimbatus* a strong sexual difference in the distribution of long white pedipalpal hairs exists: In the female white hairs exist on all articles except the basal part of the femur, longest and most striking on the tarsus. Contrarily in the male long white hairs exist in the distal half of the femur (few basally on the patella, too) but not on the tarsus.
In June 2025 I observed the intraspecific behaviour of *semilimbatus*:
(a) The meeting of two females. Both spiders were spaced by ca. 20 cm from each other. “As usual” both spiders moved their pedipalpi fast up and down, presenting the conspicuous brush of white hairs mainly on their pedipalpal tarsi. After about half a minute one female turned around and jumped away. In this case the pedipalpal moving can apparently be interpreted as antagonistic behaviour.
(b) The meeting of a male and a female. Both spiders were spaced by ca. 15 cm from each other. “As usual” both spiders moved their pedipalpi fast up and down. Shortly after the spiders recognized each other the male raised its prosoma and stretched its dark and strong forelegs widely sidewards. This was the beginning of the courtship behaviour, similar known

in many other salticid species. But the present female was not interested in mating; after about half a minute it turned around and disappeared.

During the courtship behaviour of *semilimbatus*, the moving of the pedipalpi of the male is connected with quite a different intraspecific behaviour, too. WESOLOWSKA (1999) treated and figured a cheliceral-pedipalpal stridulatory organ of several species of the genus *Menemerus* (HAHN 1827). This organ has been found in several but not all congeneric species; it has been first described in the family Salticidae by PETRUNKEVITCH (1926) in *Menemerus bivittatus* (under *Stridulattus stridulans*), and is believed to be connected with courtship behaviour. PETRUNKEVITCH (1926: Fig. 25) figured retrolateral cheliceral “stridulation ridges” as well as long probasal “stridulation setae” (fig. 26). Long setae in this position were rarely observed/drawn by WESOLOWSKA and not by me, but only “humps” were recognized; they apparently represent the bases of stronger setae which were broken (rubbed) off.

This kind of spiders' stridulatory organs consists usually of one or several prolateral spines of the pedipalpal femur which are rubbed over retrolateral files – similar to a washboard - of the basal articles of the chelicerae, see fig. 44. Such kind of a cheliceral-pedipalpal stridulatory organ is not rare in spiders of various families. In certain families like Linyphiidae it exists even as a family characteristic pattern and exists even in the female sex. From the family Salticidae I know the existence of such a pedipalpal-cheliceral organ only in the male sex of the genus *Menemerus*. WESOLOWSKA (1999: 346) did not mention *Menemerus semilimbatus* in her list of species possessing such stridulatory organ. In males of *semilimbatus* I found (1) a larger number of retrolateral (more retroventral) files – or simply file-shaped structures? - on the basal cheliceral articles which are best recognizable in the dorsal-apical aspect (fig. 44); in females such a structure seems to be absent. - (2) a field of “humps” or “nodes” (see above) exist which may be placed in rows, see WESOLOWSKA (1999: Fig. 111). The “nodes” of this field are situated on a probasal *concave* area of the male pedipalpal femur opposite to the cheliceral files/ribbs and are apparently be connected with a stridulatory function, but further studies are needed, best in nature and not in the laboratory. WESOLOWSKA (1999: Fig. 63) figured long basal-prolateral pedipalpal hairs in a male of *M. congoensis* LESSERT 1927. In females I found only thin pedipalpal femoral hairs in the probasal position.

I suppose that this kind of a well developed cheliceral-pedipalpal stridulatory organ of the male sex may well be a basal characteristic/diagnostic pattern of the genus *Menemerus,* reduced or overlooked in certain species of this genus.

Notes: Usually a pedipalpal ventral-basal outgrowth of the femur is well developed in the male sex of *Menemerus*, distinctly pointed in certain species. but absent in few species, e. g. in *M. bivittatus* (DUFOUR 1831). - Is the prolateral tibial tooth of the male pedipalpus of *M. animatus* O. PICKARD-CAMBRIDGE 1876 probably used for stridulating?

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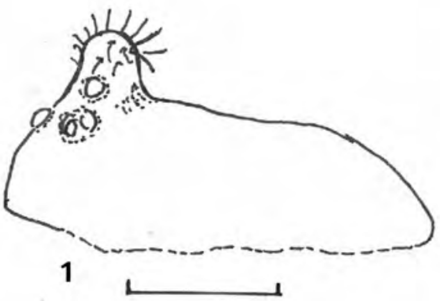
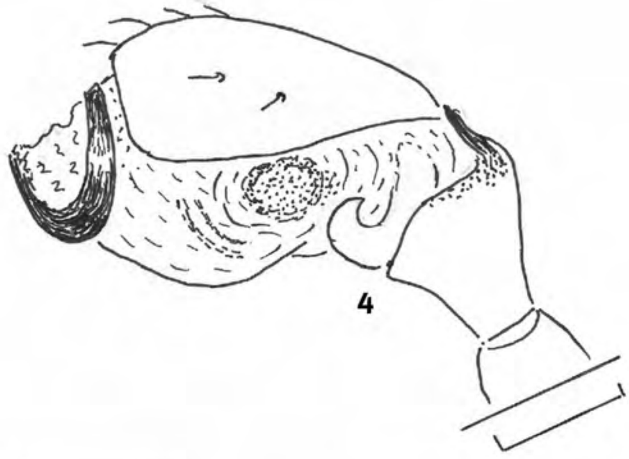
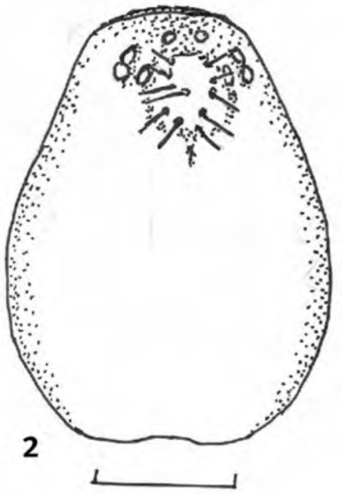
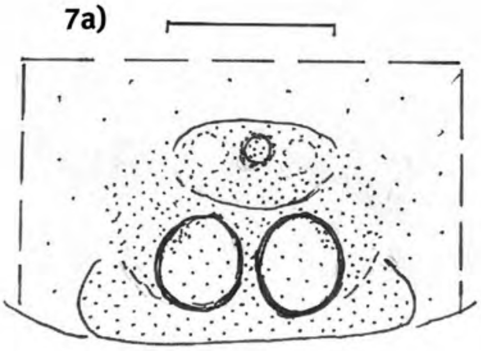
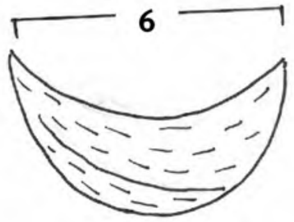
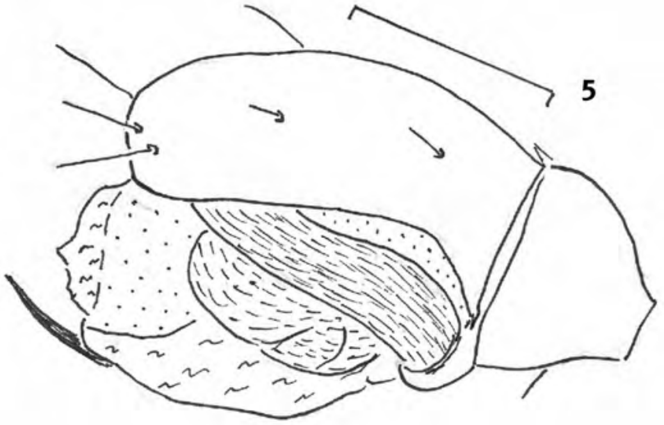




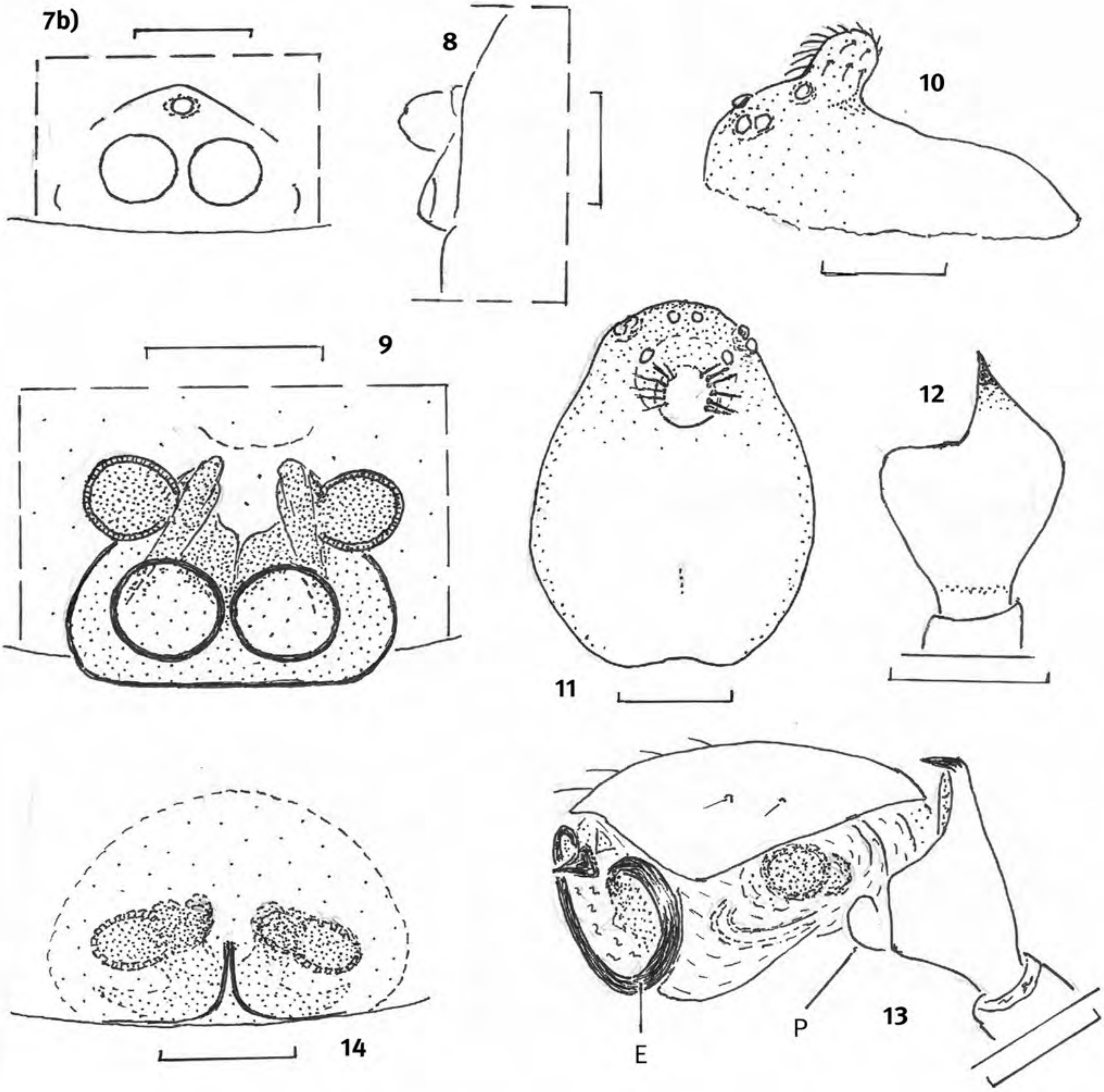








Figs. 1-6: ***Macrargpelecopsis ascutata* n. gen. n. sp.**, ♂; 1-2) lateral and dorsal aspect of the prosoma; 3) dorsal aspect of the tibia of the left pedipalpus; 4) retrolateral aspect of the left pedipalpus; 5) prolateral aspect of the right pedipalpus; 6) apical-ventral aspect of a part of the embolus of the right pedipalpus. - Scale: 0.2 mm in figs. 1-2, 0.1 mm in the remaining figs.;
fig. 7a) ***Macrargpelecopsis ascutata* n. gen. n. sp.**, ♀, epigyne. - Scale: 0.1 mm.

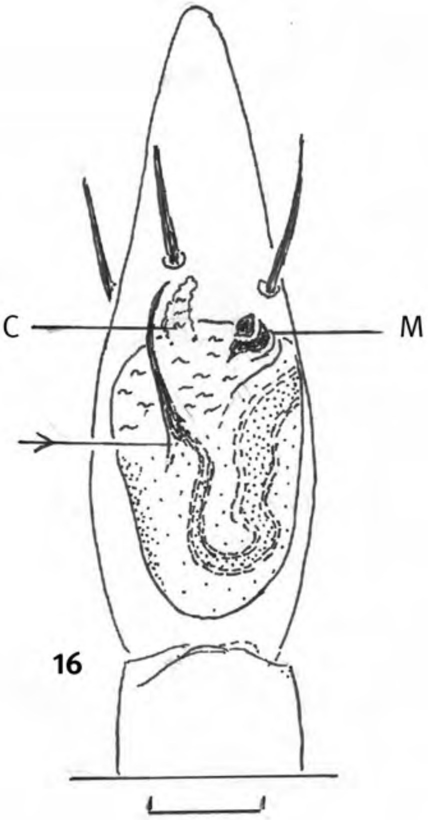


figs. 7b-9: ***Macrargpelecopsis ascutata* n. gen. n. sp.**, ♀; 7b) ventral-posterior aspect of the epigyne. Pigmentation and sclerotics are not drawn; 8) lateral aspect of the epigyne, outline; 9) dorsal aspect of the vulva;

10-13) ***Macrargelecopsis spinosa* n. gen. n. sp.**, ♂; 10-11) lateral and dorsal aspect of the prosoma; 12) dorsal aspect of the tibia of the left pedipalpus; 13) retrolateral aspect of the left pedipalpus;

14) ***Silometopus furcatus*** WUNDERLICH 2024, ♀, epigyne.

E = embolus, P = paracymbium. Scales: 0.2 mm in figs. 10-11, 0.1 in the remaining figs.;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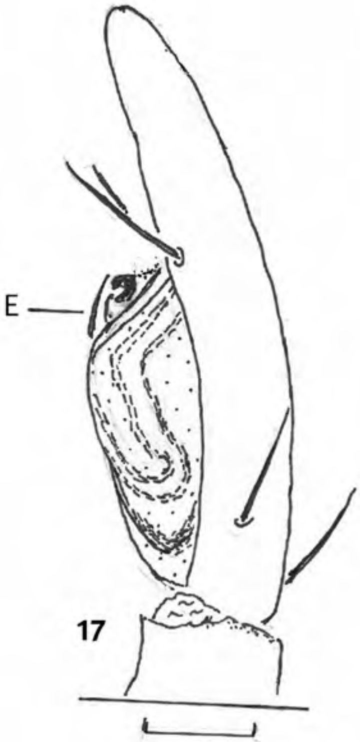
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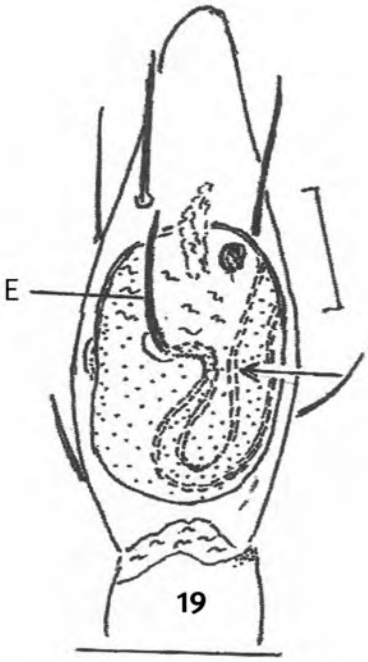
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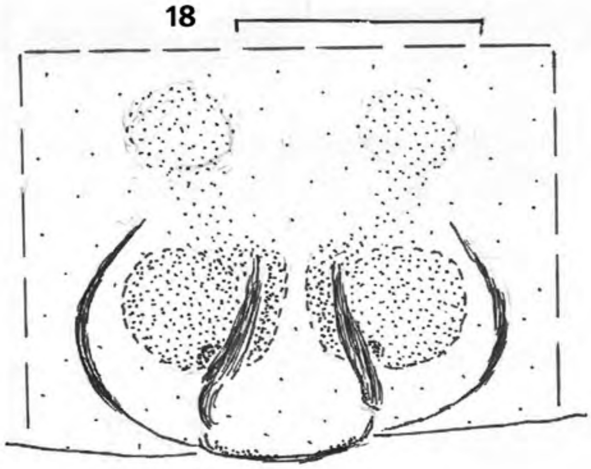
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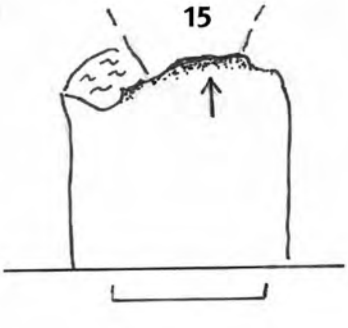
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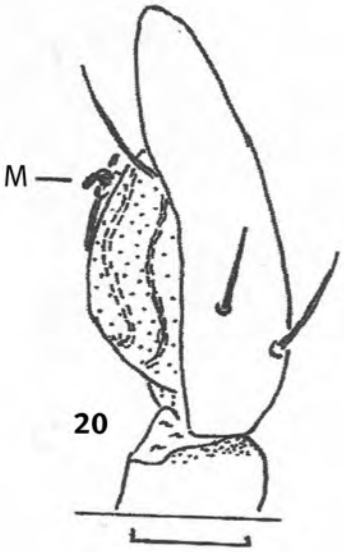
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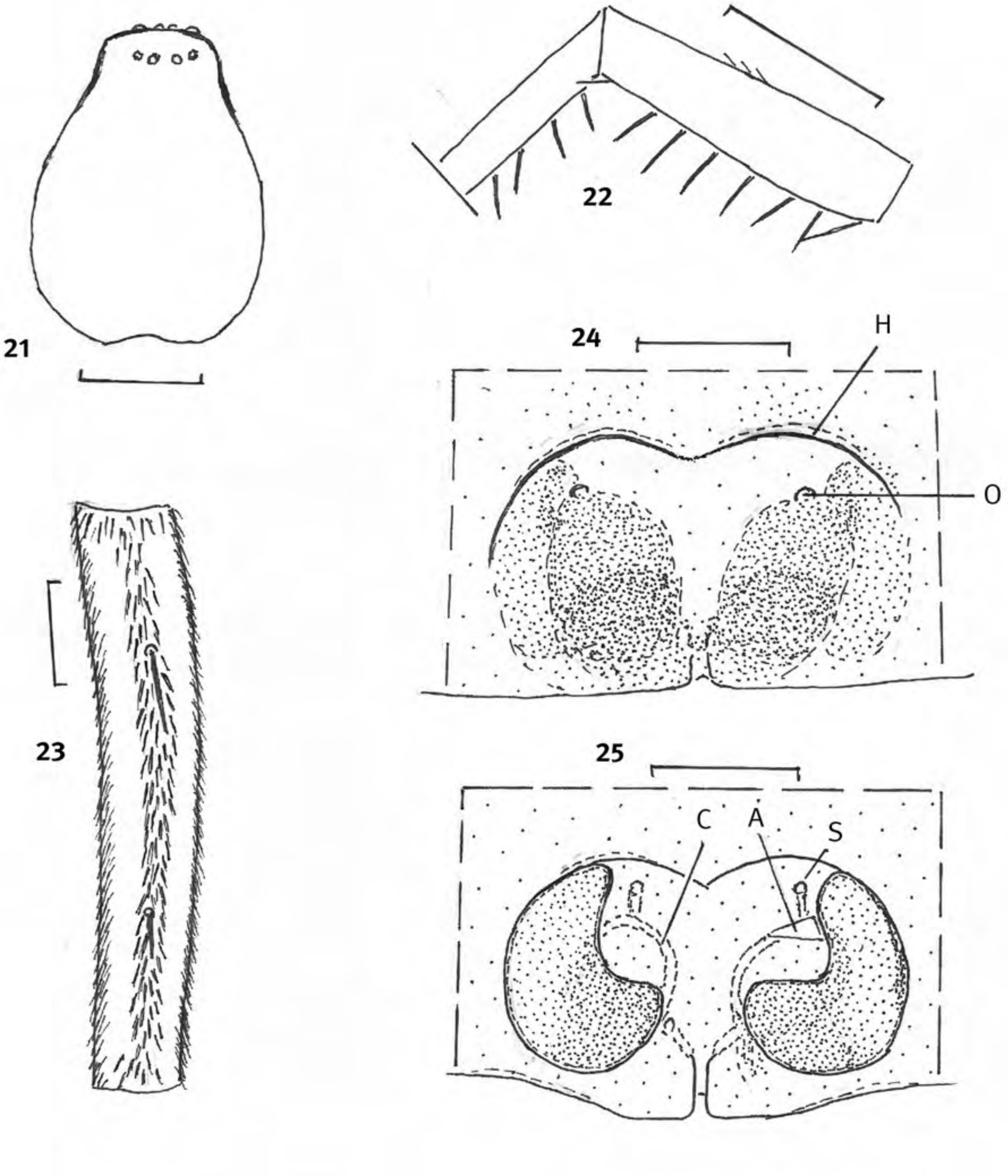
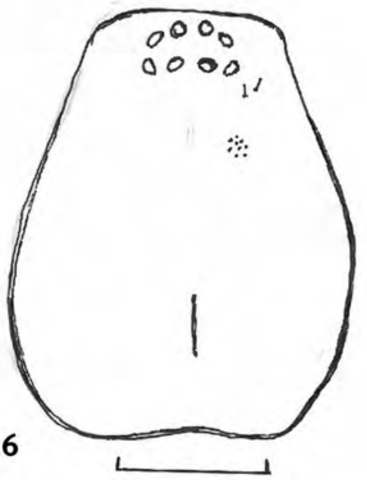
figs. 15-18: ***Drassodes balneum* n. sp.**; 15-17) ♂; 15) retrolateral aspect of the distal part of the left pedipalpal tibia. The arrow points to the sclerotised lamellate apical margin; 16-17) ventral and retrolateral aspect of the left pedipalpus; the arrow points to the base of the embolus; 18) ♀, epigyne;

figs. 19-20: ***Drassodes arenosus*** WUNDERLICH 2023 ♂, ventral and retrolateral aspect of the left pedipalpus. - C = conductor, E = embolus, M = median apophysis. Scales: 0.2 mm.



figs. 21-25: ***Micaria*** ?***triguttata*** SIMON 1884, ♀; 21) dorsal aspect of the prosoma; 22) retrolateral aspect of the left tibia and the basal part of the metatarsus I (prolateral bristles are not drawn); 23) dorsal aspect of the right femur IV. The light longitudinal bands are covered with yellowish hairs which are not drawn; 24-25) epigyne and dorsal aspect of the vulva. Scales: 0.2 mm in figs. 21-23, 0.1 mm in figs. 24-25. - A = artefact, C = copulatory duct, H = hood, O = copulatory opening, S = secondary receptacula seminis sensu LI & ZHANG (2025);



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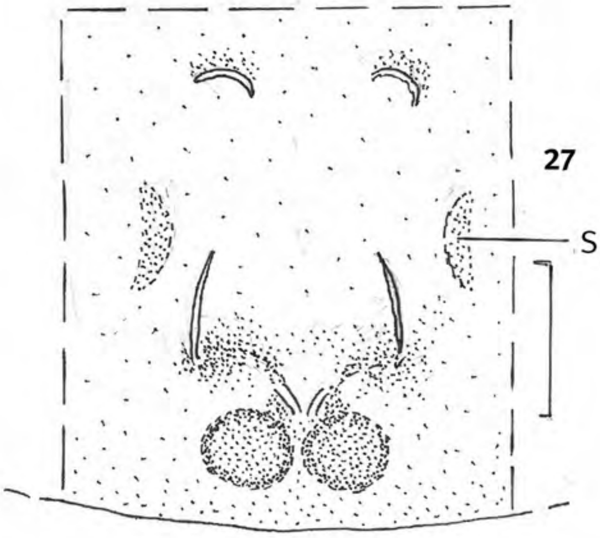

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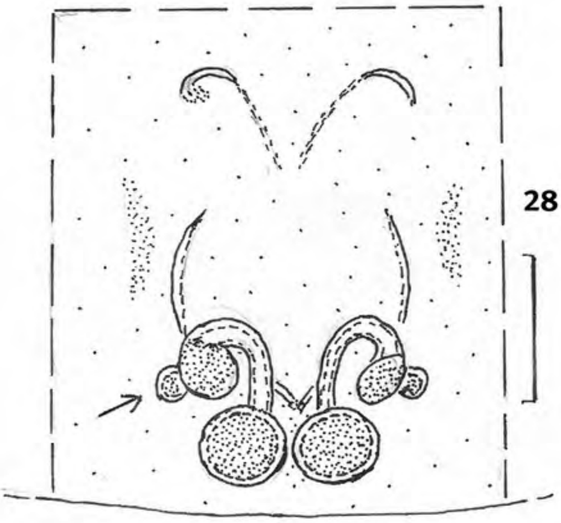

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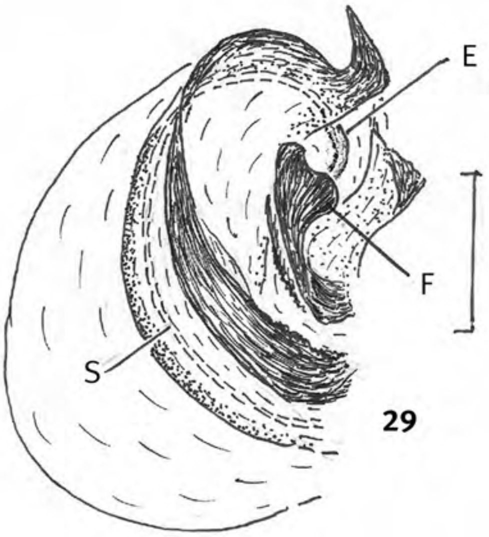

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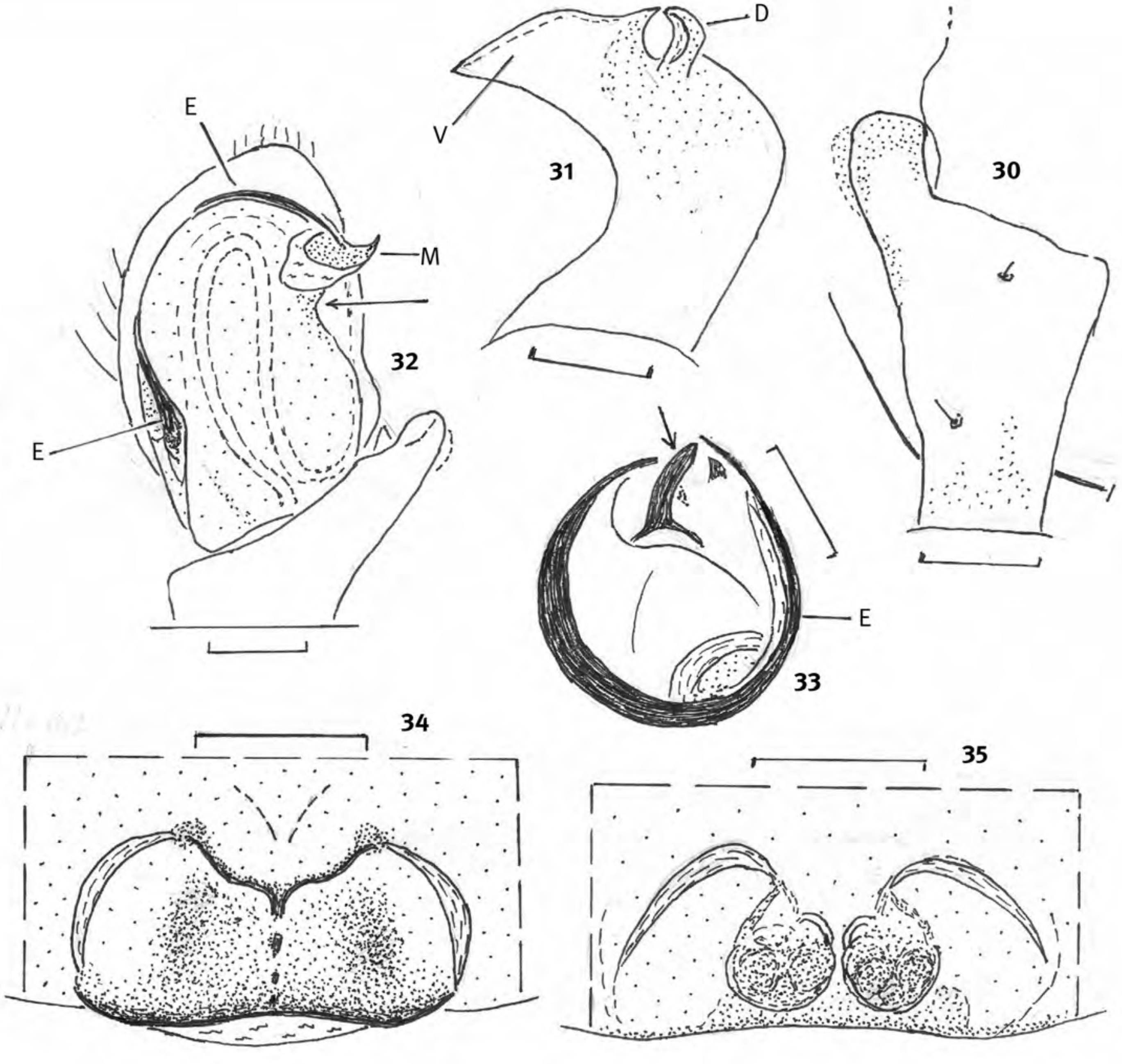
figs. 26-28: ***Zelotes nigropunctatus* n. sp.**, ♀; 26) dorsal aspect of the prosoma; 27) epigyne (S = sclerotized field); 28) dorsal aspect of the vulva. The arrow points to a globular structure of unknown function. Scales: 1.0 mm in fig. 26, 0.2 mm in figs. 27-28);

fig. 29) ***Micrommata ligurica*** (C. L. KOCH 1848), freshly moulted ♂, ventral aspect of the bulbus. The free part of the embolus is slightly enlarged. - Scale: 0.1. E = embolus, F = functional conductor, S = sperm duct;



figs. 30-32: ***Emargidromus lusitanicus*** (KULCZYNSKI 1911), ♂; 30) dorsal aspect pf the left pedipalpal tibia; 31) retrolateral aspect of the left pedipalpal tibia; 32) ventral aspect of the left pedipalpus. The arrow points to the tegular inclination;

33-35: ***Aelurillus*** ?***luctuosus*** (LUCAS 1846) from Campeiros, R344/CJW; 33) ♂, dorsal aspect of the embolic division. The arrow points to the long sclerite; 34-35) ♀, epigyne and dorsal aspect of the vulva. - Scale: 0.2 mm in figs. 30-32, 0.1 in figs. 33-35. D = retrodorsal tibial apophysis, E = embolus, M = median apophysis, V = retroventral tibial apophysis;

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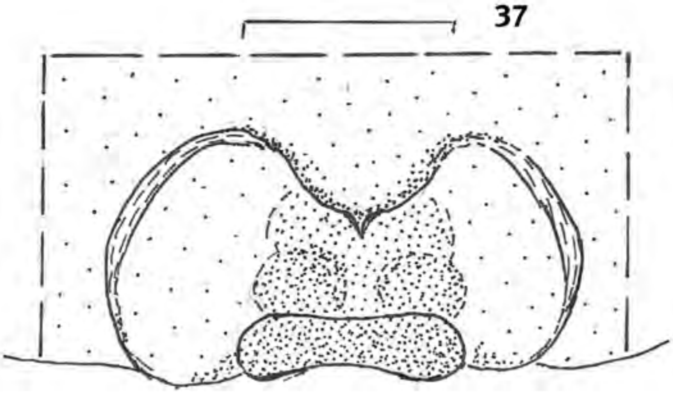

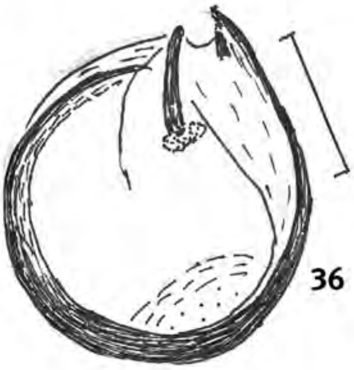

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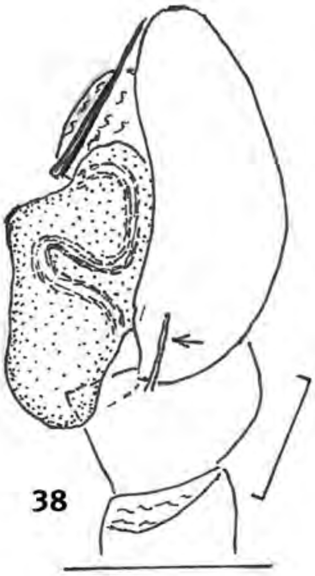

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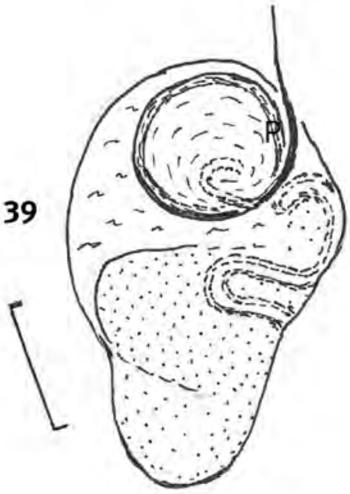

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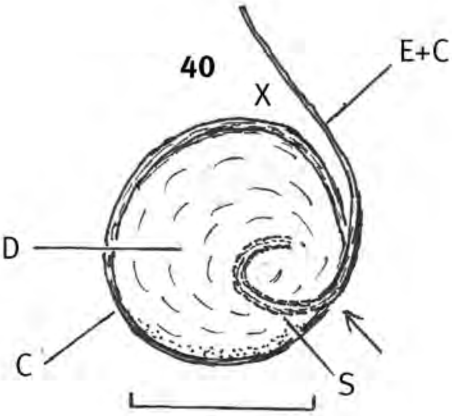
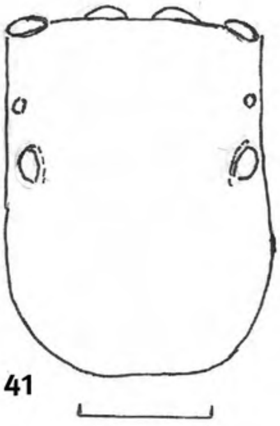


figs. 36-37: ***Aelurillus*** ?***luctuosus*** (LUCAS 1846), lake Beliche, R345/CJW; 36) ♂, dorsal aspect of the embolic devision; 37) ♀, epigyne. Scales 0.1 and 0.2 mm;

figs. 38-40) ***Euophrys parvireceptacula*** **n. sp**., ♂; 38) retrolateral aspect of the left pedipalpus. The arrow points to the thin tibia apophysis. Hairs are not drawn; 39) ventral aspect of the bulbus; 40) embolus + conductor (E+C), disc (D) and sperm duct (S); the arrow points to the entrance of the sperm duct into the embolus. - Scale: 0.2 mm. X = little space between embolus and conductor in this species;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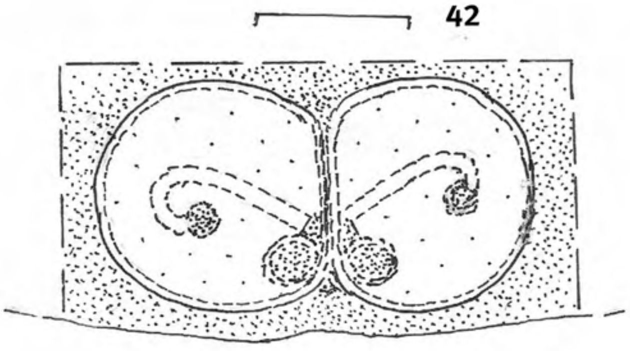
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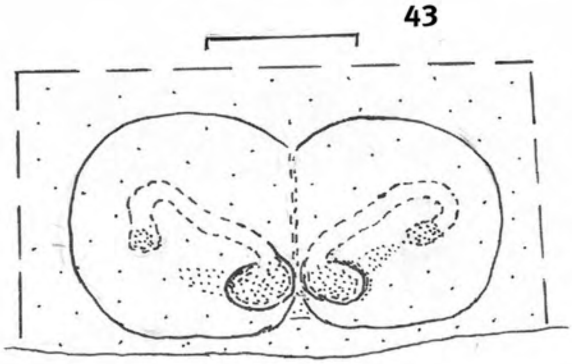
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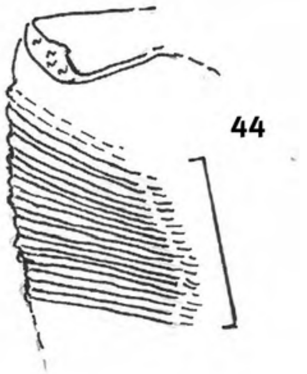
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figs. 41-43: ***Euophrys parvireceptacula*** **n. sp.**, ♀; 41) dorsal aspect of the prosoma; 42-43) epigyne and dorsal aspect of the vulva. - Scales: 1.0 mm in figs. 41, 0.2 mm in figs. 42-43.

fig. 44) ***Menemerus semilimbatus*** (HAHN 1827), ♂, retroapical aspect of the distal part of the right chelicera. - Scale: 0.5 mm.

BEITR. ARANEOL., 18 (2025: 37–63)

CONTRIBUTION TO TAXONOMY AND PHYLOGENY OF THE ARCHAEOID SPIDER BRANCH OF THE SUPERFAMILY PALPIMANOIDEA (ARANEAE), WITH NEW DESCRIPTIONS OF FOSSIL TAXA

.

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Abstract and summary: The 12 fossil and extant higher genera of 6 families of the archaeoid branch of the superfamily Palpimanoidea (= Archaeoidea) (Araneae) are treated. In my opinion the family Archaeidae in the recent sense is not monophyletical and the diverse Mesozoic Archaeidae has to be split up as proposed in the present paper, see tabs. 1-2. Only 2 families – Archaeidae and Mecysmaucheniidae – survived, both in the Southern Hemisphere; so by far most families are extinct. Archaeidae is the most diverse and longevity family of this branch: it is the only family known as fossil from Cretaceous Burmese (Kachin) amber, from Eocene European – Baltic, Bitterfeld and Ukrainean Rovno - ambers as well as from extant genera. To my current knowledge the family Mecysmauchniidae has to be deleted from Kachin amber. The construction of an improved cladogram of the families of the archaeoid branch is a matter of the future. We are far from knowing satisfactorily all family diagnoses or sure relationships. - The existence of *parthenogenesis* is suggested for extinct members of the families Archaeidae (*Baltarchaea* and *Myrmecarchaea*) and Eoarchaeidae n. fam. (*Eoarchaea*) - New descriptions, relationships and ranks: (1) In Eocene European ambers: Eoarchaeidae **n. fam**. *Baltplanarchaea oblonga* (WUNDERLICH 2017): This taxon – erroneously described from Cretaceous Burmese Kachin amber - is transferred from *Planarchaea* of the family Archaeidae: Planarchaeini to the new genus *Baltplanarchaea* of the family Planarchaeidae (**n. comb.& n. relat**.). The holotype is actually preserved in Eocene Baltic amber. The family Planarchaeidae was only known from the Cretaceous and is new to Baltic amber and to the Palaeogene. - (2) in Lower (Mid) Cretaceous Kachin (Burmese) amber: *Planarchaea brevipalpitibia* **n. sp**., *P. longipalpitibia* **n. sp.**, *P. petersi* **n**. **sp**. and *P. quinquespinae* **n. sp**. of the Planarchaeidae and *Burmesarchaea spinicaput* **n. sp**. of the Archaeidae. Lacunaucheniidae WUNDERLICH 2008 **n. stat.** is raised from subfamily rank of the Archaeidae. Planarchaeidae WUNDERLICH 2017 (**n. stat.**) is raised from tribe rank of the Archaeidae to a family of its own. - (3) The Jurassic Jurarchaeinae ESKOV 1987 (under Archaeidae) is elevated to family rank (**n. stat**.) - <u>Further new relationships and synonyms</u>: *Archaemecys arcantiensis.* SAUPE & SELDEN 2009 (Cretaceous France amber) is transferred from the family Mecysmaucheniidae to the Archaeidae (**n. relat**.) and so a Cretaceous report of the Mecysmaucheniidae is absent. Spiniarchaeinae WUNDERLICH 2021 (Cretaceous Kachin amber, under Archaeidae) is regarded as a taxon of the Planarchaeidae WUNDERLICH 2017, probably as tribe of the nominate subfamily (**n. relat**.).

Key words: Araneae, Archaeidae, *Burmesarchaea*, Burmese amber, Cretaceous, Eoarchaeidae, Eocene, fossils, Jurarchaeidae, Kachin amber, Lacunaucheniidae, Mecysmaucheniidae, parthenogenesis, Planarchaeidae, spiders, Spiniarchaeinae, Zearchaeinae.

Most **material** is still kept in my private collection and will later probably be given to the Palaeontology of the University of Hamburg, Ulrich Kotthoff.

This study is partly based on new material of excellently preserved male spiders.

Notes on the method

A cladogram is based on the selection of characters. Usually the choice of diagnostic family characters is fundamentally more or less *arbitrary,* and chosen by me in this paper only provisionally. Few examples in this matter: The characteristics of the families Archaeidae and Mecysmaucheniidae are quite different from the characters selected by FORSTER & PLATNICK (1984: 20, 32). SCHÜTT (2002: 95) lists a large number of – plesiomorphic as well as apomorphic - characteristics of her “true archaeids”; I did not recognize all of them. In both papers I miss more focus on (in my opinion) important characters like a sclerotized ring around the spinnerets, a quite short (reduced) female pedipalpus and - partly - strong opisthosomal folds, see tab. 1 and 2. I tried to find special/rare/apomorphic family characters *which are linked with each other;* two examples: In the Archaeidae I regard as most important the sclerotized ring around the spinnerets (fig. 1), strong opisthosomal folds (fig. 1) and the very short pedipalpus in the female sex. In the Lacunaucheniidae short legs and the unique paired clypeal “horns” (fig. 7) are linked with each other. See also the family Eoarchaeidae.

To my current knowledge the mainly (sub)tropical relic superfamily Palpimanoidea (= Archaeoidea which has priority from the date) includes 14 families of which 9 – ca. two thirds! - are extinct (*). 5 of 7 families of the archeoid branch are extinct. The archaeoid branch of this superfamily is **characterized** by its large cheliceral *foramen* and usually long “*neck*” as well as chelicerae surrounded by a sclerotized ring (fig. 1, photo 2) (**). The basal cheliceral articles are powerful/long (figs. 1, 14, photo 3), the cephalic part is usually more (e g. fig. 22) or less (fig. 9) raised. Cheliceral peg teeth (fig. 19), lateral cheliceral stridulatory files (fig. 1) and araneophagy – except in the Mecysmaucheniidae - exist in most taxa like in other taxa of the Palpimanoidea. In most archaeoid families 3 pairs of well developed spinnerets and frequently dorsal femoral humps (fig. 9) exist in contrast to the members of the extant family Mecysmaucheniidae whose opisthosoma bears, *well developed*, only a single pair of spinnerets, the anterior laterals, in a close position.
Most often 8 eyes exist but most members of the - extant - Mecysmaucheniidae possess only 6 eyes (see the key). Leg bristles are usually absent; the genus *Spiniarchaea* (Planarchaeidae) is one of the very rare exceptions (figs. 15-16, see tab. 2). See also *Baltplanarchaea* n. gen. in Eocene Baltic amber..

(*) I suppose the existence of a further - not low – number of unknown extinct archaeoid genera and even families.

(**) A *distinct* long “neck” is absent in the unusual Eocene family Eoarchaeidae n. fam.

Notes on phylogenetics

I suppose that the ancient family Jurarchaeidae possessed the most primitive - and probaly apomorphic - characters of the archaeoid branch: See tab. 1. Sure relationships/branchings of the families Lacunaucheniidae and Planarchaeidae are unknown to me. Close relationships of the family Eoarchaeidae - the male sex is unknown! - remain doubtful to me. The most diverse, long-living and probably ancient family Archaeidae possesses a mixture of more primitive as well as of derived characters, see below. Members of the family Mecysmaucheniidae possess only a single pair of well developed spinnerets, lost prosomal tubercles, opisthosomal furrows as well as araneophagy and have the strong tendency to lose the anterior median eyes. In my opinion this is the most derived and youngest family of the archaeoid branch. A very long “neck” and a raised cephalic part of the prosoma evolved apparently several times independently, in Archaeidae, Lacunaucheniidae and Planarchaeidae. Femoral humps (fig. 9) exist in quite different taxa, e. g., of the Archaeidae and Planarchaeidae.

The distribution of the higher archaeoid taxa in time (periods) and space:

(a) Extant: Archaeidae and Mecysmaucheniidae (Mecysmaucheniinae and Zearchaeinae). - Southern Hemisphere.

(b) Palaeogene (Eocene): Archaeidae (*Archaea, Baltarchaea*, *Myrmecarchaea* and Saxonarchaea*)*, Eoarchaeidae (only *Eoarchaea*) and Planarchaeidae (only *Baltplanarchaea*). - Baltic, Bitterfeld and Rovno ambers of Europe.

(c) Cretaceous: Archaeidae (*Burmesarchaea*), Lacunaucheniidae (*Lacunauchenius*) and Planarchaeidae (*Planarchaea*, *Platythele* and *Spiniarchaea*). - Kachin amber of Myanmar.

(d) Jurassic: Jurarchaeidae (only *Jurarchaea*). - Kazaksthan.

The families **Archaeidae** KOCH & BERENDT 1854 and **Mecysmaucheniidae** SIMON 1895: See the key below as well as tab. 1 and 2.

New material of the genus *Myrmecarchaea*:

Mymecarchaea sp. indet., 1♀ in Eocene Baltic amber, F3885/BB/CJW, photo 10. It is excellently and completely preserved, its body is 2.5 mm long, its tibia I is 2.1 mm long, the caput is slightly/fairly gradually raised, the anterior median eyes are widely spaced, a claw of the pedipalpal tarsus is absent, the opisthosoma bears narrow furrows, the spinnerets are well preserved, short.

Key to the extinct and extant families and subfamilies of the archaeoid branch:

Notes: The dorsal femoral hump (fig. 9) and the tarsal inclination of certain taxa are difficult to recognize in fossil spiders and are not taken into account in the key. Frequently – apparently by natural heating of the pieces of amber – the body of the fossil spiders and the structures of the bulbus are more (frequently) or less deformed. - Jurarchaeidae is not included, see tab. 1.

1 6 eyes except the 8-eyed genera *Aotaora* of the Mecysmaucheniinae and *Zearchaea* of the Zearchaeinae. Only anterior lateral spinnerets well developed. Extant .... **Mecysmaucheniidae** 2

- 8 eyes (e. g. fig. 14). Three pairs of well developed spinnerets (e. g. fig. 12). Extant (Archaeidae) and fossil (Archaeidae as well as the remaining extinct families) 3

2(1) Only 1-3 peg teeth on the cheliceral promargin. Paracymbium absent...... Zearchaeinae

- Several to numerous cheliceral pro- and retromarginal peg teeth. Cymbium with a bristle-bearing retrobasal paracymbium.. Mecysmaucheniinae

3(1) Sclerotized ring around spinnerets (fig. 1, photo 2). Strong prosomal tubercles (figs. 1, 4, photo 2) and strong opisthosomal folds (fig. 1, photo 2). ♀-pedipalpus very small (photo 4). Cretaceous to extant .... **Archaeidae**

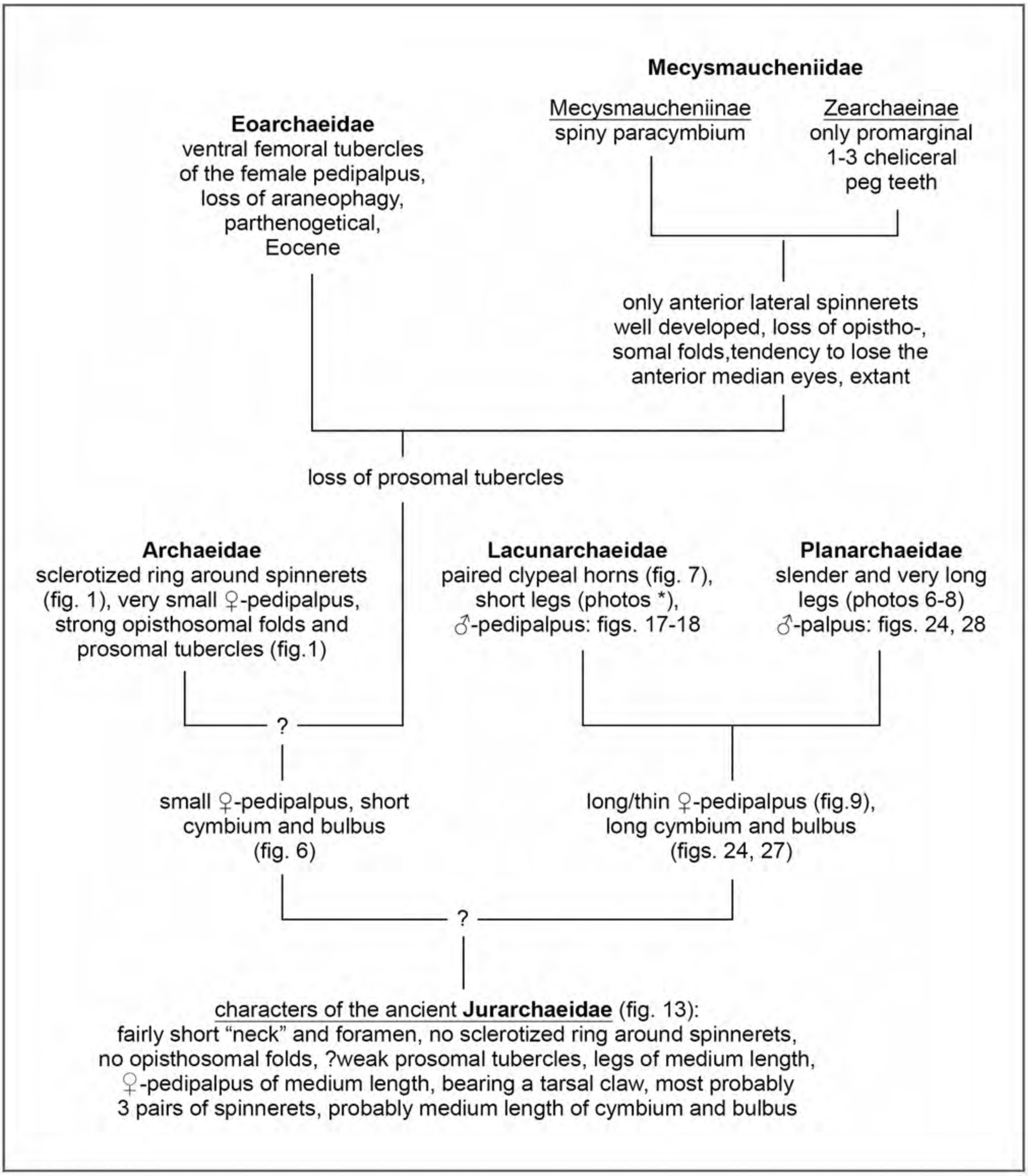
- No ring around spinnerets (fig. 2). Distinct prosomal tubercles and opisthosomal folds absent (figs. 2, 9). ♀-pedipalpus quite long (Planarchaeidae, fig. 9, photo 4), slender (Lacunaucheniidae, photo 4) or rather short/ small (Eoarchaeidae) 4

4(3) ♀-pedipalpus bearing ventral femoral tubercles. Prosoma not abruptly raised, tubercles completely absent. ♂ unknown; probably parthenogenetical. Eocene European ambers. Only *Eoarchaea* .... **Eoarchaeidae**

- ♀-pedipalpus without ventral tubercles. Most often Cretaceous taxa; in Eocene Baltic amber only *Baltplanarchaea* of the family Planarchaeidae 5

5(4) Legs short (photo 4), tibia I usually only 0.5-0.6 times of the prosomal length. Clypeus bearing a pair of small "horns" in both sexes (fig. 7). *Lacunauchenius* .....**Lacunaucheniidae**

- Legs (and ♀-pedipalpus, fig. 9) quite long and slender, tibia I usually 1.1-2.2 times longer than the prosoma. Clypeal "horns" absent. *Baltplanarchaea*, *Planarchaea*, *Platythelae* and pobably *Spiniarchaea* .... **Planarchaeidae**



Tab.1. Possible relationships of the fossil and extant families of the archaeoid branch
(*) See WUNDERLICH (2015: photo 127) and (2017: photo 85).

Description of a new extinct family and a new genus in Eocene Baltic amber:

EOARCHAEIDAE n. fam.

The name is based on the type genus *Eoarchaea* FORSTER & PLATNICK 1984, the only known genus of the family.

Type species (by monotypy): *Archaea hypocrita* MENGE 1854.- Further species: *Eoarchaea vidua* WUNDERLICH 2004.

Diagnostic characters (♀; ♂ unknown): Longer and thin opisthosomal hairs arranged in relatively regular rows, pedipalpal femur with a row of well developed ventral tubercles, cephalic part not abruptly raised, see FORSTER & PLATNICK (1984: Figs. 13, 15 and 17; absent are: A sclerotized ring around (three pairs) of spinnerets, prosomal tubercles and distinct opisthosomal folds. Apparently parthenogenetical (*).

Further characters: Lateral cheliceral stridulatory files (similar to fig. 1) existing, legs only fairly long, opisthosomal scuta absent, female pedipalpus rather small; see WUNDERLICH (2004: 784-786, figs. 29-30, photos 71-73).

Relationships: Apparently Archaeidae and Mysmauchniidae are most related, see tab. 1. In the Archaeidae a sclerotized ring around the spinnerets as well as strong prosomal tubercles exist. In the Mecysmaucheniidae only the anterior median spinnerets are well developed.

Distribution: Eocene European amber forests.

(*) I saw more than 40 adult female specimens of this family but not a single male. Usually males preserved in amber are far more frequent than females, see, e. g., the species of the family Archaeidae like *Archaea paradoxa;* see WUNDERLICH (2004: 177-178). Thus the complete absence of males of *Eoarchaea* in Eocene ambers point to the existence of parthenogenesis in this genus. From the rather rare taxa *Baltarchaea conica* (KOCH & BERENDT 1854), Baltplanarchaea oblonga WUNDERLICH 2017 and *Myrmecarchaea* WUNDERLICH 2004 – family Archaeidae, Baltic amber, too -, also never a male has been reported; I know more than a dozen female specimens of these taxa.
To my knowledge parthenogenesis in *extant* spiders has only been reported from each a single species of the families Dysderidae, Oonopidae, Ochyroceratidae, Symphytognathidae, Agelenidae and probably Hahniidae; extant and Eocene (in Baltic amber) Hahniidae: See WUNDERLICH (2004: 177).

Baltplanarchaea **n. gen.**

Etymology: The name refers to the Baltic area of preservation and to the genus name *Planarchaea*.

Type species (by monotypy): *Planarchaea oblonga* WUNDERLICH 2017.

Diagnostic characters (♀; ♂ unknown): Prosoma low, quite long and slender (photo 9), opisthosoma (fig. 2, photo 9) very long and slender, spinnerets set forward, metatarsi III-IV with a ring of thin bristles (fig. 3), femoral humps absent.

Further characters: Probably parthenogenetical. See the tab. 2 of the family Planarchaeidae in Kachin amber below and the original description of the type species.

Relationships: The shape of body and legs is quite similar to *Planarchaea* WUNDERLICH 2017 which may be related and is known from the older (100 m. a. old) Mid Cretaceous Kachin (Burmese) amber but the position of the spinnerets is at the end of the opisthosoma in *Planarchaea*, the cephalic part is stronger raised (photo 7), femoral humps may exist, apical metatarsal bristles are absent and the position of the eyes is different. In *Spiniarchaea* WUNDERLICH 2021 (see below) exists a ring of apical short metatarsal strong hairs or bristles, too, but further leg bristles exist and the cephalic part is distinctly raised. - Based on its characters the erection of a subfamily of its own is probably justified.

Ecology/climate: In my opinion this extremely rare taxon may well be a relic survivor of the tropical Cretaceous family Planarchaeidae which is known from Kachin amber from Myanmar (Burma). Among more than 100 000 spiders in Baltic amber I did not find a further confamiliar spider. Further mainly tropical and extremely rare Eocene spider families are, e. g., Deinopidae, Telemidae and Tetrablemmidae. Did members of these families exist only in areas near the southernmost border of the Baltic amber forest?

Distribution: Eocene Baltic amber forest.

Baltplanarchaea oblonga **(**WUNDERLICH 2017) (figs. 2-3), photo 9

2017 *Planarchaea oblonga* WUNDERLICH, Beitr. Araneol., 10: 187-188, photos 95-96.

Material: Holotype F2939/BU/CJW. - Note: The holotype was bought from a Chinese dealer as preserved in Cretaceous Kachin (Burmese) amber. The piece of amber was probably slightly heated, the size of the piece is 4.7x3.3x1.5 mm, the spider is only slightly deformed. In my original description I wrote “The <amber> piece looks like Baltic amber....”. After a restudy I exclude now that this piece is Kachin amber but actually it is Baltic amber: A small plant “stellate” hair – typical for Baltic amber – is placed near the right leg IV of the spider and several large bent layers (“Schlauben” in German) exist which are typical for Baltic amber, too, the smell during dry grinding is fairly sweet as in weakly heated Baltic amber; a thin white emulsion may exist on the ventral side of the spider which is hidden in main parts. I erroneously described the taxon from Cretaceous Burmese Kachin amber which is transferred now from *Planarchaea* of the family Archaeidae: Planarchaeini to the new genus *Baltplanarchaea* of the raised family Planarchaeidae (**n. comb**.). The family Planarchaeidae was only known from the Cretaceous and is new to the Eocene Baltic amber and to the Palaeogene.

Diagnostic characters (♀; ♂ unknown) and **relationships**: See above.

Added/corrected description (♀): The spider is completely preserved, the cephalic part is not raised, the 8 eyes are fairly well preserved, the anterior median eyes are widely spaced, the basal cheliceral articles are not or only slightly diverging, e “neck” and a foramen exist, the soft opisthosoma (fig. 2) is laterally not depressed, the spinnerets are partly hidden, in an advanced position. Leg I is extremely long, almost twice as long as II or IV, III is distinctly the shortest; probably a dorsal hump on the femora is completely absent. Bristles are absent except a ring of fairly slender apical bristles on metatarsi III and IV (fig. 3). I did not find metatarsal trichobothria but they should exist.

Distribution: Eocene Baltic amber forest.

The spiders in Cretaceous Kachin amber from Myanmar (Burma)

Notes on two spider taxa described in Kachin amber

(1) *Planarchaea oblonga* WUNDERLICH 2017 (Planarchaeidae), figs. 2-3, photo 9, described under Archaeidae: Planarchaeini from Kachin amber, has turned out to be preserved in *Baltic* amber, and is transferred to *Baltplanarchaea* (**n. comb**.), see above. It is the only known member of the family Planarchaeidae in Eocene Baltic amber and in the Palaeogene.

(2) *Palaeozearchaea* WUNDERLICH 2021. Single species: *Palaeozearchaea depressa* WUNDERLICH 2021, described under Mecysmaucheniidae. Its spinnerets are unknown, its opisthosoma bears probably a dorsal scutum. This enigmatic taxon may probably be near the families Vetiatoridae or Stenochilidae; in my opinion it is not a member of the Mecysmaucheniidae nor even of the archaeoid branch (**quest. rel.).**

character	**Archeidae**	**Planchaeidae**	**Lacunaucheniidae**
sclerotized ring around spinnerets	**+ (!)**	–	–
distinct opisthosomal folds	**+ (!)** (photo 2)	–	–
legs long or short	+/- long (1) (photos 2-3)	**very** long (photos 6-7)	**Short (!)** (2) (photo 4)
♀-pedipalpus	**small (!),** short (3)	Long (fig. 9)	fairly long (photo 4)
a pair of clypeal “horns”	–	–	**+** (!) (fig. 7)
♂-pedipalpus	fig. 6	figs. 24, 28	fig. 8
genera	*Burmesarchaea*	*Planarchaea* (4)	*Lacunauchenius*

(1) Legs slender, *fairly* short in certain species.

(2) Tibia I usually only 0.5-0.6 times of the prosomal length; in the remaining families tibia I usually 1.3-2.2 times longer than the prosoma, in *Spiniarchaea* 1.1 times.

(3) Short means shorter than the basal cheliceral articles; long means distinctly longer than the basal cheliceral articles.

(4) As well as *Platythelae* and probably *Siniarchaea*. See also below, the Eocene genus *Baltplanarchaea* n. gen. in Baltic amber.

Tab. 2. Selected characters of the families of the archaeoid branch in Kachin (Burmese) amber

Additional list of n. comb. and n. relat. of fossil taxa in Kachin (Burmese) amber (see the abstract, WUNDERLICH (2008) and WUNDERLICH (2021: 93)):

Burmesarchaea crassicaput WUNDERLICH 2017 (under Archaeidae) = *Lacunauchenius crassicaput* (WUNDERLICH 2017) (Lacunaucheniidae) (**n. comb.** & **n. relat.**),

Burmesarchaea crassichelae WUNDERLICH 2017 (under Archaeidae) = *Lacunauchenius crassichelae* (WUNDERLICH 2017) (Lacunaucheniidae) (**n. comb. & n. relat**.),

Burmesarchaea longicollum WUNDERLICH 2017 (under Archaeidae) = *Planarchaea longicollum* (WUNDERLICH 2017) (Planarchaeidae) (**n. comb** & **n. relat**.),

Burmesarchaea propinqua WUNDERLICH 2017 (under Archaeidae) = *Lacunauchenius propinquus* (Lacunaucheniidae) (**n. comb**. & **n. relat**.),

Burmesarchaea quadrata WUNDERLICH 2017 (under Archaeidae) = *Lacunauchenius quadratus* (WUNDERLICH 2017) (Lacunaucheniidae) (**n. comb.** & **n. relat**.),

Eomysmauchenius dubius WUNDERLICH 2017 (under Archaeidae) = *Planarchaea dubia* (WUNDERLICH 2017) (Planarchaeidae) (**n. comb. & n. relat.**),

Eomysmauchenius septentrionalis (WUNDERLICH 2008) (under Archaeidae) = *Planarchaea septentrionalis* (WUNDERLICH 2008) (Planarchaeidae) (**n. comb**. **& n. relat,**),

Filiauchenius paucidentatus WUNDERLICH 2008 (under Archaeidae) = *Planarchaea paucidentata* (WUNDERLICH 2008) (Planarchaeidae) (**n. comb**. & **n. relat**.),

Lacunauchenius longissipes WUNDERLICH 2015 (under Archaeidae: Lacunaucheniinae) = *Planarchaea longissipes* (WUNDERLICH 2915) (Planarchaeidae) (**n. comb**. & **n. relat**.),

Lacunauchenius pilosus WUNDERLICH 2015 (under Archaeidae: Lacunaucheniinae) = *Planarchaea pilosa* (WUNDERLICH 2015) (Planarchaeidae) (**n. comb**. & **n. relat**.).

(1) **Archaeidae** KOCH & BERENDT 1854

Type genus: *Archaea* KOCH & BEREND 1854 in Eocene Baltic amber.

Diagnostic characters: Sclerotized ring around spinnerets (fig. 1), *very* small ♀-pedipalpus (photo 1), strong opisthosomal folds (fig. 1) with a thick cuticula and strong prosomal tubercles (fig. 1), body shape very variable. - At least in extant spiders anterior surface of the opisthosoma with “stridulatory file (pick on dorsal surface of petiole; Legendre (1970b); FORSTER & PLATNICK (1984: 8)). I did not recognize such structures in fossils of the Cretaceous genus *Burmesarchaea*.

Relationships: Eoarchaeidae is probably the sister group. In eoarchaeid taxa a sclerotized ring around the spinnerets, prosomal tubercles and opisthosomal folds are absent.

Distribution: Cretaceous (diverse in Cretaceous Burmese Kachin amber the genus *Burmesarchaea* WUNDERLICH 2008 is quite diverse; its new combinations: See the list above); Eocene to extant. The longest existing and most diverse family of the archaeoid branch and probably all other spiders so far known to me. - *Spiniarchaea* WUNDERLICH 2021: See Planarchaeidae.

***Burmesarchaea spinicaput* n. sp.** (figs. 4-5), photo 3

Etymology: The species name refers as a contraction to the existence of spines (lat. spina) on the cephalic part (caput) of the spider.

Material: Holotype (♂) in Upper (Mid) Cretaceous Kachin amber from Myanmar (Burma), F3887/BU/CJW.

Preservation and syninclusions: The spider is completely and very well preserved in a thin, 1.9 cm long clear piece of amber. - Syninclusions are few tiny plant hairs, excrement of insects, particles of detritus and tiny bubbles.

Diagnostic characters (♂; ♀ unknown): Cephalic part bearing few short spines on an elevation of the cephalic part (caput) (fig. 4), basal cheliceral articles longer than the prosoma (photo 3); pedipalpus as in fig. 5.

Description (♂):
Measurements (in mm): Body length 1.9; prosoma: Length 0.65, height 0.65, basal cheliceral article 0.75; opisthosoma: Length 0.9, width 0.5, height 0.8; leg I: Femur 1.0, patella 0.22, tibia 0.75, metatarsus 0.45, tarsus 0.3; femur IV ca. 0.85.

Colour: Prosoma dark brown, legs medium brown, not annulated, opisthosoma light grey.
Prosoma (fig. 4, photo) about as high as long, strongly tuberculate, bearing few short spines on an elevation of the cephalic part, most eyes difficult to recognize, clypeus very long, basal cheliceral articles slender and very long, I did not find lateral stridulatory files, teeth hidden, pedicel quite long. - Legs (photo) long and slender, order I/?IV/II/III, hairs short, bristles absent. - Opisthosoma (photo) distinctly tuberculate, bearing large furrows and a large sclerotized ring around the hidden spinnerets. - Pedipalpus with slightly deformed long and slender articles, femur distinctly bent, bulbus with a furcate and strongly sclerotized sclerite.

Relationships: In *B. pustulata* WUNDERLICH 2017 the shape of the prosoma is different, spines of the cephalic part are absent, the articles of the pedipalpus are shorter and the sclerites of the bulbus are different. - Note: Dorsal prosomal spines exist also in extant Archaeidae.

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

(2) **Lacunaucheniidae** WUNDERLICH 2008

Lacunaucheniidae WUNDERLICH 2008 **n. stat.** (raised from subfamily rank of the Archaeidae).

Type genus: *Lacunauchenius* WUNDERLICH 2008, the only known genus of the family.

Type species: *Lacunauchenus speciosus* WUNDERLICH 2008.
Further species: (see the list above): *crassicaput, crassichelas, propinquus* and *quadratus*.

Diagnostic characters: Legs short (photo 4), tibia I usually only 0.5-0.6 times of the prosoma length, prosoma strongly raised bearing distinct tubercles (photo 4), clypeus bearing a pair of rather small “horns” in both sexes (fig. 7) (overlooked in the original description), ♀-pedipalpus quite slender, only fairly long (photo 4), ♂-pedipalpus as in fig. 8.

Close **relationships** are unknown to me; see tab. 2, the key and the family Planarchaeidae.

Distribution: Cretaceous Kachin (Burmese) amber forest.

New Material: *Lacunauchenius* sp. indet., 1♀, F3838/BU/CJW. Its clypeal “horns” are well observable, body length 1.7 mm, photo 4.

(3) **Planarchaeidae** WUNDERLICH 2017 (**n. stat**.; raised from tribe rank Planarchaeini WUNDERLICH of the Archaeidae)

Type genus: *Planarchaea* WUNDERLICH 2015.
Further – monotypic – genera in Kachin amber: The unusual genus *Platythelae* WUNDERLICH 2021 and the special genus *Spiniarchaea* WUNDERLICH 2021 (**n. relat.**, from Archaeidae). - See also above, the Eocene genus *Baltplanarchaea* n. gen. in Baltic amber.

Diagnostic characters: Cephalic part quite variable, low to strongly raised, "neck" very long in the Cretaceous Burmese Kachin amber taxa (figs. 19, 22, photos 5-8) (*) but flat in *P. kopp* (WUNDERLICH 2015) (♀) and low in the Eocene genus *Baltplanarchaea* in Baltic amber (see above, ♀), legs long to very long (photos 5-8), tibia I usually 1.5-2.2 times longer than the prosoma, femoral humps (fig. 29) frequently existing, sclerotized ring around spinnerets and distinct opisthosomal folds absent, cymbium and bulbus long, tegulum with a long, slender and pointed basal apophysis which is directed basally and a distal apophysis (figs. 17-18). See tab. 2.

The **relationships** (tab. 1 p. 44) are quite different from tab. 1, provided by WUNDERLICH & MÜLLER (2021: 82). See the key and tab. 1-2. - In *Spiniarchaea* WUNDERLICH 2021 few leg bristles exist (figs. 15-16) and tibia I is only 1.1 times longer than the prosoma; ♂-pedipalpus as in figs. 17-18. Spiniarchaeinae WUNDERLICH 2021 may represent a subfamily of its own. - In the probably related family Lacunarchaeidae the legs are short (tibia I usually 0.5-0.6 times longer than the prosoma), the prosomal shape is quite different (shorter and bearing clypeal horns, fig. 7), and a basally directed basal tegular apophysis is absent. - See also above, the Eocene genus *Baltplanarchaea* n. gen. in Baltic amber.

Distribution: Cretaceous Kachin (Burmese) amber forest and Eocene Baltic amber forest (*Baltplanarchaea* n. gen., see above.

(*) Mainly the first described specimens of this family were strongly deformed and their "neck" was seemingly quite short; therefore the cephalic part was regarded as low; see, e. g., WUNDERLICH (2021: 82).

Key to the Cretaceous genera of the family Planarchaeidae in Kachin amber:

1 Spinnerets in the anterior position contiguous and quite thick (fig. 12). Tibia I ca. 2 1/2 times the length of the prosoma. ♂ unknown. *P. longicorpus* WUNDERLICH 2021 .... Platythelae

- Spinnerets in the anterior position slender and distinctly spaced. Legs fairly long or very long 2

2(1) Few leg bristles existing (figs. 15-16). Tibia I only 1.1 times longer than the prosoma. ♂-pedipalpus as in figs. 17-18. ♀ unknown. *S. aberrans* WUNDERLICH 2021 .... Spiniarchaea

- Leg bristles absent. Tibia I 1.5-2.2 times longer than the prosoma. ♂-pedipalpus, e. g. as in figs. 24, 27. Several species .... Planarchaea

Planarchaea WUNDERLICH 2015

In *Planarchaea* a strongly raised cephalic part exists (figs. 19, 22), leg bristles are absent, tibia I is usually 1.5-2.2 times longer than the prosoma, a dorsal femoral hump – more distinct on I-II – may exist and may be well developed (in *quinquespinae*, fig. 29), distinct (in *longipalpitibia*), indistinct or absent in the remaining species. ♂-pedipalpus, e. g., as in figs. 24, 27. - Questionable relationships: See above, the family Planarchaeidae.

Note: The shape of the prosomal profile - in an exact lateral position - allows best the identification of the species; the structures of the bulbus are frequently more or less deformed.

***Planarchaea humilis* n. sp.** (figs. 19-21), photo 5

Etymology: The name of the species refers to its low cephalic area, from (lat.) humilis.

Material: Holotypus ♂ in Upper (Mid) Cretaceous Kachin amber from Myanmar (Burma), F8384/BU/CJW.

Preservation and syninclusions: Besides the bulbi the spider is excellently preserved in a clear yellow-orange piece of amber, the right leg I is cut off near the end of the femur, the distal articles of the left leg II are lose and placed a bit away. - Syninclusions are a part of a Cicadina and 4 tiny Diptera: Nematocera.

Diagnostic characters (♂; ♀ unknown): Prosoma (figs. 19, 23, photo) rather low, basal cheliceral articles only fairly long, legs (photo) extremely long, femur I 2.37 times longer than the body (!), pedipalpus (fig. 21) with a very long tibia, bulbus strongly deformed.

Description (♂):
Measurements (in mm): Body length 1.9; prosoma: Length 0.9, width in the middle 0.53 but anteriorly only 0.28; basal cheliceral article 0.4; opisthosoma: Length 1.0, width 0.6; leg I: Femur 4.5, patella 0.35, tibia 4.5, metatarsus 4.3, tarsus 2.9; tibia II ca. 1.8, tibia III 1.1, tibia IV 1.6, pedipalpal tibia 0.55.
Colour: Prosoma and legs grey brown, legs not annulated, opisthosoma light grey.
Prosoma (figs. 19-20, photo) low, anteriorly narrow, posteriorly wide, covered with tiny tubercles and quite short hairs, fovea indistinct, 8 eyes which are covered with tiny bubbles or emulsions, basal cheliceral articles only fairly long, distinctly thickened in the middle, bearing large “peg teeth”, fangs long, mouth parts hidden. - Legs (photo) extremely long, slender, order I/II/IV/III, hairs indistinct, bristles absent, position of the metatarsal trichobothrium unknown, tarsal claws not studied. - Opisthosoma (photo) 1.6 times longer than wide, bearing quite short hairs, spinnerets hidden. - Pedipalpus (fig. 21) with very long and slender articles and a strongly deformed bulbus.

Relationships: In *P. longipalpitibia* n. sp. the pedipalpal tibia is also very long but the cephalic part is strongly raised and the legs are shorter.

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

***Planarchaea longipalpitibia* n. sp.** (figs. 22-24), photo 6

Etymology: The name of the species refers to its long (lat. longus) pedipalpal tibia.

Material: Holotypus ♂ in Upper (Mid) Cretaceous Kachin amber from Myanmar (Burma), F3883/BU/CJW.

Preservation and syninclusions: The spider's amber piece has been cut off from a 5 cm long piece of amber to a few mm long piece; it is almost completely and very well preserved, the basal half of the right metatarsus II is cut off, the opisthosoma is deformed. - Syninclusions are a longer thread from a spider web and few tiny pieces of amber. In the large piece of amber preserved are a tiny Coleoptera, few tiny insects, a large oxidated piece of a plant and some bubbles from a boring shell.

Diagnostic characters (♂; ♀ unknown): Prosoma (figs. 22-23) long as high, with a quite slender cephalic part; pedipalpal tibia long, structures of the bulbus as in fig. 24.

Description (♂):
Measurements (in mm): Body length 1.5; prosoma length and height 1.0, width 0.3-0.5 (basally); length of a basal cheliceral article 0.8; opisthosoma: Length 0.9, width 0.4, height 0.5; leg I: Femur ca. 1.7, patella 0.3, 1ibia 1.6, metatarsus 1.1, tarsus 0.55, tibia II 1.1, tibia III ca. 0.6, tibia IV ca. 0.7; pedipalpal tibia 0.5.
Colour: Prosoma and legs medium brown, legs not annulated, opisthosoma medium brown.
Prosoma (figs. 22-23) strongly raised, as long as high, distinctly longer than wide, posteriorly widened, bearing tiny tubercles, 8 deformed eyes, basal cheliceral articles large, thickest in the middle bearing long "peg teeth", fangs slender. - Legs (photo) quite long and slender, order I/II/IV/III, hairs indistinct, bristles absent, position of the metatarsal trichobothrium unknown, tarsal claws not studied. - Opisthosoma 2.2 times longer than wide, bearing quite short hairs, spinnerets hidden and deformed. - Pedipalpus (fig. 24) with long articles similar to *P. humilis* n. sp., structures of the bulbus only fairly deformed.

Relationships: In *P. petersi* n. sp. the cephalic part is wider, in *P. humilis* n. sp. the cephalic part is low.

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

***Planarchaea petersi* n. sp.** (figs. 25-27), photo 7

Derivatio nominis: It is a great pleasure to me to name this interesting species after Thorsten Peters who will give it to the Palaeonological Institute of the University of Hamburg.

Material: Holotypus ♂ in Upper (Mid) Cretaceous Kachin amber from Myanmar (Burma), Palaeonological Institut of the University of Hamburg.

Preservation and syninclusions: The spider is almost completely and very well preserved in a rather flat, 2.7 mm long and clear yellow-orange piece of amber, the left leg II is cut off beyond the femur, the right leg I is broken through the tibia, the cymbium of the left pedipalpus is broken through in the distal half, both bulbi are fairly deformed. - Syninclusions are few small plant hairs.

Diagnostic characters (♂; ♀ unknown): Prosoma (fig. 25) strongly raised, with a large cephalic part, basal cheliceral articles powerful, pedipalpus as in figs. 26-27, tibia long and slender

Description (♂):
Measurements (in mm): Body length 1.6; prosoma: Length 0.8, height 1.0, basal cheliceral article 0.9; opisthosoma: Length 0.7, height 0.5; leg I: Femur 1.9, patella 0.23, tibia 1.6, metatarsus 1.35, tarsus 0.6; tibia II 1.7, tibia III 0.6, tibia IV 0.9; pedipalpal tibia 0.3.
Colour: Prosoma and legs medium brown, legs not annulated, opisthosoma light grey.
Prosoma (fig. 25, photo) higher than long, with a large cephalic pat, distinctly tuberculate, 8 eyes, anterior medians largest, basal cheliceral articles powerful, lateral files not recognizable, fangs long and slender, most “peg teeth” hidden, petiolus well developed. - Legs (photo) quite long and slender, order I/II/IV/III, hairs indistinct, bristles absent, position of the metatarsal trichobothrium unknown, tarsal claws not studied. - Opisthosoma (photo) almost egg-shaped, hairs short, folds indistinct, spinnerets deformed.- Pedipalpus (figs. 26-27): Tibia and cymbium long and slender, bulbus basally with a long and sickle-shaped apophysis, distally with a long, slender and pointed apophysis.

Relationships: In *P. longipes* WUNDERLICH 2015 (under *Burmesarchaea*) the shape of the prosoma is similar but the structures of the bulbus are different and the pedipalpal tibia possesses a dorsal-apical outgrowth. See also *P. quinquespinae* n. sp.

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

***Planarchaea quinquespinae* n. sp**. (figs. 28-33), photo 8

Etymology: The species name refers to the five or more tibial and femoral pedipalpal spines, from quinque (lat.) = five and spina (lat.) = spine.

Material: Holotype ♂ in Upper (Mid) Cretaceous Kachin amber from Myanmar (Burma), F3939/KA/CJW.

Preservation and syninclusions: The spider is well and almost completely preserved in a flat and clear yellow-orange piece of amber, parts of the left leg I and the right leg II are cut off, the body is fairly deformed: Prosoma and opisthosoma are dorsally depressed. - Syninclusions are 1 Diptera, 1 Psocoptera, an insect larva, parts of articulate arthropod legs and half of a bubble at the margin of the amber piece which has been produced by a boring shell.

Diagnostic characters (♂; ♀ unknown): Prosoma (fig. 28) high, posterior margin of the cephalic part vertical, femoral I-II humps (fig. 29) well developed, their position in 0.18; pedipalpus (figs. 30-33): The long tibia bears at least three larger and few tiny retrolateral spines, the femur bears similar but ventral spines in the distal half, bulbus with a long retrolateral apophysis which stands widely out, questionable embolus in a distal position.

Description (♂):
Measurements (in mm): Body length 1.7; prosoma: Length 1.0, width 0.55, height ca. 0.8; opisthosoma:Length 0.75, width 0.5, height ca. 0.6; leg I: Femur 2.0, patella 0.2, tibia 1.75, metatarsus 1.45, tarsus 0.65; tibia II 1.35, tibia III ca.0.65, tibia IV ca. 0.85.
Colour: Prosoma dark brown, legs and opisthosoma medium grey, legs not annulated.
Prosoma (fig. 28, photo) 1.7 times longer than wide, wrinkled, strongly raised, posterior margin of the cephalic part vertical, 8 eyes in a deformed field, anterior medians largest, lateral eyes touching, clypeus short, basal cheliceral articles long and distally distinctly diverging, bearing two rows of “peg teeth”, anterior row with 5 quite long besides some small teeth in an irregular position; I did not recognize retrolateral files, fangs long, labium a free sclerite, longer than wide. - Legs long and thin, order I/II/IV/III, tibia I 1.75 times longer than the prosoma, hairs of medium length, bristles absent, position of the well developed dorsal femur I hump in 0.18 (fig. 29). - Opisthosoma (photo) oval, 1.5 times longer than wide, hairs of medium length, spinnerets short/retracted, sclerotized ring around spinnerets absent. - Pedipalpus: See above, patella short.

Relationships: The shape of the prosoma is unique, the femoral hump is larger developed than in other congeneric species. According to the structures of the bulbus *P. petersi* n. sp. may be most related in which the femoral hump is only weakly developed and the shape of the prosoma is quite different.

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

Note on the Cretaceous taxon *Archaemecys arcantiensis* SAUPE & SELDEN 2009, Archaeidae (n. relat.)

This taxon was published from Lower Cretaceous amber from France, under the family Mecysmaucheniidae, based on a single subadult male. According the existence of a sclerotized ring around the spinnerets, of two pairs of well developed spinnerets as well as of distinct furrows of the opisthosoma, which are typical characters of the family Archaeidae but absent absent in the Mecysmaucheniidae, I transfer *Archaemecys arcantiensis* from the Mecysmaucheniidae to the Archaeidae (**n. relat**.).

The Jurassic family JURARCHAEIDAE ESKOV 1987 (n. stat.) (fig. 13)

This taxon is based on a single species and specimen of the archaeid subfamily Jurarachninae ESKOV 1987. It is preserved in stone.

Type (by monotypy): *Jurarachne zherikhini* ESKOV 1987.

Diagnostic characters (♀; ♂ unknown) (see fig. 13 tab. 1 and ESKOV (1987: 82 and 83)): Fairly short "neck" and foramen, no sclerotized ring around spinnerets, no opisthosomal folds, probably weak prosomal tubercles, legs of medium length, ♀-pedipalpus of medium length, bearing a tarsal claw, most probably 3 pairs of spinnerets, epigyne strongly sclerotized, body length 3.85 mm. I will not exclude a medium length of cymbium and bulbus.

Relationships (see tab. 1): According to the diagnostic characters I regard this - in the geological sense - very old taxon as the most ancient/primitive member of the archaeoid branch which can not be included in a described family. Therefore I elevate its status from subfamiliar rank – Jurarachninae of the Archaeidae - to familiar rank (**n. stat**.).

Distribution: Upper Jurassic of Kazakhstan.

Index of higher taxa, most species and a term (parthenogenesis)

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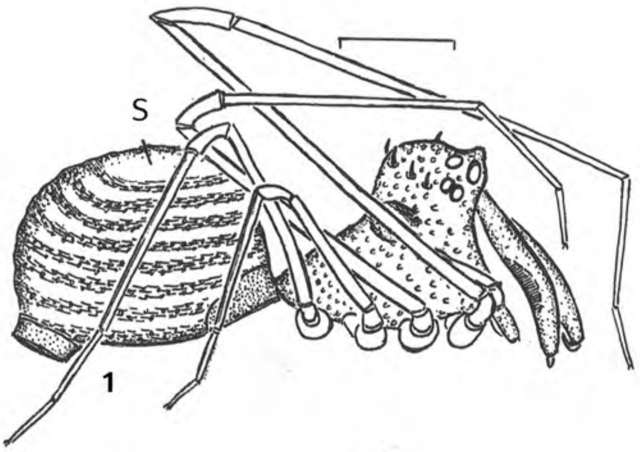

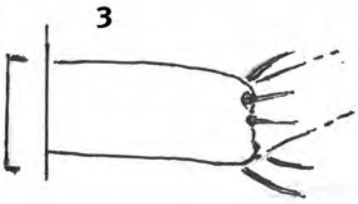

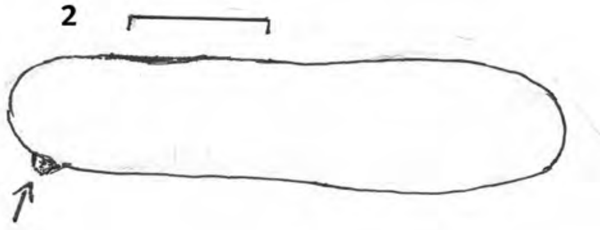

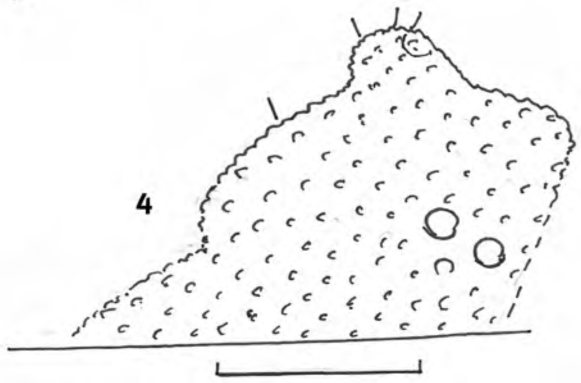

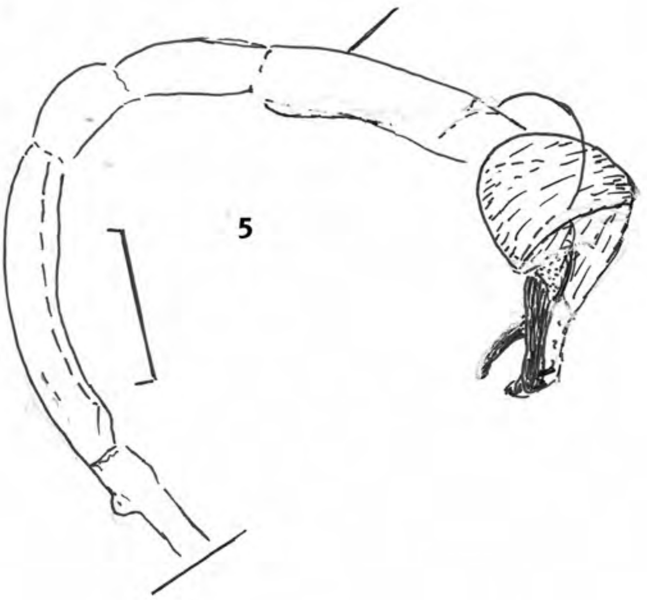

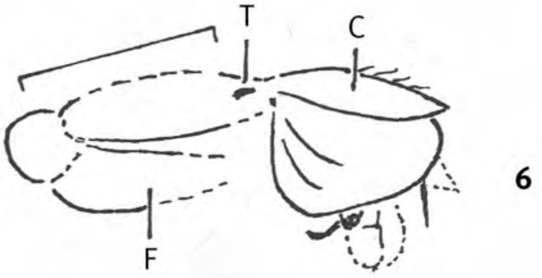

Fig. 1) ***Saxonarchaea pediculus*** WUNDERLICH 2004 (Archaeidae, Bitterfeld amber), ♂, lateral aspect. Note the cheliceral stridulatory field and the large sclerotized ring around the spinnerets. - S = scutum. Scale: 0.5 mm;

figs. 2-3: ***Baltplanarchaea oblonga*** (WUNDERLICH 2017) (Planarchaeidae, Baltic amber), ♂ holotype; 2) retrolateral aspect of the opisthosoma, outline. The arrow points to the advanced position of the spinnerets; 3) prodorsal aspect of the distal part of the right tibia IV which bears a ring of weak bristles. Hairs are not drawn. - Scale: 0.5 and 0.1 mm;

figs. 4-5: ***Burmearchaea spinicaput* n. sp**. (Archaeidae, Kachin (Burmese) amber), ♂; 4) lateral aspect of the caput. Note the strong wrinkles and the few short spines; 5) retrolateral aspect of the partly deformed right pedipalpus. - Scale: 0. 2mm;

fig.6) ***Burmesarchaea pseudogibber*** WUNDERLICH 2017 (Archaeidae, Kachin (Burmese) amber), ♂, retrodorsal aspect of the right pedipalpus. - T = tibial spine. Scale: 0.1 mm;

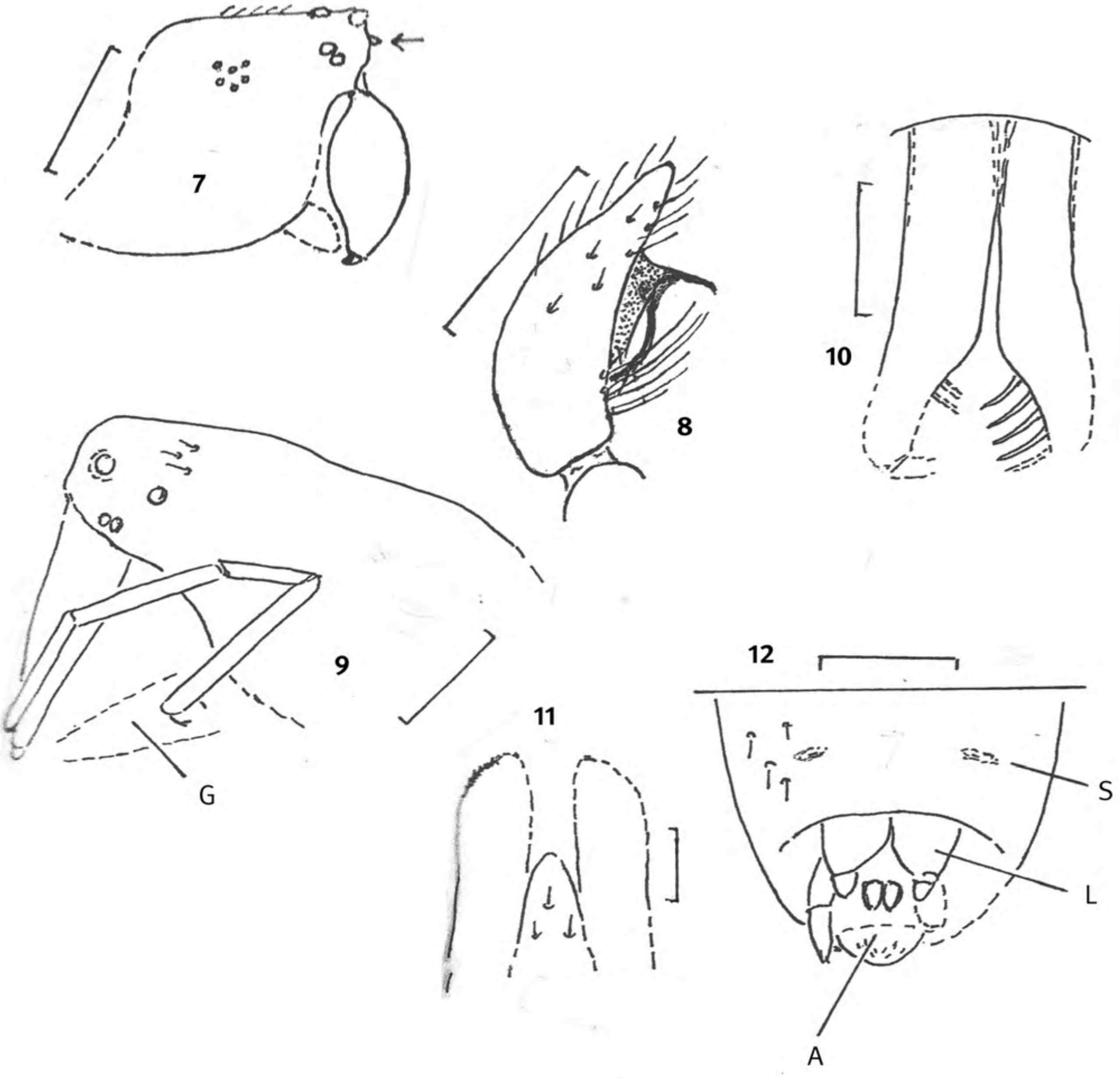

fig. 7) ***Lacunauchenius crassichelae*** WUNDERLICH 2017 (Lacunaucheniidae, Kachin amber), ♂, lateral aspect of the prosoma. The arrow points to the pair of small anterior “horns”. - Scale: 0.5 mm:

fig. 8) ***Lacunauchenius propinquus*** (WUNDERLICH 2017), (Lacunaucheniidae, Kachin amber, ♂, retrolateral aspect of the right pedipalpus. - Scale: 0.2 mm;

figs. 9-12: ***Platythelae longicorpus*** WUNDERLICH 2021 (?Planarchaeidae, Kachin amber), ♀; 9) lateral aspect of the deformed and partly hidden prosoma; 10) anterior aspect of the chelicerae which are partly hidden; 11) ventral aspect of gnathocoxae and labium; 12) ventral aspect of the posterior part of the opisthosoma; the left posterior spinneret is deformed and incomplete. - A = anal tubercle, G = gnathocoxa, L = left anterior spinneret, S = questionable left spiracle. - Scales: 0.5 in figs. 9) and 12), 0.4 in fig. 10), 0.2 in fig. 11);

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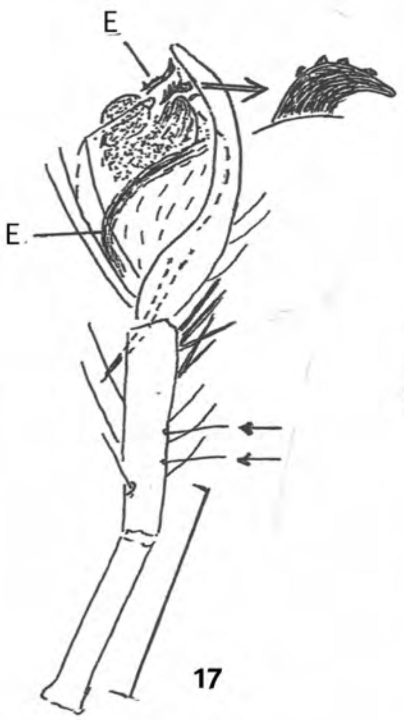

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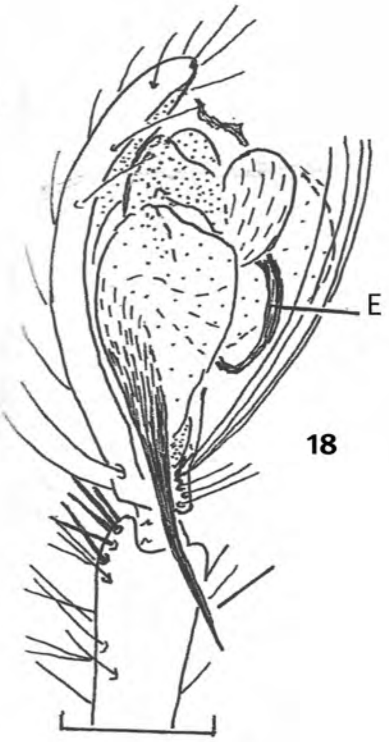

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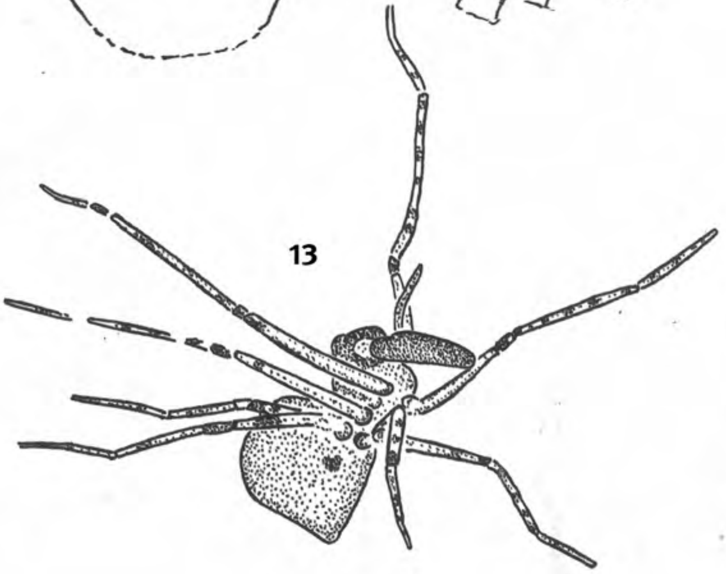

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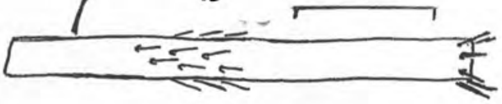

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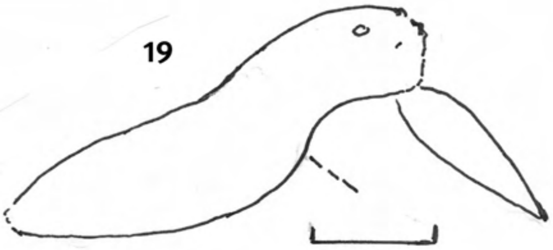
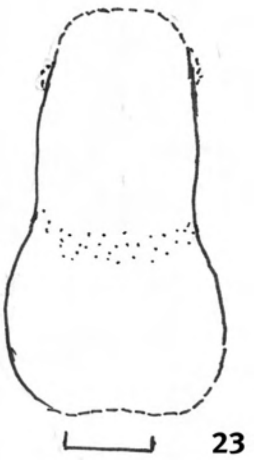
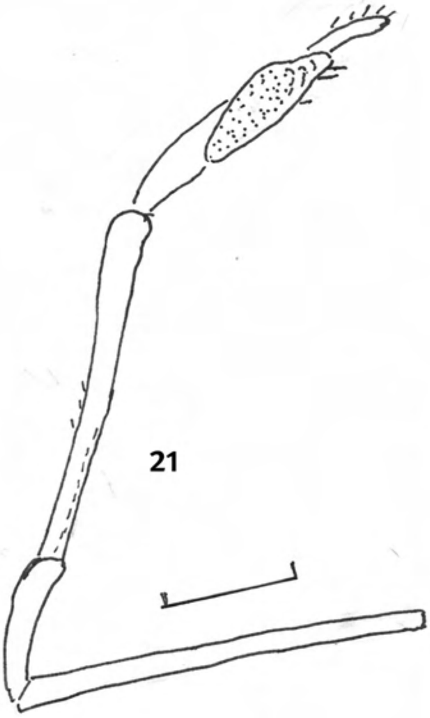
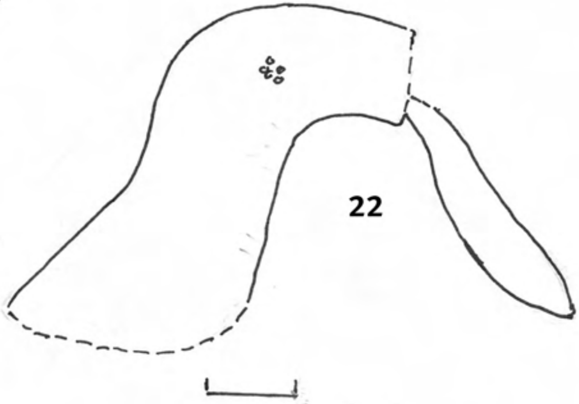
fig. 13) ***Jurarchaea zherikhini*** ESKOV 1987 (Jurarchaeidae, in stone from Kazakhstan), ♀, body length 3.85 mm, retroventral aspect. -Taken from ESKOV (1987);

figs. 14-18: ***Spiniarchaea aberrans*** WUNDERLICH 2021 (Planarchaeidae, Kachin amber), ♂; 14) dorsal aspect of the prosoma. The chelicerae are stretched forward in an unnatural position; 15) prodorsal aspect of the left metatarsus IV; 16) dorsal aspect of the distal part of the left femur I, showing the retroapical bristle; 17) prolateral aspect of the right pedipalpus; the thin arrows point to the tibial trichobothria, the thick arrow points to the enlarged toothed tegular apophysis; 18) retroventral aspect of the partly deformed right pedipalpus. - E = embolus, T = basal tegular apophysis. Scales: 0.5 mm in figs. 14) and 17), remaining figs. 0.2;



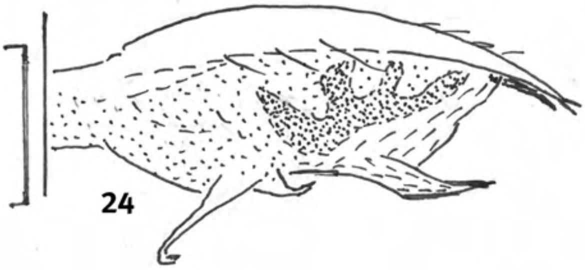






figs. 19- 21: ***Planarchaea humilis* n. sp**. (Planarchaeidae, Kachin amber), ♂; 19) lateral aspect of the prosoma (under water); the eye region is deformed; 22) dorsal-basal aspect of the right chelicera; 21) prolateral aspect of the left pedipalpus; mainly the structures of the bulbus are deformed. - Scale: 0.2 mm;

figs. 22-23: ***Planarchaea longipalpitibia* n. sp**. (Planarchaeidae, Kachin amber), ♂; 22) lateral aspect of the prosoma; the eyes are hidden; 23) dorsal aspect of the prosoma, outline; most eyes are hidden. - Scale: 0.2 mm;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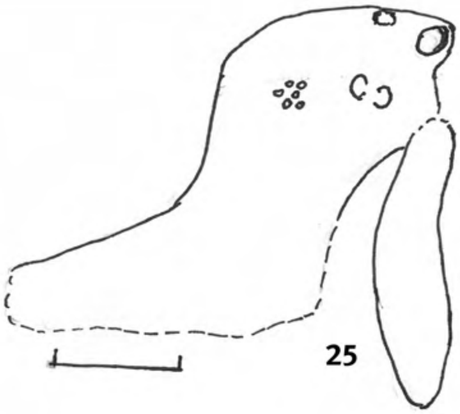
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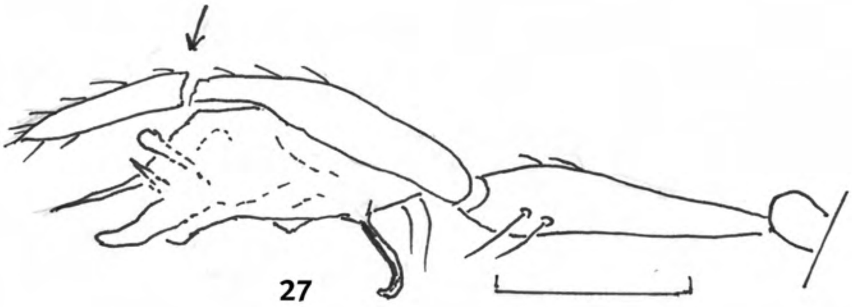
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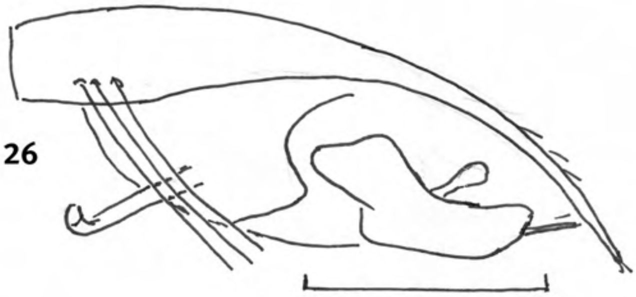
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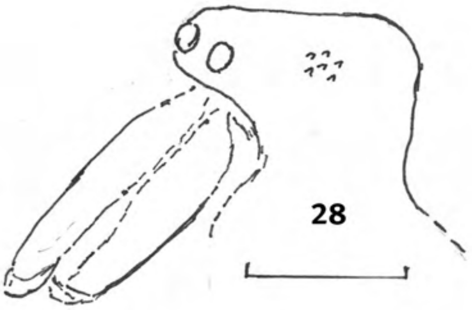
fig. 24) ***Planarchaea longipalpitibia*** **n. sp.** (Planarchaeidae, Kachin amber), ♂, retrolateral aspect of the deformed right pedipalpus. Scale: 0.2 mm;

figs. 25-27: ***Planarchaea petersi*** **n. sp.** (Planarchaeidae, Kachin amber), ♂; 25) lateral aspect of the prosoma; 26) retrolateral aspect of the deformed right pedipalpus; only few hairs are drawn; 27) retrolateral aspect of the partly deformed left pedipalpus. The cymbium (arrow) is broken. - Scales: 0.2 mm;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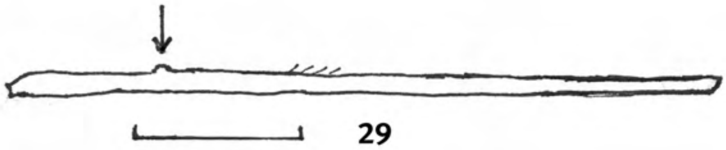
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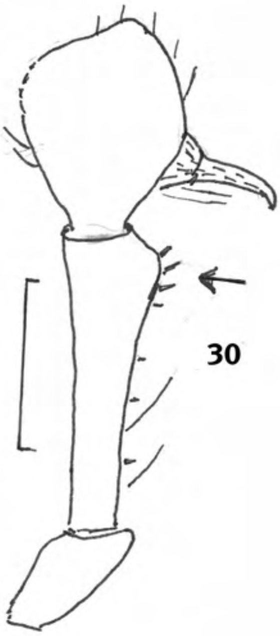
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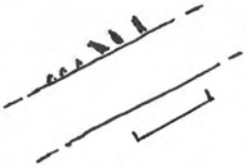
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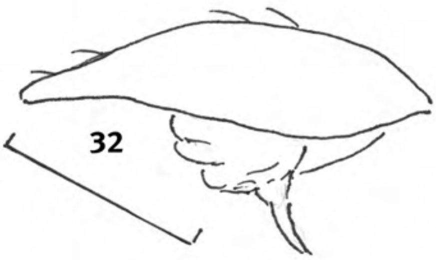
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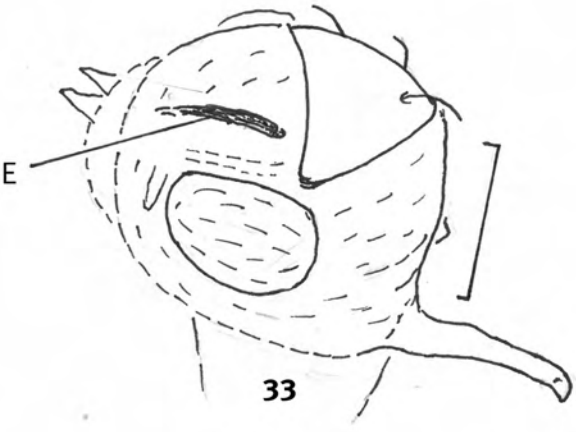

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figs. 28-33: ***Planarchaea quinquespinae* n. sp.** (Planarchaeidae, Kachin amber) ♂; 28) lateral aspect of the prosoma, parts are hidden; only the anterior median eyes are drawn, the cheliceral "peg teeth" are not drawn; 29) prolateral aspect of the right femur I; the arrow points to the dorsal hump; 30) dorsal aspect of the right pedipalpus; the arrow points to the larger tibial spines; 31) prodorsal aspect of the distal part of the right pedipalpal femur; 32) retrolateral aspect of the left cymbium and bulbus; 33) apical aspect of the left pedipalpus; parts are hidden. - E = questionable embolus. Scales: 0.2 mm in figs. 28-29), 0.1 mm in fig. 33), 0.05 mm in fig. 31, 0.2 mm in figs. 30) and 32).

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NEW FOSSIL SPIDER (ARANEAE) TAXA IN EOCENE BALTIC AND BITTERFELD AMBERS

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Abstract: The following taxa are treated: *Baltplanarchaea* **n. gen**. (Palpimanoidea: PLANARCHAEIDAE) with the type species *oblonga* WUNDERLICH 2017 which is transferred from the genus *Planarchaea* WUNDERLICH 2017 (**n. comb**.); it is preserved in Eocene Baltic amber but not in Cetaceous Kachin (Burmese) amber as erroneously published in 2017; family SYNOTAXIDAE: *Cornuanandrus scutatus* **n. sp**., *Pseudoacrometa gracilipes* WUNDERLICH 1986, *Succinitaxus* WUNDERLICH 2004 (key), *Succinitaus pusillus* **n. sp**., *Succinitaxus strepidus* **n. sp.** *Succinitaxus* sp. indet. 1 and 2; family MIMETIDAE: ?*Mimetus flexuosus* **n**. **sp**.; family NESTICIDAE: *Balticonesticus* WUNDERLICH 1986, *Balticonesticus rectus* **n. sp**., *Heteronesticus* WUNDERLICH 1986, *Heteronesticus magnocymbialis* WUNDERLICH 1986, *Heteronesticus acuminatus* **n. sp**., *Heteronesticus bitterfeldensis* **n. sp**., Heteronesticus sp. indet.; family ZODARIIDAE: *Pectenzodarion unicum* **n. gen. n. sp**. - Synonymy: *Pseudoacrometa wittmanni* WUNDERLICH 2004 is synonymized with *Pseudoacrometa gracilipes* WUNDERLICH 1986 (**n. syn**.).

Key words: Archaeiod brach, Baltic amber, Bitterfeld amber, climate, Cretaceous, Eocene, Palpimanoidea.

Family PLANARCHAEIDAE WUNDERLICH 2017

Baltplanarchaea **n. gen**. (see the paper above in this volume on fossil taxa of the Archaeoid branch: Planarchaeidae of the superfamily Palpimanoidea) - with the type species *oblonga* WUNDERLICH 2017 (photo 9) - is transferred from the genus *Planarchaea* WUNDERLICH 2017 (**n**. **comb**.) and from Cretaceous Kachin (Burmese) amber to Eocene Baltic amber. The discovery of this unusually tropical taxon in Baltic amber is a great surprise to me!

Family SYNOTAXIDAE

This (sub)tropical family is one of the most diverse spider families in Baltic amber besides Anapidae, Linyphiidae and Theridiidae; the families Cyatholipidae and Nesticidae are less diverse. All these families are members of the superfamily Araneoidea and - except Anapidae - construct irregular capture webs; Anapidae construct modifies orb webs.

The separation of fossil members of the similar families Cyatholipidae, Nesticidae and Synotaxidae may be difficult, also by their copulatory organs: A typical nesticid ventral comb of tarsus IV is absent in some fossil taxa of this family or difficult to recognize and exists at least in few extant taxa of the Synotaxidae, too. A typical cyatholipid elongated opisthosoma, mating spines on an article of the male anterior leg – and other characteristics, vgl. WUNDERLICH (2004: 1155-1188) – are absent in few taxa of this family, and its widely spaced posterior spiracles are usually not recognizable in fossils spiders. A quite long anterior leg and quite diverse shaped paracymbia exist in certain members of these families. To my knowledge the most tiny fossil species of the three families in Baltic amber - body length less than 2 mm – exist in certain members of the families Cyatholipidae and Synotaxidae but not in the Nesticidae.

Fossil females of the families in question are very rarely reported; example of an external copulatory organ: See below, *Pseudoacrometa gracilipes.*

In this paper I describe 3 new species of 2 genera besides *Pseudoacrometa* WUNDERLICH 1986 and its hitherto unknown female; an upgraded key to the males of *Succinitaxus* is provided.

<u>Cornuanandrus</u> WUNDERLICH 1986

In 2004 I described 5 species of this genus in Baltic amber. In this paper I describe one new species and treat in short the following 3 species:

C. ?*bitterfeldensis* WUNDERLICH 2004: A probably conspecific ♂ in Bitterfeld amber, badly preserved, body length ca. 3 mm, F3903/BI/CJW.

C. ?*minor* WUNDERLICH 2004: A probably conspecific ♂ in Baltic amber, body length ca. 2.3 mm, F3904/BB/CJW.

C. ?*maior* WUNDERLICH 1986: A probably conspecific ♂ in Baltic amber, body length 2.7 mm, F39057BB/CJW.

<u>Notes</u>: (1) Certain differences between the present males and the holotypes of these species may be caused by their different position in the amber, by intraspecific variation of structures of the spiders which furthermore partly may be hidden. - (2) In the present 3 males the epigastric area is hidden by an emulsion; so a leathery or even scutate epigastrum like in *C. scutatus* may exist or not. - (3) Usually the embolus is guided by a conductor; apparently it makes no sense - and is quite unusual - if the parembolic process (PP) (figs. 1-2) is guided by the conductor.

Cornuanandrus scutatus n. sp. (figs. 1-2), photo 11

<u>Etymology</u>: The species name refers to the leathery or even scutate epigaster, from scutum (lat.) = shield.

<u>Material</u>: Holotype ♂ in Eocene Baltic amber, F3906/BB/CJW.

Preservation and syninclusions: The spider is very well preserved in a clear yellow-orange piece of amber, the right side of its opisthosoma is covered with a white emulsion, the left leg II is lost beyond the coxa by autotomy, most parts of both legs I, the left patella II and the distal articles of the left leg II are cut off. - <u>Syninclusions</u> are three bubbles on the anterior part of the prosoma of the spider and numerous stellate plant hairs.

Diagnostic characters (♂; ♀ unknown): Pedipalpus (figs. 1-2) with a quite large/wide conductor which bears denticles.

Description (♂):
Measurements (in mm): Body length ca. 3.0; prosomal length ca. 1.2; opisthosoma: Length ca. 2.0, height 1.1; Leg I: Femur 3.3, patella 0.5, leg II: Femur 2.4, tibia 1.8, tibia III 0.8, tibia IV 1.45.
Colour: Prosoma and legs light brown, legs not annulated, opisthosoma light grey.
Prosoma (photo) longer than wide, hairs of medium length, fovea well developed, 8 small eyes, median eyes widely spaced from each other, posterior row slightly procurved, clypeus quite long, basal cheliceral articles of medium size, fangs and mouth parts hidden, sternum longer than wide. - Legs (photo) long, partly cut off, order I/II/IV/III, I very long, probably ca. 19 mm, tarsi short, hairs short, position of the metatarsal trichobothrium unknown, all patellae and tibiae bear 1/1 dorsal bristles, 3 tarsal claws which are not closely studied. - Opisthosoma (photo) almost twice as long a heigh, hairs short, epigaster hair-less, at least leathery but probably with a large scutum like the lung covers, too, spinnerets short. - Pedipalpus (figs. 1-2, see also above: Note (3)) with stout patella and tibia, paracymbium large, pointed and standing out, conductor large, denticulate.

Relationships: The shape of the much smaller conductor of the remaining congeneric species is different.

Distribution: Eocene Baltic amber forest.

<u>Pseudoacrometa</u> WUNDERLICH 1986

Spiders of this extinct genus are only known from Eocene European ambers. Only a single species is known:

Pseudoacrometa gracilipes WUNDERLICH 1986 (fig. 3), photo 12

Synonymy: After the study of numerous conspecific males I regard now *Pseudoacrometa wittmanni* WUNDERLICH 2004 (: 1201) as younger synonym of *Pseudoacrometa gracilipes* WUNDERLICH 1986 (**n. syn**.). The paracymbium of this species may partly be hidden in certain specimens and its size/shape is a bit variable.

<u>Material</u> in Baltic amber: Holotype ♂: Bayerische Staatssammlung, Paläont. Histor. Geologie München (BSP); paratype ♂ in Hamburg, PIUH (F3896/BB/CJW); 11♂ without no., 1♂; F3897/BB/CJW; 1♀ together with a questionable egg sac and threads, F3895/BB/CJW.

Males of this very long-legged species (photo) are not too rare in Baltic amber. The **female** is described here for the first time:

Preservation and syninclusions: The spider is almost completely preserved in a clear orange piece of amber, the right leg I is lost after the coxa by autotomy, the opisthosoma is deformed, most parts of the body – except parts of the sternum and ventral parts of the opisthosoma – are covered with a white emulsion. - Syninclusions: At a corner of the piece of amber, 5 mm in front of the spiders body, an almost globular structure is preserved among few thin spider threads, diameter ca. 0.5 mm, partly hidden by two fissures in the amber and covered with tiny structures which are similar to tiny plant hairs. I do not want to exclude that it may be the *egg sac* of the present female. Certain female Synotaxidae are known to carry their egg sac with the help of their chelicerae. - Further syninclusions are some thin spider threads which may be part of the irregular capture web of the present female, numerous plant hairs, two tiny Acari and two small Diptera.

Description:
Measurements (in mm): Body length almost 1.6; prosomal length almost 0.8; opisthosoma: Length 0.85, height 0.6; leg I: Femur 2.5, patella 0.25, tibia 2.7, metatarsus 2.1, tarsus 0.9, tibia II 1.4, tibia III 0.9, tibia IV 1.2.
Colour light yellow brown, legs non annulated.
Prosoma (most parts are hidden) low, fangs of median size. - Pedipalpus rather long, slender, tarsus bearing a large claw which may be smooth. - legs (photo) quite slender and very long, especially I (its tibia is 3.2 times of the prosomal length), order I/II/IV/III, hairs quite short and indistinct, bristles very thin, existing 1/1 on patellae and apparently also 1/1 on tibiae, metatarsal trichobothria in almost 0.7, 3 small tarsal claws. - Opisthosoma (deformed, photo), 1.2 times longer than high, posteriorly high, bearing longitudinal furrows which may be caused by the preservation, hairs and spinnerets short. - Epigyne (fig. 3) a flat sclerotized plate which is only slightly protruding. - Note: Most often the epigyne of extant Synotaxidae is poorly developed, lobes are rarely existing. (Contrarily in the Nesticidae the epigyne is protruding or bearing a scape, and in the Cyatholipidae a scape at the anterior edge of the epigyne or a median lobe exist.

Distribution: Eocene Baltic amber forest.

Succinitaxus WUNDERLICH 2004

In 2004 I described *S. brevis* (the generotype) and *S. minutus*, both in Baltic amber. *Succinitaxus* is characterized by a leathery dorsal opisthosoma which bears hair-shaped bristles placed on tiny plates. The body length of the tiny spiders is 0.92-1.25 mm. Here I describe two further species of this genus.

Key to the species of Succinitaxus (♂):

1 Dorsal opisthosomal plates and hairs relative large/long (fig. 5). Pedipalpus (figs. 7-8): Paracymbium distally strongly bent .... *strepitus* **n. sp.**

- Dorsal opisthosomal plates and hairs short, see WUNDERLICH (2004: 1236, fig. 82). Paracymbium distally not strongly bent (fig. 9) 2

2(1) Paracymbium short, see WUNDERLICH (2004: 1237, fig. 90 (*) ....
.... *minutus* WUNDERLICH 2004

- Paracymbium larger (figs. 4, 7) 3

3(2) coxa IV-epigastric stridulatory organ and opisthosomal sigilla existing, see WUNDERLICH (2004: 1236, figs. 80a and 82) .... *brevis* WUNDERLICH 2004

- coxa IV-epigastric stidulatory organ (incl. a tooth of coxa IV) absent like in *strepitus* and probably in *minutus.* Pedipalpus: Fig. 4... *pusillus* **n. sp**.

(*) According to WUNDERLICH (2004: 1219) dorsal tibial bristles are absent in *minutus* but probably these indistinct bristles have been overlooked by me.

***Succinitaxus pusillus* n. sp**. (fig. 4)

Etymology: The name of the species refers to its tiny (lat. = pusillus) body.

Material: Holotype male in Eocene Baltic amber and a separated piece of amber, F3902/BB/CJW.

Preservation and Syninclusions: The spider is completely preserved in a clear yellow-orange piece of amber, its right bulbus is fairly expanded, mainly the dorsal parts of the body are covered with a white emulsion, fissures exist directly around the spider and hide it partly. - Syninclusions are absent.

Diagnostic characters (♂; ♀ unknown): Dorsal opisthosomal plates tiny, their bristles short as in *S. brevis* WUNDERLICH (2004: 1236, fig. 82); pedipalpus (fig. 4): Tegulum with at least one large apophysis, embolus quite long.

Description (♂; fissures and an emulsion hide most parts):
Measurements (in mm): Body length 1.0; prosomal length ca. 0.47; opisthosoma: Length ca. 0.57, height 0.5; tibia IV ca. 0.28.
Colour light brown.
Prosoma with large eyes, posterior row straight. - Legs only fairly long, patellae and tibiae most probably bearing 1/1 indistinct dorsal bristles, coxae IV toothless.. - Opisthosoma almost globular, dorsal plates small, bristles short (see above), epigaster sclerotized. - Pedipalpus: See above; tibia and patella stout.

Relationships: See the key above.

Distribution: Eocene Baltic amber forest.

***Succinitaxus strepitus* n. sp.** (figs. 5-8)

Etymology: The species is named after its tiny dorsal opisthosomal plates (lat.= strepitus).

Material: 2 ♂ in Eocene European ambers: Holotype in Baltic amber, F3900/BB/CJW, paratype in amber from Bitterfeld, F3901/BI/CJW.

Preservation and syninclusions: *Holotype*: The fairly deformed spider is preserved in a clear yellow-orange piece of amber which is broken off and lost in front of the spider including the distal parts of the anterior legs, the left leg II is cut off through the patella, the left leg IV is lost beyond the coxa by autotomy, the opisthosoma is ventrally distinctly concave/shrunk, a white emulsion is absent. The left cymbium/bulbus is turned by 180°, the right cymbium/bulbus is turned ba ca. 90° to the outside. - Syninclusions are a ca. 1 mm long juv. Araneae, a ca. 1 cm long part of the leg of an Opiliones, 1 Collembola and few stellate hairs.. - The *paratype* is incompletely preserved in a clear yellow-orange piece of amber, not covered with a white emulsion because it probably has been artificially been heated. The opisthosoma is lost as well as the right leg II beyond the coxa by autotomy, mouth partrs and sternum are strongly deformed, the left tarsus IV is deformed/shrunk, both copulatory organs are excellently preserved. - Syninclusions are a partly dissected 1.5 mm long Diptera near the spider, a similar Diptera near a corner of the piece of amber, a tiny insect indet. and 2 tiny insect larvae.

Diagnostic characters (♂; ♀ unknown): Pedipalpus as in figs. 7-8 paracymbium distally strongly bent, tegulum bearing prodistally a straight and a hook-shaped apophyses. Epigaster and opisthosomal plates: See below.

Description (♂):
Measurements (in mm): Holotype: Body length 1.35; prosoma: Length 0.75, width 0.7; opisthosoma: Length 0.7, width 0.67; diameter of a tiny dorsal opisthosomal plate 0.02, length of a dorsal bristle up to 0.1; legs: Femur I 1.0, patella I ca. 0.3, metatarsus II 0.55, tarsus II 0.32. - Paratype: Prosomal length 0.9; femur I 0.95, femur IV 1.0.
Colour: Prosoma medium to dark brown, opisthosoma and legs medium grey brown, legs apparently not annulated.
Prosoma almost as wide as long, hairs short, fovea well developed, deformed, eyes large, as in *S. brevis* WUNDERLICH 2004 (: 1236, fig. 80a), clypeus ventrally distinctly protruding, fangs fairly slender labium deformed or hidden. - Opisthosoma (holotype, fig. 5) slightly longer than wide, dorsally leathery, bearing numerous almost hair-shaped bristles placed on tiny plates, sigillae absent, lateral hairs long, epigaster bearing a large scutum, slightly longer than wide, most spinnerets retracted, anterior medians stout and close together. – Legs (fig. 6): I and IV similar in length, hairs short, coxa IV smooth, metatarsi distinctly longer than tarsi, all patellae and tibiae bear 1/1/ thin dorsal bristle (probably tibia IV bears a single bristle only), three thin tarsal claws, position of the metatarsal IV trichobothrium of the holotype in 0.82. - *Note*: Only the right femur I of the holotype bears a retroventral bristle in the middle. Usually femoral bristles are absent in the family Synotaxidae. - Pedipalpus (figs. 7-8) with short patella and tibia, paracymbium distally strongly bent, tegulum bearing prodistally a straight and a hook-shaped apophyses, embolus long, distally describing half a circle.

Relationships: See the key above.

Distribution: Eocene Baltic and Bitterfeld amber forests. This is one of the not frequently documented existence of species in both kinds of these ambers.

Synotaxidae indet. 1 (fig. 9)

Material: 1♂ in Eocene Baltic amber, F3898/BB/CJW.

Preservation and syninclusions: The spider is incompletely preserved in a 2.5 cm red-orange piece of amber, placed on a long piece of a plant, the body is deformed, only the right legs I and II are completely preserved, the left legs I, II and IV are lost beyond the coxa by autotomy, a white emulsion is absent, the reason my be that the piece of amber has been heated/cleared.

Description (♂):
Measurements (in mm): Body length 2.2; prosomal length 1.2; opisthosoma: Length 1.2, height 0.4; leg I: Femur ca. 3.3, patella ca. 0.5, tibia ca. 3.3, metatarsus + tarsus ca. 3.2.
Colour light grey, legs not annulated.
Prosoma: 8 large eyes, posterior row procurved. - Legs - especially I – long and slender, order probably I/II/IV/III, tarsi distinctly shorter than metatarsi, hairs of medium length, patellae and tibiae with 1/1 thin dorsal bristles. - Opisthosoma three times longer than heigh, hairs short. - Pedipalpus (fig. 9): Paracymbium apparently simple (a hidden outgrowth may exist), standing widely out, bulbus large, bearing at least a pair of apophyses, reminding on the open bill of a bird, embolus long, apparently in a circular position.

Close **relationships** are unknown.

Distribution: Eocene Baltic amber forest.

Synotaxidae indet. 2 (figs. 10-11)

Material: 1♂ in Eocene Baltic amber, F3899/BB/CJW.

Preservation: The spider is incompletely preserved in a flat yellowish piece of amber, placed on a fissure in the amber, most parts of body and legs are covered with a white emulsion, the posterior part of the opisthosoma is cut off, both legs I and the left legs III-IV are lost beyond the coxa by autotomy, the distal part of the left tarsus II and the right patella IV are cut off, the copulatory structures are partly hidden or deformed.

Description (♂):
Measurements (in mm): Body length 3.0; prosoma: Length 1.4, width 1.3; opisthosoma: Length ca. 2.0, width 1.0; leg II: Femur 2.4, patella 0.6, tibia ca. 2.4, metatarsus 2.3, tarsus 0.4; femur IV ca. 2.2.
Colour light grey, legs not annulated.
Prosoma not much longer than wide, ventrally hidden, hairs short, thoracal fissure long, clypeus long, 8 large eyes, posterior row distinctly procurved. - Legs (I is lost): II quite long, hairs partly long, patellae with 1/1 thin dorsal bristles, tibia II with 1/1 well developed dorsal bristles. - Opisthosoma twice as long as wide, hairs not long. - Pedipalpus (figs. 10-11) bearing two larger tegular apophyses; embolus long, apparently in an at least half circular position.

Close **relationships** are unknown.

Distribution: Eocene Baltic amber forest.

Family MIMETIDAE

See WUNDERLICH (2004:1260f) and (2011: 521f).

In the ant eating members of the family Mimetidae tibia and metatarsus I-II bear long prolateral bristles and between them a row of short and bent bristle increasing in length fig. 12).
Here I describe a new species.

Mimetus HENTZ 1832

In the genus *Mimetus* (see below) femur I bears a row of short retrolateral bristles see WUNDERLICH (2004: 1274, fig. 14).

?***Mimetus flexuosus* n. sp**. (figs. 12-15), photo 16

Etymology: The species name refers to its winding/flexible tibia, metatarsus and tarsus I-II, from lat. flexuosus.

<u>Material</u>: Holotypus (♂) in Eocene Baltic amber, F3912/BB/CJW.

Preservation and syninclusions: The spider is excellently and completely preserved in a clear yellow-orange piece of amber which is slender and 2.5 cm long. The left bulbus is partly expanded. A white emulsion covers all parts of the body and most part of legs and pedipalpi; the spider was not cleared by the sun, therefore the emulsion did not disappear, probably because the piece of resin was hidden below bark of a tree. So the spider was probably a dweller of the bark of trees like certain extant Mimetidae. - <u>Syninclusions</u>: The branch of a tiny plant hair is preserved near the spider, lose dorsal opisthosomal hairs exist within a fissure dorsally of the opisthosoma.

Diagnostic characters (♂; ♀ unknown): Legs I-II quite long, tiba I 2.8 mm long, tibia, metatarsus and tarsus I-II flexible and winding (photo); pedipalpus (figs. 13-15), see below.

Description (♂):
Measurements (in mm): Body length 4.0; prosoma: Length 1.8, width ca. 1.6; opisthosoma: Length 2.7, width 2.3; leg I: Femur 4.0, patella 1.0, tibia 2.8, metatarsus ca. 2.75, tarsus 1.25; tibia II 2.0, tibia III 1.2, tibia IV 2.0.
Colour of the legs light brown.
Prosoma (photo) 1.13 times longer than wide, not raised, hairs short to medium in length, 8 eyes in two rows, posterior row straight, anterior median eyes largest, spaced by about their diameter, clypeus short, basal cheliceral articles fairly long, bearing about half a dozen “peg teeth”, lateral files nor recognizable, fangs robust, gnathocoxae strongly converging, labium a free sclerite, about as long as wide, sternum distinctly longer than wide, only fairly spacing the coxae IV. - Legs (fig. 12, photo): Order I/II/IV/III, I not much longer than II, tibia, metatarsus and tarsus I-II distinctly undulating/flexible, tarsi short, femur I rather thick, bearing a retrolateral row of short bristles in the basal half, 5 resp.8 dorsal bristles and 3 apicals, patellae dorsally with 1/1 bristles, the basal one short. - Opisthosoma (photo) 1.17 times longer than wide, almost egg-shaped, hairs short, spinnerets hidden. - Pedipalpus (figs. 13-15) with long articles which bear long bristles, I did not recognize prolateral stridulatory teeth on the femora, patella distally distinctly thickened, bearing 3 dorsal-distal bristles, tibia with 2 dorsal bristles, cymbium wide, paracymbium well developed, pointed, bulbus bearing at least 2 strongly sclerotized sclerites, thin part of the questionable embolus are observable.

Relationships: The quite diverse genus *Mimetus* HENTZ 1832 has probably to split up in the future. In the three known questionable species of *Mimetus* in Baltic aber the pedipalpal patella is distinctly thickened distally. Long legs exist also in ?*Mimetus longipes* WUNDERLICH 2004 in which tibia I is 3.1 mm long and the structures of the bulbus are different.
<u>Notes</u>: (1) Similar *undulating* leg article exist also in most – but not all (!) - males of *Balticonestius flexuosus* WUNDERLICH 1986 of the family Nesticidae in Baltic amber, see below.
(2) In the dubious and preoccupied fossil genus *Corynitis* MENGE in KOCH & BERENDT 1854 – type species *C. flexuosus* MENGE 1854 - in Baltic amber the opisthosoma possesses folds and the anterior leg articles are not “undulating”.

Distribution: Eocene Baltic amber forest.

Family NESTICIDAE

Sticky droplets of the capture web – otherwise they are existing in other members of the superfamily Araneoidea and in the family Pholcidae - are well known in extant as well as in fossil Nesticidae (fig. 16 together with the holotype of Balticonesticus flexuosus WUNDERLICH 1986).

Identification of the species: Frequently it is impossible to observe the pedipalpi of conspecific specimen in the exact identical position; therefore the structures of the paracymbium – see figs. 25f of *Balticonesticus rectus* n. sp., paratype F3913 - and of the bulbus (figs.) may appear quite different in a slightly different position in specimens which are most probably conspecific. Furthermore a certain intraspecific variability may exist or the species may be members of quite similar and strongly related morphospecies!

Balticonesticus WUNDERLICH 1986

Type species: *Balticonesticus flexuosus* WUNDERLICH 1986; male holotype (figs. 19-20); further male: F3891/BB/CJW (fig. 21), body length 2.6 mm, length of tibia I 3.5 mm.

Relationships: *Balticonesticus* is a member of the Nesticini, in my opinion close - or even synonymous? - with the extant genus *Nesticus* and close to *Heteronesticus*, see below. Relationships to the extinct genus *Eopopino* PETRUNKEVITCH 1942: See WUNDERLICH (1986: 129).

Diagnostic characters of the genus: See WUNDERLICH (1986: 129). In *B. rectus* n. sp. metatarsus I is not flexible (undulated) but straight in contrast to the generotype; therefore a flexible metatarsus I is not a character of the genus *Balticonesticus*.

Here I describe a second species of this probably extinct genus which is only known by the male sex.

***Balticonesticus rectus* n. sp.** (figs. 22-28), photos 14-15

Etymology: The name of the species refers to its straight metatarsus I, from rectus (lat.) straight.

Material in Eocene Baltic amber: Holotype F3914/BB/CJW; male paratpes: F3913/BB/CJW, F3915/BB/CJW + 1 separated piece of amber, F3916/BB/CJW, F3917/BB/CJW.

Preservation, syninclusions and figs.: Holotype (photo 14): The spider is well and almost completely preserved in a clear yellow-orange piece of amber, a weak white emulsion exists on the left side of the body and some leg articles; most leg articles are preserved but parts of the left legs III and IV are cut off. *Syninclusion*: A single stellate plant hair. - Paratype F3913 is well but incompletely preserved in a clear yellow-orange piece of amber, the ventral side is covered with a white emulsion, several leg articles are cut off, the left legs I and II are lost beyond the coxa by autotomy, the right leg I is cut at the end of the femur, the right leg II is completely preserved, both pedipalpi are very well preserved and observable, the spinnerets are covered by a bubble. Organic *syninclusions* are absent. - Paratype F3915 is fairly well and completely preserved in a clear yellow-oange piece of amber, the body is deformed, parts of body and legs are dorsally and ventrally covered with a white emulsion.- Syninclusions are 3 tiny arthropods: A juv. spider, a mite and a Collembola. In the separated piece of amber is a larger Diptera preserved. - Paratype F3916 (photo 15) is well and almost completely preserved in a clear yellow-orange piece of amber, the opisthosoma is slightly deformed, a white emulsion is absent, some leg articles are cut off, one leg is lose and preserved left in front of the spider, some leg articles are broken within the piece of amber. A *syninclusion* is a tiny part of a Diptera: Nematocera. - Paratype F3917 is fairly well (the pedipalpi not well) preserved in a clear yellow-orange piece of amber, its dorsal side is covered with a white emulsion, the right leg I is lost beyond the coxa by autotomy, the left leg II is a regenerate or a deformation, only a small “stump” of the coxa is preserved, the left legs I, III and IV as well as the right legs III and IV are completely preserved. A *syninclusion* is a tiny beetle.

Diagnostic characters (♂; ♀ unknown): Metatarsus I straight (photos 14-15); pedipalpus (e. g., figs. 22, 27): Tibia about 1 1/2 times longer than wide, distinctly longer than the patella.

Description (♂):
Measurements (in mm): Holotype: Body length 2.7; prosomal length 1.2; opisthosoma: Length 1.6, width 0.7, height 0.7; leg I: Femur 4.5, patella ca. 0.7, tibia ca. 5.5, metatarsus 4.5, tarsus 1.3; tibia II 3.6, tibia III 2.0, tibia IV (partly lost) ca. 2.9. - Paratypes: F3913: Body length ca. 3.0; prosoma: Length 1.5, width ca. 1.3; F3915: Body length ca. 2.3, prosomal length ca. 1.0, tibia I 3.6; F3916: Body length 3.0; prosoma: Length 1.5, width ca. 1.35; F3917: Body length ca. 2.9, prosomal length ca. 1.2.
Colour: Prosoma and legs medium brown, legs not annulated, opisthosoma light grey.
Prosoma (photos 14-15) clearly longer than wide, bearing few short and long hairs, cuticula almost smooth, fovea well developed, 8 eyes of medium size, posterior row straight, posterior median eyes spaced by about their diameter, clypeus not protruding, about as long as the field of the median eyes, basal cheliceral articles robust and not diverging, teeth of the furrow margins hidden, fangs basally thick, labium distinctly wider than long, gnathocoxae not converging, sternum 1.14 times longer than wide, spacing coxae IV by ca 3/4 of their diameter. - Legs (photos) long and slender, I-II very long, tarsi short, order I/II/IV/III, metatarsus I straight, tibia I 3.6-4.6 times longer than the prosoma, cuticula smooth, hairs partly long, all patellae and tibiae bear 1/1 thin dorsal bristles, position of the metatarsal trichobothrium unknown, tarsal claws not studied. - Opisthosoma (photos) up to more than 2 times longer than wide or high, dorsal hairs of medium length, anterior and posterior spinnerets stout, best preserved in the holotype. - Pedipalpus (figs. 22-28): Femur long and slender, patella only slightly longer than wide, tibia ca. 1 1/2 times longer than wide, fairly thickened, cymbium wide, paracymbium very large, standing widely out and divided, median apophysis, radix and terminal apophysis well developed, embolus originating basally at the

bulbus, long and thin, describing half a circle in a prolateral position, guided by a long conductor.

Relationships: In *B. flexuosus* WUNDERLICH 1986 metatarsus I is distinctly undulating (fig. 17), the pedipalpal tibia (figs. 19-21 is about as long as wide like the patella, the shape of the paracymbium and the sclerites of the bulbus are similar to *rectus*.

Distribution: Eocene Baltic amber forest.

Heteronesticus WUNDERLICH 1986

Heteronesticus has been based on *H. magnocymbialis* WUNDERLICH 1986. It is close to *Balticonesticus* WUNDERLICH 1986 (see above) in which the paracymbium is less complicated and a large pointed outgrowth of the paracymbium, directed to the bulbus (fig. 26) is absent. In both genera the prosoma is wide, 1.1-1.35 times longer than wide, the legs are long; the opisthosoma is egg-shaped to distinctly longer than wide or high. - Problems regarding the determination of species: See above.

Heteronesticus magnoparacymbialis WUNDERLICH 1986 (figs. 29-32; compare photo of *H.* sp. indet.1, F3920, see below)

Material: Holotype ♂ in Eocene Baltic amber and a separated piece of amber, F3888/CJW. The male will soon be given to the Palaeontological Institute of the University Hamburg. - Further material: 1♂ in a bad condition, incomplete and probably conspecific (fig. 32), body length 1.6 mm, length of tibia I 1.1 mm, and a separated piece of amber, F3918/BB/CJW. See also below: 2♂ *H*. sp. indet.

Distribution: Eocene Baltic and Bitterfeld amber forests.

***Heteronesticus acuminatus* n. sp**. (figs. 33-34), photo 13

Heteronesticus sp.: WUNDERLICH, Beitr. Araneol., 3 (1986: 231).

Etymology: The species name refers to its well developed and well observable pointed paracymbial apophysis, from acumen (lat.) = point. This apophysis exists in all species of *Heteronesticus* but may be hidden.

<u>Material</u>: Holotypus ♂ in Eocene Baltic amber and a separated piece of amber, F1085/BB/CJW.

Preservation and syninclusions: The spider is completely and well preserved in a clear yellow-orange piece of amber; the left side of body and legs are covered with a white emulsion. - <u>Syninclusions</u> are some small stellate plant hairs and - at the margin of the piece - parts of a spider and parts of a questionable Collembola.

Diagnosis (♂; ♀ unknown): Pedipalpus (figs. 33-34) with a quite long terminal apophysis.

Description (♂):
Measurements (in mm): Body length 2.0; prosomal length 1.0; opisthosoma: Length 1.1, height 0.9; leg I: Femur 1.3, patella ca. 0.3, tibia ca. 1.35, metatarsus 1.2, tarsus 0.55; tibia III ca. 0.8,tibia IV 1.2.
Colour mainly light brown, legs not annulated.
Prosoma partly hidden, 8 eyes, dorsal hairs indistinct, clypeus about as long as the field of the median eyes. - Legs fairly long, hairs short, bristles thin, most are rubbed off. - Opisthosoma ovoid, hairs short.

Relationships: Compare the figs. of the pedipalpi of the remaining congeneric species which are closely related.

Distribution: Eocene Baltic amber forest.

***Heteronesticus bitterfeldensis* n. sp.** (fig. 35)

<u>Etymology</u>: The name of the species refers to its deposit near Bitterfeld.

<u>Material</u>: Holotype ♂ in Eocene amber from Bitterfeld, Germany, F3919/BI/CJW.

Preservation and syninclusions: The spider is completely and fairly well preserved in a yellow-orange piece of amber, well observable from the left side; its right pedipalpus is hidden. - <u>Syninclusions</u>: At a layer of the amber near the ventral side of the spider exists a strongly developed white emulsion. Further included are a 2 mm long probably congeneric or even conspecific male spider which is observable from the ventral side and is partly covered with a white emulsion as well a bubble, 1 Formicidae, 1 Collembola and small stellate plant hairs.

Diagnostic characters (♂; ♀ unknown): The longest branch of the paracymbium (P in fig. 35) is widened distally.

Description (♂):
Measurements (in mm): Body length ca. 1.9; prosomal length 0.85; opisthosoma: Length 1.05, height 0.65; leg I: Patella 0.3, tibia 1.2, metatarsus 1.0, tarsus 0.55; tibia IV 1.2.
Colour: Prosoma and legs medium brown, legs not annulated, opisthosoma medium grey.
Prosoma with few hairs of medium size, fovea well developed, 8 eyes of medium size, clypeus, mouth parts and sternum hidden. - Legs fairly long and slender, hairs short, all patellae

and tibiae bear 1/1 thin dorsal bristles, position of the metatarsal IV trichobothrium in ca. 0.4. - Opisthosoma oval, scarcely covered with hairs of medium length. - Pedipalpus: Patella and tibia short, longest branch of the paracymbium (P in fig. 35) widened distally.

Relationships: In the other congeneric species the long paracymbial branch (P in fig. 35) is distally less widened.

Distribution: Eocene Bitterfeld amber forest.

Heteronesticus **sp. indet**. 1 (photo 15a)

Material: 1♂ in Eocene Baltic amber, F3920/BB/CJW.

Preservation and syninclusions: The spider (photo) is excellently and almost completely preserved, ventrally laying on a weakly translucent layer of the amber, the right leg I is lost beyond the coxa by autotomy. - Syninclusions are several long and slender leg articles of an Opiliones and some small stellate plant hairs.

Relationships: I do not want to exclude the conspecifity of the present male with *H. magnoparacymbialis* WUNDERLICH 1986.

Distribution: Eocene Baltic amber forest.

Heteronesticus **sp. indet**. 2

Material: 1♂ in Eocene Baltic amber, F3921/BB/CJW.

Preservation and syninclusions: The spider is very well and almost completely preserved in a yellow-orange piece of amber, only the right leg II is lost beyond the coxa by autotomy. - Syninlusions are a tiny Acari, a Hymenoptera, small stellate plant hairs and particles of detritus.

Measurements (in mm): Body length 1.8; prosoma: Length 0.75, width 0.7; opisthosoma: Length 0.85, width 0.45; tibia I 1.2, tibia IV 1.0.

Relationships: I do not want to exclude the conspecifity of the present male with *H. magnoparacymbialis* WUNDERLICH 1986.

Distribution: Eocene Baltic amber forest.

Family ZODARIIDAE

The still not well studied Eocene amber fauna of the ant-hunting spider family Zodariidae on generic level - at least half a dozen genera exist - was more diverse than the extant European zodariid fauna (4 genera); see WUNDERLICH (in 2004: 1576-1611): The fossil spiders (Araneae) of the family Zodariidae in Baltic amber with remarks on the subfamilies Cryptothelinae and Homalonychinae.
To my knowledge all Eocene zodariid genera are extinct. Here I add further material in Baltic amber, including a new genus. Some indet. taxa are kept in my private collection, waiting for a study.

Angusdarion humilis WUNDERLICH 2004 (photo 17)

Material: 1♂ in Eocene Baltic amber and a larger separated piece of amber, F3893/BB/CJW.

The present male is the second known specimen besides the male holotype.
The spider (photo) is partly well preserved, the mouth parts are hidden, the distal articles of the right legs are split off, the opisthosoma is mainly dorsally covered with a white emulsion, the bullbi are bent below the pedipalpal femora.
Measurements (in mm): Body length 3.5; prosoma: Length 1.7, width 1.3; opisthosoma: Length 1.85, width 1.2; leg I: Femur 1.0, patella 0.4, tibia 1.1; tibia IV 1.0.
Colour of prosoma and legs dark brown. Tibia I is distinctly thickened and bears 4 pairs of long and thin ventral bristles mainly in the basal half.

Distribution: Eocene Baltic amber forest.

Pectenzodarion **n. gen.** (figs. 36-38), photo 18

Etymology: The name refers to the quite unusual existence of a comb on tibia I as well as the unusual shape of the posterior margin of the prosoma (the peltidium), from unicus (lat.) = unique.

The gender of the name is neuter.

Type species (by monotypy): *Pectenzodarion unicum* n. sp.

Diagnostic characters (♂; ♀ unknown): 8 small eyes in two rows, posterior row fairly procurved, posterior median eyes largest and spaced by their diameter, anterior median eyes smallest and spaced by more than their diameter, cephalic part raised fairly convex, posterior margin of the prosoma (the peltidium) (fig. 36) distinctly elongated (convex), unpaired tarsal claw existing, leg bristles few and slender, tibia I bearing a transverse apical-ventral comb of a row of stout and spine-shaped bristles (fig. 37), dorsal opisthosomal scutum absent, epigaster (photo) bearing a large scutum; pedipalpus (fig. 38): Cymbium without spines or strong bristles, retrobasally bearing a long spoon-shaped outgrowth which fits into a space between the tibia and a ventral tibial apophysis. The sclerites of the bulbus are badly observable, the embolus is unknown.

Relationships: A member of the subfamily Zodariinae. Close relationships are unknown to me. See the key to the Eocene genera, WUNDERLICH (2004: 1588-1589).

Distribution: Eocene Baltic amber forest.

***Pectenzodarion unicum* n. gen. n. sp.** (figs. 36-38), photo 18

Etymology: The species name refers to its unique tibial I comb and the special convex posterior dorsal shape of its prosoma (the peltidium), from latin unicus = unique.

Material: ♂ holotype in Eocene Baltic amber, F3926/BB/CJW.

Preservation and syninclusions: The spider is completely and fairly well preserved in a 4 cm long piece of amber which includes several layers of amber and possesses partly an oxidated surface bearing tiny fissures. Few dorsal parts of the spider are covered with a white emulsion, the dorsal part of the opisthosoma is hurt (inclined), the bulbi are directed to the chelicerae. - Synincluions are some tiny stellate plant hairs.

Diagnostic characters and **syninclusions**: See above.

Description (♂):
Measurements (in mm): Body length 4.3; prosoma: Length 2.5, width 1.7; opisthosoma: Length 2.1, width 1.4; leg I: Tibia 0.9, metatarsus 0.8, tarsus 0.6; tibia IV 0.9.
Colour: Prosoma and legs medium to dark brown, legs not annulated,, opisthosoma light grey brown, epigaster dark brown.
Prosoma (fig. 36) 1.5 times longer than wide, bearing few short hairs, eyes and peltidium see above, clypeus not long, basal cheliceral articles robust, fangs hidden, labium a free sclerite, longer than wide, sternum fairly convex, 1.43 times longer than wide, weakly spacing coxae IV. - Legs (fig. 37) robust, I and IV of about the same length, tibia I bearing a transverse apical-ventral comb of a row of stout and spine-shaped bristles (fig. 37) of an unknown function (the diversity of stridulatory organs in Zodariidae see JOCQUE (2005)), leg bristles few and slender, partly hidden, femur I dorsally 1/1/1/1, femur IV dorsally probably only 1/1; patella I probably none, patella III with a strong lateral pair, tibia I (fig. 37) and IV with 5 not paired bristles, tibia III at least with 1/1 pro- and retrolateral bristles, metatarsus ventrally and laterally at least 3 bristles and apicals. Scopulae and tarsal tufts absent, unpaired tarsal claw existing, teeth of paired claws not studied. - Opisthosoma 1.5 times longer

than wide, hairs short, dorsal scutum absent, epigaster (photo) with a large scutum, spinnerets only partly recognizable, anteriors stout. - Pedipalpus see above, partly hidden, with slender femur and short patella and tibia, cymbium probably with a basal depression.

Distribution: Eocene Baltic amber forest.

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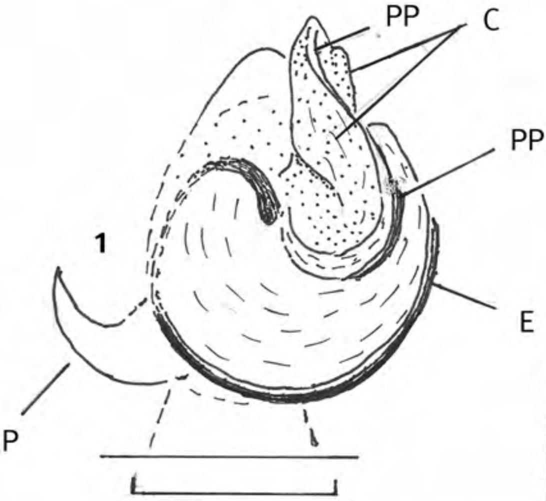

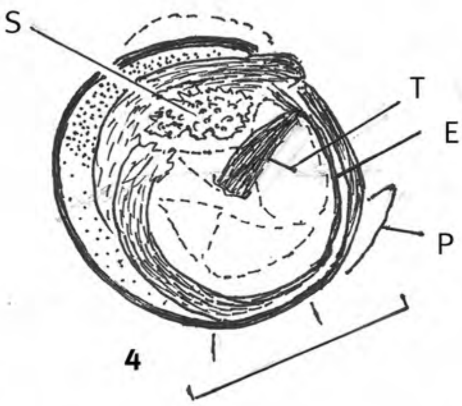

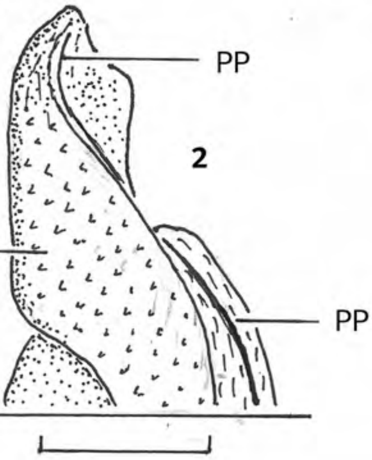

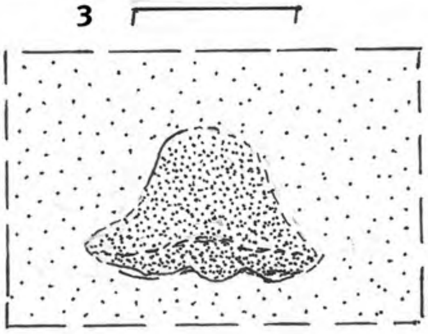

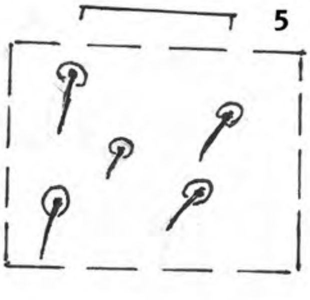

Figs. 1-2: ***Cornuanandrus scutatus*** **n. sp.** (Synotaxidae), ♂; 1) ventral and slightly retrolateral aspect of the right pedipalpus, hairs not drawn; 2) retroventral aspect of conductor (C) and parembolic process (PP). - E = embolus, P = paracymbium. Scales 0.2 and 0.1 mm;

fig. 3) ***Pseudoacrometa gracilipes*** WUNDERLICH 1986, ♀, epigyne. - Scale: 0.2 mm;

fig. 4) ***Succinitaxus pusillus n. sp.*** (Synotaxidae), ♂;,ventral aspect of the left pedipalpus. Most structures are difficult to observe. E= embolus, P= paracymbium, S= sperm. Scale 0.1;

figs. 5-6: ***Succinitaxus strepitus*** **n. sp., ♂** holotype; 5) dorsal bristles of the middle of the opisthosoma; 6) retrodorsal aspect of the right femur **I**. - Scales 0.1 and 0.2 mm;

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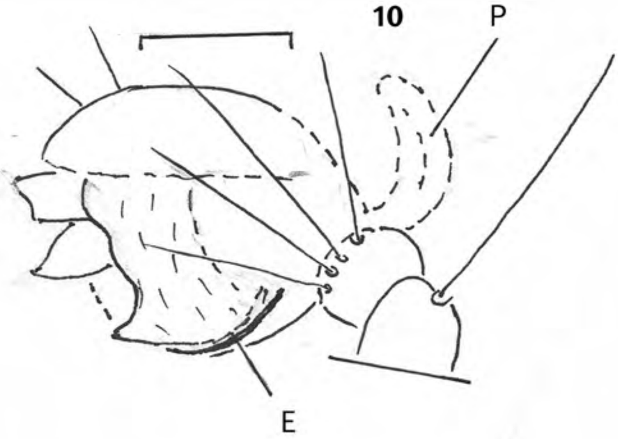

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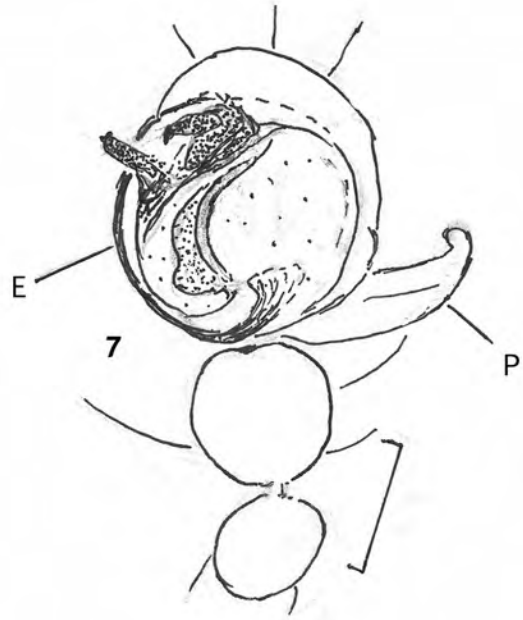

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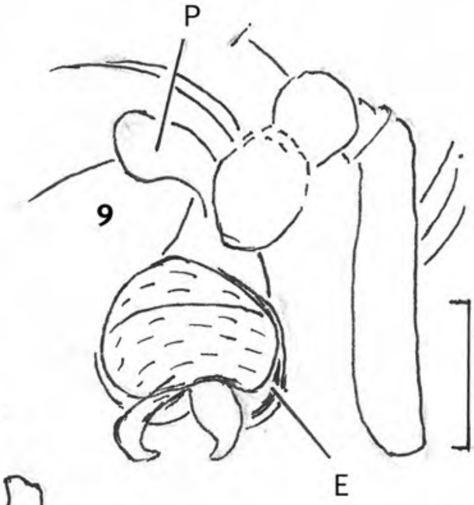

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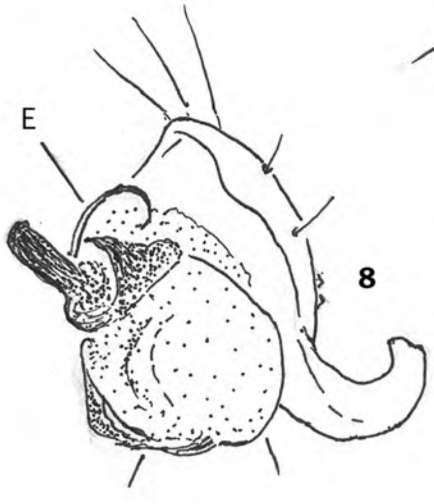

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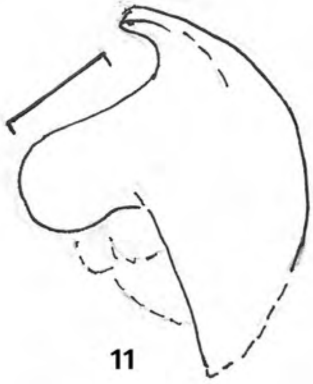
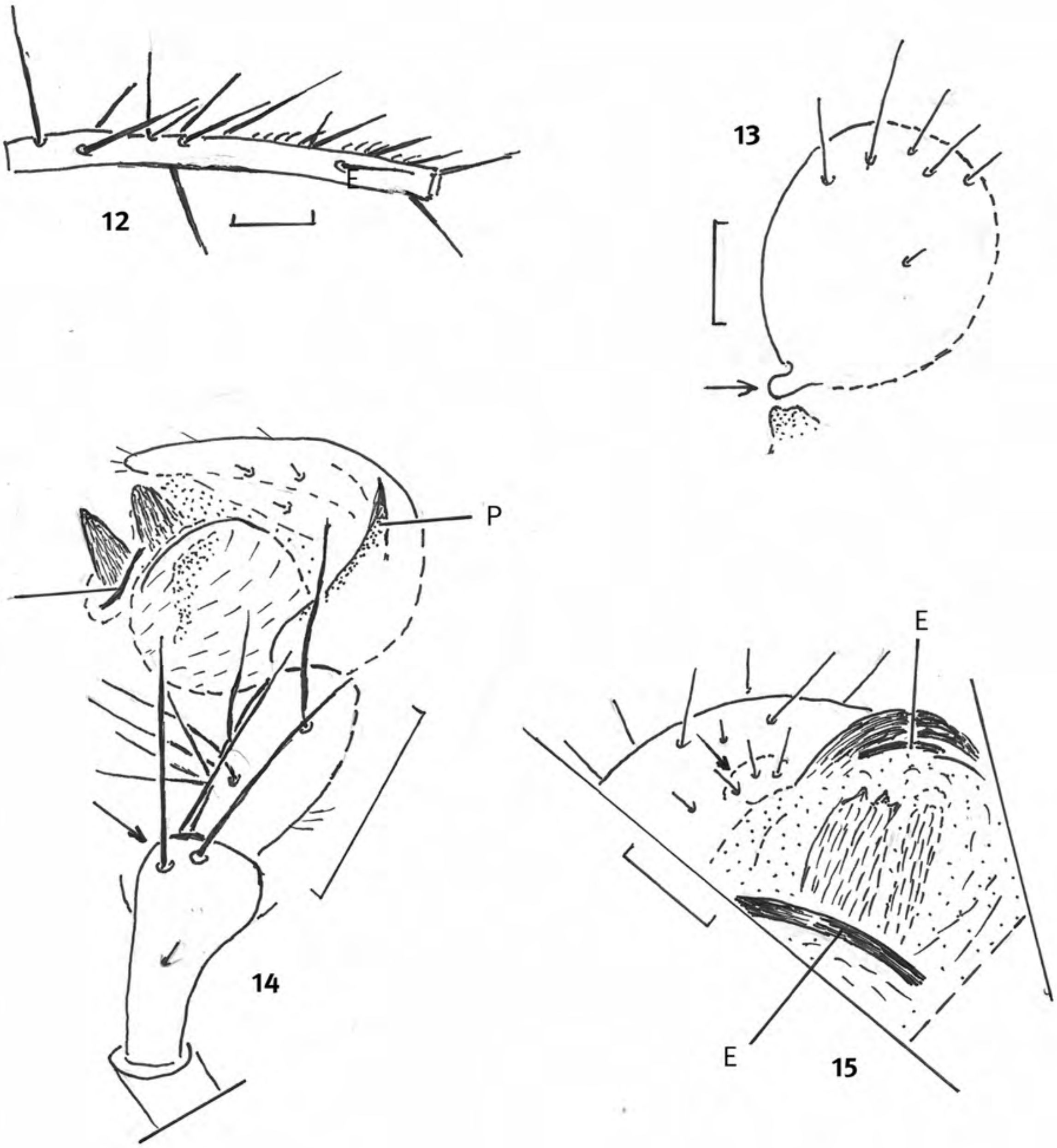


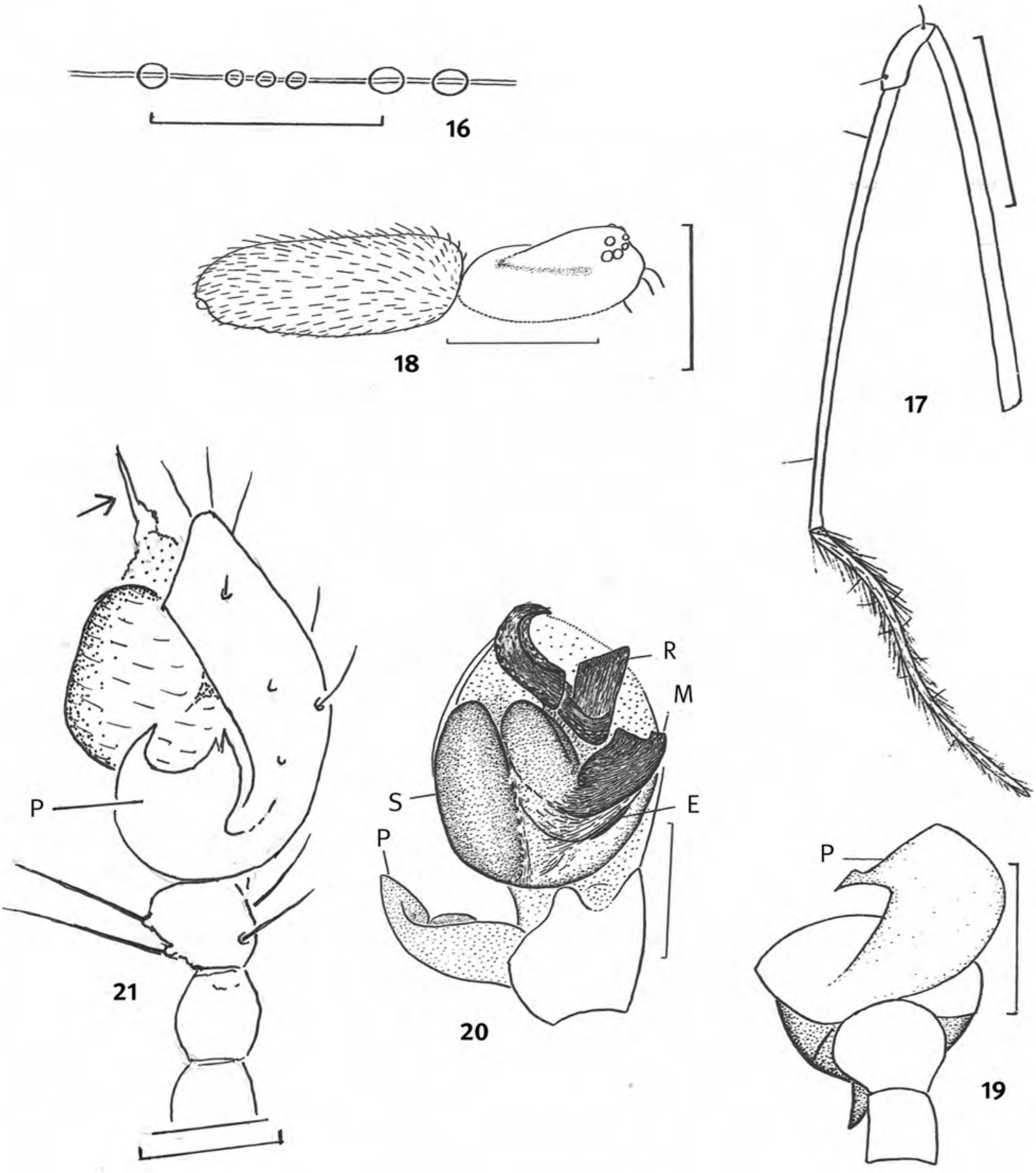
figs. 7-8: ***Succinitaxus strepitus* n. sp.**, ♂; 7) holotype, dorsal aspect of patella and tibia but ventral aspect of the bulbus of the right pedipalpus. Some structures are badly observable/hidden; 8) paratype, retroventral-apical aspect of the partly expanded right pedipalpus;

fig. 9) **Succinitaxidae sp. indet. 1** (F3898), ♂, retrolateral aspect of the left pedipalpus;

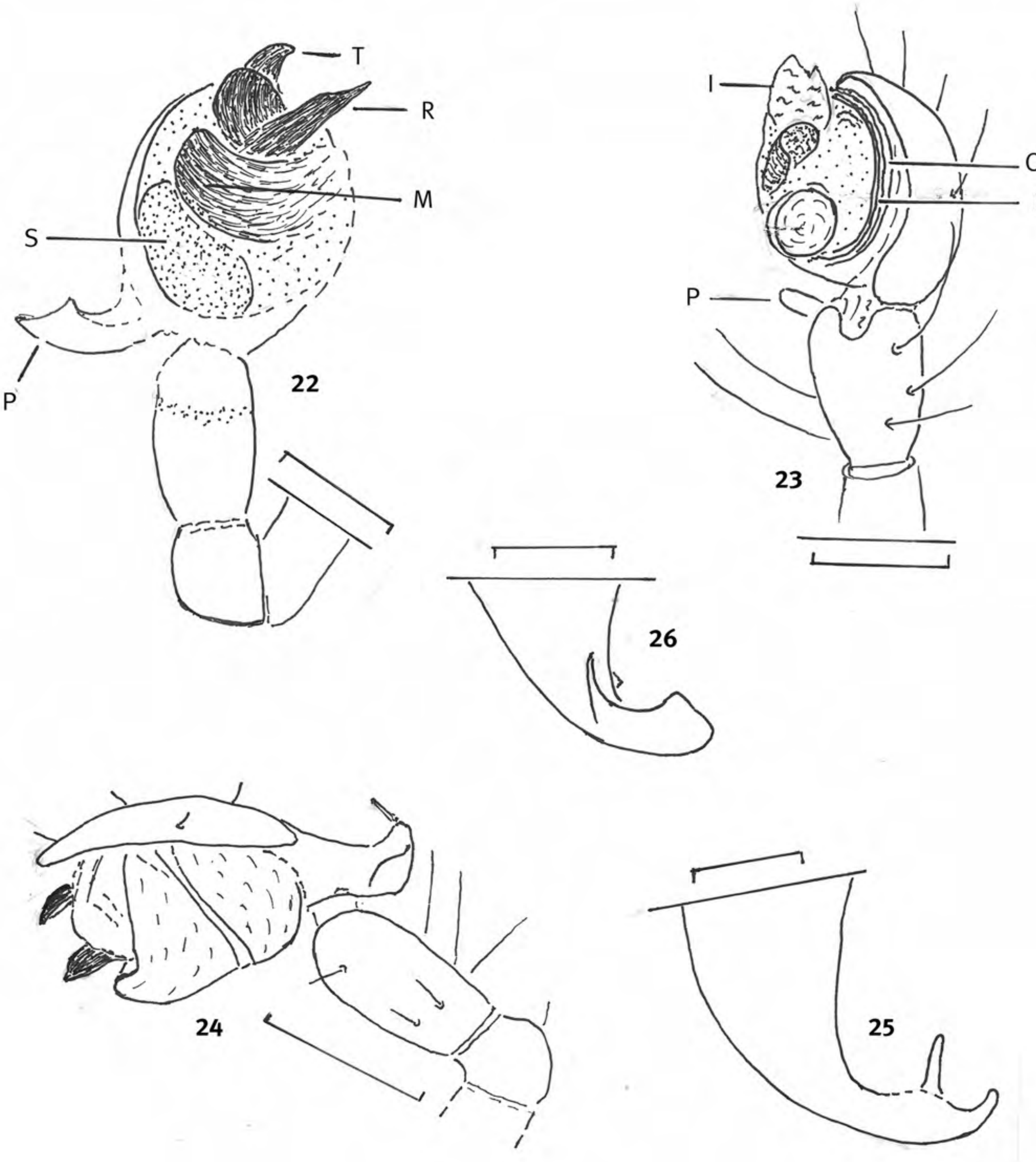
figs. 10-11: S**uccinitaxidae sp. indet. 2** (F3899), ♂; 10) retrolateral aspect of the left pedipalpus; 11) ca. retrolateral aspect of the right pedipalpus; large parts are hidden. - E = embolus, P = paracymbium. Scales: 0.2 mm in figs. 9-10), 0.1 mm in the remaining figs.;



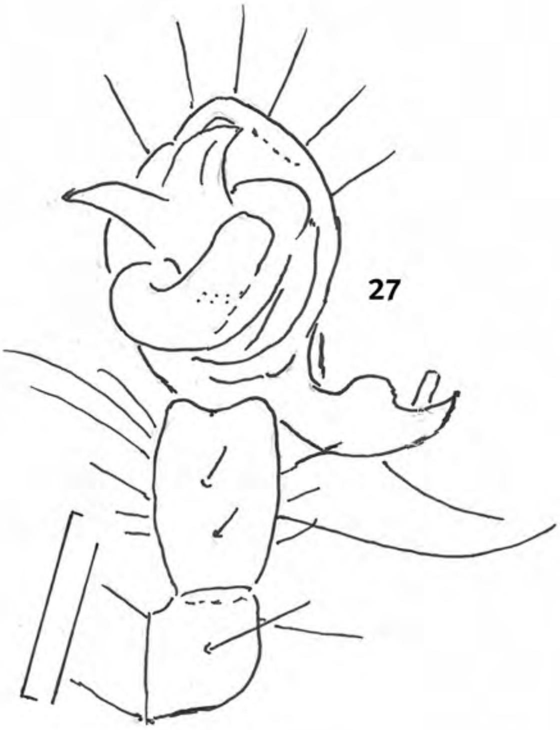
figs. 12-15: ?***Mimetus flexuosus*** **n. sp**. (Mimetidae), ♂; 12) retrolateral aspect of the righrt tibia **I**; 13)dorsal aspect of the cymbium and the tibial margin of the right pedipalpus. The arrow points to the questionable cymbial outgrowth. Only few hairs are drawn; 14) retroventral aspect of the left cymbium and bulbus but probasal aspect of the patella and tibia. The arrow points to the end of the patella which is distinctly thickened; 15) distal aspect of the right pedipalpus, partly hidden by leg articles and an emulsion. The arrow points to the tip of the cymbium. - E = embolus, P = paracymbium. Scales: 0.5 mm in figs. 12) and 14), 0.2 mm in figs. 13) and 15);



figs. 16-21: ***Balticonesticus flexuosus*** WUNDERLICH 1986 (Nesticidae); 16) part of a thread bearing sticky droplets near the holotype; 17-20) holotype ♂, 21) ♂ F3891; 17) retrolateral aspect of the left leg I without tarsus, hairs are drawn only on the metatarsus. Note the thin and hair-shaped dorsal bristles on patella and tibia; 18) lateral aspect of the body; 19) dorsal-basal and slightly prolateral aspect of the right pedipalpus; 20) ventral aspect of the right pedipalpus; 21 retroventral aspect of the left pedipalus. The arrow points to an artefact. Only few hairs are drawn.- E = embolus, M = median apophysis, P = paracymbium, R = radix, S = subtegulum. Scales: Fig. 18) 1 mm, 16) 0.1 mm, remaining figs. 0.2 mm;



figs. 22-26: ***Balticonesticus rectus* n. sp**. (Nesticidae), ♂, holotype and paratype F3913: Figs. 25-26; 22) ventral and slightly basal aspect of the right pedipalpus, partly hidden; 23) proventral aspect of the right pedipalpus; 24) retrolateral aspect of the left pedipalpus; 25) dorsal aspect of the paracymbium of the right pedipalpus; 26) slightly retrodorsal aspect of the paracymbium of the right pedipalpus. - C = conductor, E = embolus, I = scinny structure, M = median apophysis, P = paracymbium, R = Radix, S = subtegulum, T = terminal apophysis. Scales: 0.1 mm in figs. 25-26), 0.2 mm in the remaining figs.;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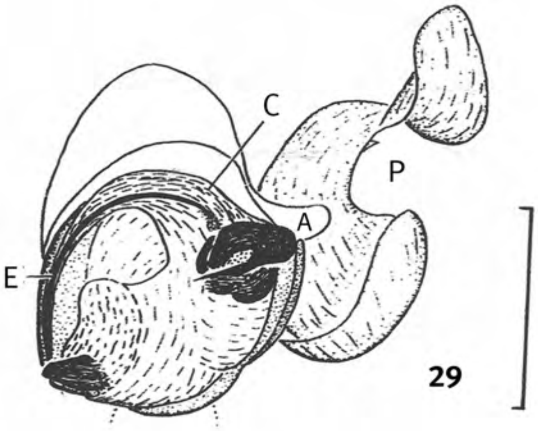

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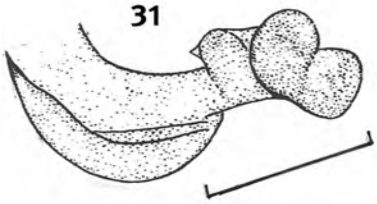

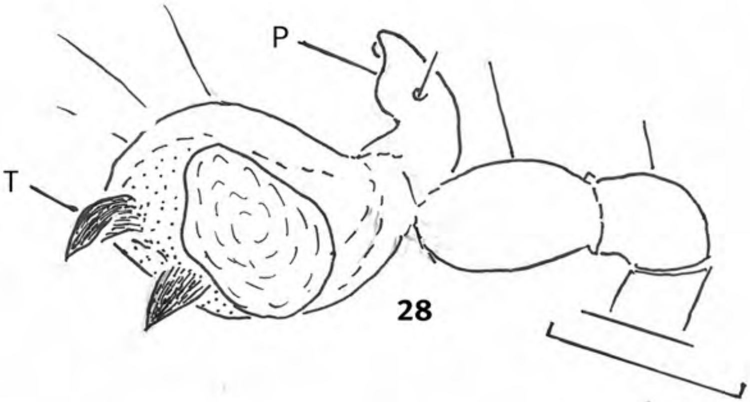

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figs. 27-28: ***Balticonesticus rectus*** **n. sp**. (Nesticidae), ♂ F3917; 27) ventral aspect of the left pedipalpus; 28) retroventral aspect of the partly hidden left pedipalpus;

figs. 29-31: ***Heteronesticus magnoparacymbium*** WUNDERLICH 1986 (Nesticidae), holotype ♂; 29) ventro-distal aspect of the left pedipalpus; 30) dorsal aspect of the left pedipalpus; 31) ventral and slightly retrolateral aspect of the paracymbium of the left pedipalpus. - A = outgrowth of the cymbium, C = conductor, E = embolus, P = paracymbium, T = terminal apophysis, TA = tegular apophysis, Y = cymbium. Scales: 0.2 mm;

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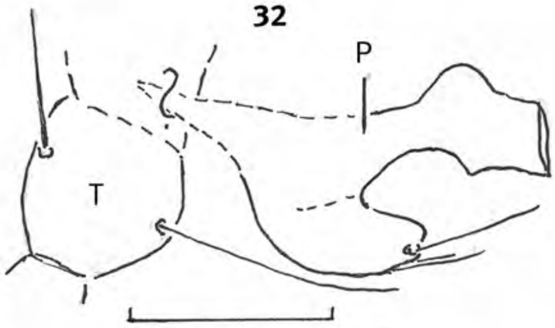

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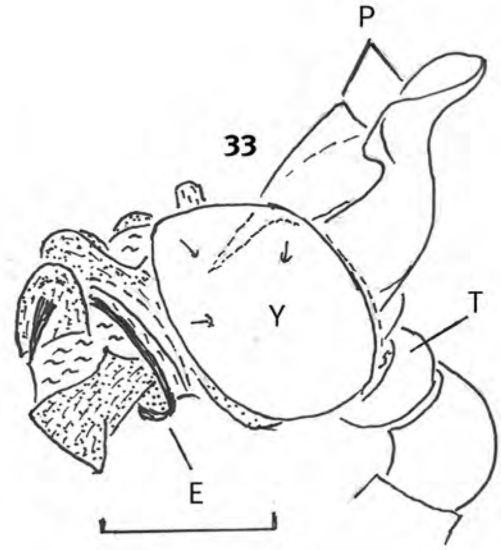

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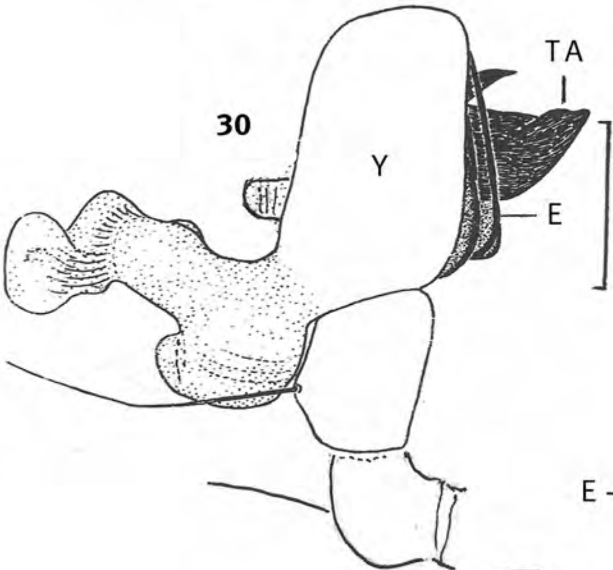

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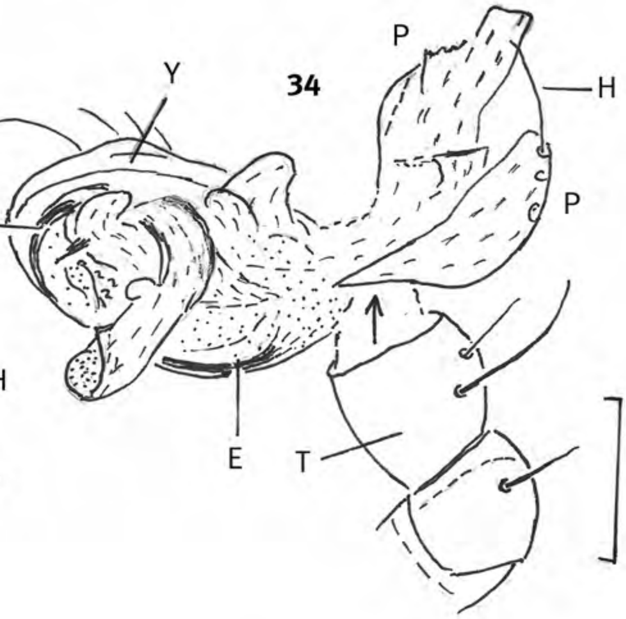

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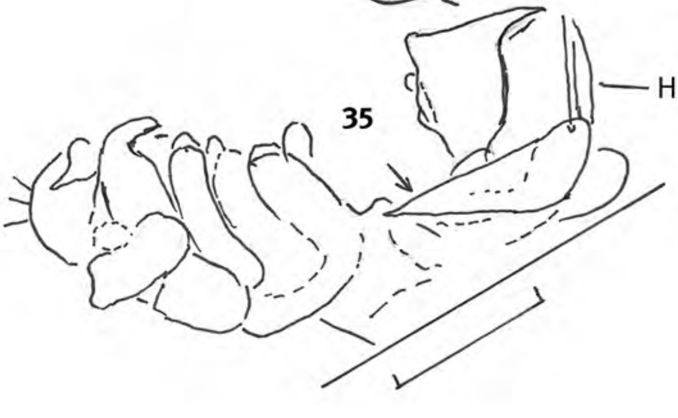
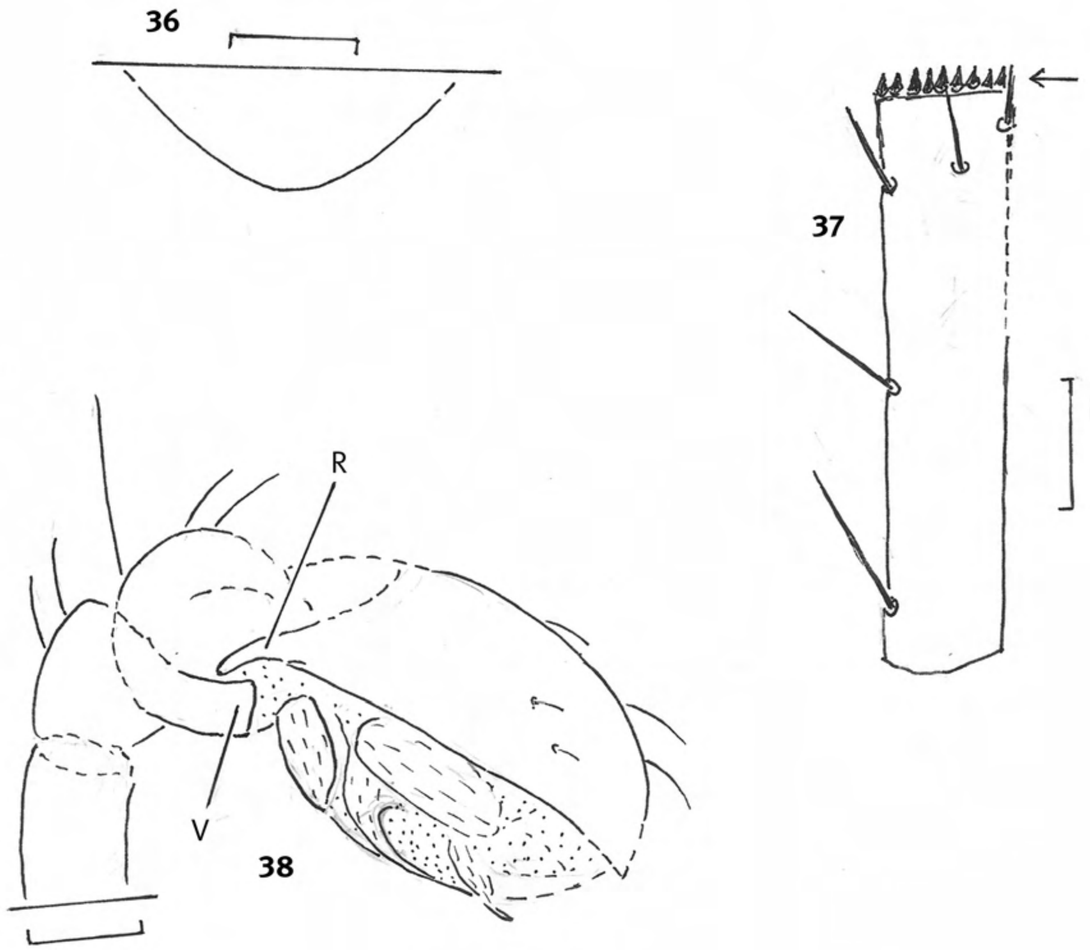


figs 32) ***Heteronesticus*** ?***magnocymbialis*** WUNDERLICH 1986 (Nesticidae), ♂ F3918, dorsal aspect of paracymbium and ventral aspect of the tibia of the partly hidden right pedipapus;

figs. 33-34) ***Heteronesticus acuminatus* n. sp**. (Nesticidae); 33) distal aspect of the right pedipalpus; 34) retroventral aspect of the left pedipalpus. The arrow points to the outgrowth of the paracymbium;

fig. 35) ***Heteronesticus bitterfeldensis* n. sp**. (Nesticidae), ♂, ventral aspect of the left pedipalpus. The arrow points to the outgrowth of the paracymbium.

E = embolus, H = hairs of the paracymbium, P = paracymbium, T = tibia, Y = cymbium. Scales: 0.2 mm;



figs. 36-38: ***Pectenzodarion unicum*** **n. gen. n. sp.** (Zodariidae), ♂; 36) dorsal aspect of the posterior part of the prosoma (the peltidium); 37) ventral aspect of the right tibia I. The arrow points to the apical comb. Hairs are not drawn; 38) retrolateral and slightly distal aspect of the right pedipalpus. Only few hairs are drawn. - R = retrobasal outgrowth of the cymbium, V = ventral tibial apophysis. Scales: 0.1 mm in fig. 36), 0.2 mm in the remaining figs.

BEITR. ARANEOL., 18 (2025: 91–93)

SHORT NOTE ON A FOSSIL BEETLE IN EOCENE BALTIC AMBER BEARING A PHORETIC AS WELL AS TWO PARASITIC ARACHNIDA (COLEOPTERA: ELATERIDAE; ARANEAE: THERIDIIDAE AND ACARI: ERYTHRAEIDAE)

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Abstract: A fossil spider (Araneae: Theridiidae) in Eocene Baltic amber attached to a beetle (Coleoptera: Elateridae) is regarded as an accidental case of phoresy. The same beetle bears furthermore two parasitic sucking mites (Acari: Erythraeidae).

Acknowledgment: I thank very much Jonas Damzen (Lithuania) for recognizing the spider's phoretic behaviour ("probable phoresy"), for having taken the photos of it and for sending the piece of amber which contains this peculiar case of "frozen behaviour" to me.

Material: A piece of Eocene Baltic amber, 2.5 x 2.0 x 1.5 cm, including numerous inclusions (det. by me) like a beetle (Coleoptera: Elateridae indet.) which bears a juv. spider (Araneae: Theridiidae indet.) and two tiny juv. mites (Acari: Erythraeidae indet.) (see below), F3928/BB/CJW. - The piece is still kept in my private collection and will most probably be given to the Palaeontological Institute of the University of Hamburg (Ulrich Kotthoff).

Preservation: The animals are preserved in a mainly clear piece of amber which was apparently slightly heated. The beetle and the attached arachnids are completely and well preserved near the margin of the piece of amber; the left side of the beetle is covered with a thin layer of a white emulsion.

Syninclusions are a juv. Araneae: ?Theridiidae, some not parasitic Acari of several families, 1 larger Diptera: Brachycera, 2 Collembola, 1 Thysanoptera, 1 ?Coccina, some tiny stellate plant hairs and detritus.

The four treated inclusions, photo 20-21

Note: Fossil members of the three arthropod taxa in Baltic amber are not rare.

Measurements (in mm): The beetle: Body length 8.0; the spider: Body length 0.85; prosomal length 0.4, femur I 0.43; the mites: Body length 0.2 and 0.25.

The juvenile mites are preserved closely together anteriorly-retrolaterally on the left elytron of the beetle, apparently at a soft area below the elytron. They apparently possess three pairs of legs (some are hidden) which are not very long and stretched sidewards-backwards. The bodies of the mites stand strongly out from the beetle's body; their mouth parts are hidden on the surface of the beetle. Because of the mites' position of body, mouth parts and legs it seems quite likely to me that they were preserved during the process of sucking blood from the beetle. In contrast to the present specimens the position of the body of phoretic mites is closer to the surface of their carrier, not standing out.
Ten fossil Acari parasitizing spiders in Eocene Baltic amber were briefly treated by WUNDERLICH (2004: 117-119, 555-559, photos 589-601 and 602-603 questionable), see also WUNDERLICH (2002). I observed only a dozen parasitic mites on fossil spiders among more than 100 000 specimens in Baltic amber.

The juvenile and apparently female spider possesses few thin leg bristles on tibiae and patellae and a short clypeus; it is directly placed with its ventral side on the left side of the beetle's head, attached at the cuticula by its left anterior and the right posterior legs; two legs are distinctly raised. Spider threads are absent. Because of the position of the spider's body and two legs attached to the beetle's body I suppose a phoretic behaviour of the spider.
In contrast to most winged insects arachnids like spiders are not able to fly actively; they need a different way for spreading. Phoresy (“hitchhiking” behaviour) of certain arthropods - arachnids like mites and pseudoscorpions or a transport by harvestmen -, is well-known, in fossil members, too. It is a usual behaviour of spreading in these wingless arthropods. In contrast to these animals spiders use quite a different innovation: Many members use threads, originating from their spinnerets, for spreading as aeronautics through the air. This is an active act (secretion of silk in a suitable free position) as well as a passive act (transport by wind).
Because of the existence of aeronautic behaviour spiders do not need phoretic behaviour for spreading, and it is only very rarely reported. Therefore I regard the present transport of a spider by a beetle to be nothing else than a rare accident. The passive transport of a fossil spider (family Comaromidae) by a beetle (family Staphylinidae) in Baltic amber may well be an accident, too; see WUNDERLICH (2004: 180, 554, photos 587-588).

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(See also the next paper in this vol. on a fossil parasitic mite).

WUNDERLICH, J. (2002): Ant mimicry by spiders and spider-mite interactions preserved in Baltic amber (Arachnida: Acari, Araneae). - In TOFT & SCHARFF (ed.): European Arachnology 2000: 355-358.

-- (2004: 115-126): Parasites, parasitoids and other enemies. In: Fossil spiders in amber and copal. Conclusions, revisions, new taxa and family diagnoses of fossil and extant taxa. -- Beitr. Araneol., 3 (A, B).

BEITR. ARANEOL., 18 (2025: 94–95)

BRIEF NOTE ON A PARASITIC FOSSIL MITE (ACARI) SUCKING ON A SPIDER (ARANEAE: ?INSECUTORIDAE) IN EOCENE BALTIC AMBER

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Abstract: A brief note is provided on a parasitic fossil mite (Acari: ?Erythraeidae) in Eocene Baltic amber sucking on the opisthosoma of a spider (Araneae: ?Insecutoridae).

Ten fossil Acari paratizing spiders in Eocene Baltic amber were briefly treated by WUNDERLICH (2004: 117-119, 555-558, photos 589-601 and 602-603 questionable), see also WUNDERLICH (2002). In this paper I treat a further pair of such arthropods, see photo 22, which has to be studied more closely in the future.

Material: The piece of Baltic amber, F2421/BB/CJW, is still kept in my private collection and will most probably be given to the Palaeontology of the University of Hamburg (Ulrich Kotthoff).

The arachnid pair is preserved in a 36x23x5 mm large piece of Baltic amber. - Syninclusions are 5 Diptera, remains of a tiny arthropod indet. and several tiny stellate plant hairs.
Both animals are completely and well preserved, both ventral sides are covered with a white emulsion, the ventral side of the spider is partly covered by two air bubbles.

The juvenile female Araneae:
Measurements (in mm): Body length 2.8; prosoma: Length: 1.5, width 1.2; opisthosomal length ca. 2.0; femur I 1.0, femur IV 1.3.
Colour of prosoma and legs medium brown, opisthosoma grey.
Prosoma: 8 eyes in two fairly wide rows, posterior row slightly procurved, thoracic fissure long, feathery hairs absent, clypeus short, basal cheliceral articles rather large. - Legs robust, feathery hairs and calamistrum absent, order IV/I/II/III, bearing numerous long bristles,

tibia I and metatarsus I with 2 pairs of ventral bristles close to their articles, metatarsi and tarsi bear long trichobothria, unpaired tarsal claw existing, paired claws with long teeth. - Opisthosoma with short hairs and fairly short spinnerets which are partly hidden. - Relationship: Mainly according to the existence of an unpaired tarsal claw, several tarsal and metatarsal trichobothria, the short spinnerets and the position of the eyes I regard the spider as a possible member of the extinct family Insecutoridae.

The inadult indet. Acari:
Measurements (in mm): Body length ca. 0.22, leg IV ca. 0.34.
Colour grey, hairs of body and legs of medium length, leg IV longest, leg I apparently quite short. - The mite, probably a member of the family Erythraeidae, is placed on the anterior dorsal side of the spider's opisthosoma, the posterior 4 of its 6 legs are stretched backwards, its mouth parts are partly hidden, the opisthosoma is thick. The mite was preserved during sucking at the spider's opisthosoma.

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-- (2004: 115-126): Parasites, parasitoids and other enemies. In: Fossil spiders in amber and copal. Conclusions, revisions, new taxa and family diagnoses of fossil and extant taxa. -- Beitr. Araneol., 3 (A, B).

BEITR. ARANEOL., 18 (2025: 96–100)

A FEMALE FOSSIL SPIDER GUARDING HER EGGS AND OFFSPRING IN CRETACEOUS KACHIN AMBER FROM MYANMAR (ARACHNIDA: ARANEAE: PARVOSEGESTRIIDAE)

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Abstract: A fossil female spider (Araneae) of the family Parvosegestriidae WUNDERLICH 2020 (genus *Parvosegestria*) guarding her clutch of eggs and offspring is reported from Cretaceous Kachin amber of Myanmar - a quite rare document of palaeobehaviour. Notes are provides on the brood care behaviour of few other arthopods in Cretaceous Kachin amber.

Material: Fossils in Mid Cretaceous Kachin amber from Myanmar (Kachin Prov.): (1) *Parvosegestria* sp. indet., 1♀ as well as half a dozen eggs and half a dozen offspring in a single piece of F3940/KA/CJW; (2) ?Diplopoda indet., “cocoon”, F3941/KA/CJW.

Determination and remarks: Mainly because of the number and the shape of the cheliceral teeth, the long and slender pedipalpal tarsus (fig. 2), the position of the eyes (fig. 1), the body size and the chaetotaxy I suppose that the present female is a member of the family Parvosegestriidae WUNDERLICH 2020: 75 and of the genus *Parvosgestria* WUNDERLICH 2015: 131 which is not very rare in Kachin amber on species and male specimens level. At least in most males of this genus a dorsal opisthosomal scutum exists which is absent in the present female. - The present specimen is one of the quite rare females of *Parvosegestria*. The female F3505/BU/CJW in the sense of WUNDERLICH (2020: 76, under *Parvosegestria* sp. indet.): Compared with other congeneric species the body length of 3.9 mm is very high, see the female described below.

Preservation, syninclusions and notes (photos 23-24): The specimens are fairly well preserved near the margin of a clear, 2 1/2 cm long and fairly flat piece of amber, enclosed by a long layer within remains of two almost tube-shaped layers which are almost as long as the piece of the amber. - The female spider: Its body is deformed, a larger bubble of decomposing gas originates apparently at the posterior end of the prosoma, the legs are preserved in an unnatural position (all preserved legs are directed forwards), the left legs III and IV are lost after the coxa by autotomy, the left leg I is loosely preserved ca. 2 mm right of the spider's body, the tip of its tarsus is lost, the right pedipalpus is broken off through the tibia and the terminal part is lost. - The clutch of eggs and hatching offspring is preserved below the prosoma, partly right below the female's body, and partly between the right legs I and II and the body. The clutch is preserved in almost a single level and not held together by threads; questionable remains of a sticky fluid between some eggs and offspring exist. Most offspring are strongly deformed and more or less covered with an emulsion or their egg cover.

The position of a loose leg of the spider right to the spider's body as well as the position of the clutch (photo) right below the spider's body – in the same direction (!) - indicate that a flow of resin moved clump and leg about two mm right of the spider. The flows of resin may well have been part of drops from a tree's bark transporting the inclusions downwards. The secretion of resin was probably the tree's reaction to an injuring event, and the spider's body is damaged, too. The existence of decomposing gas out of the spider's body may indicate that the female was captured alive by the resin, lost here one leg, and still held the clutch of eggs and offspring with the help of her legs.

Descriptions

The female spider (figs. 1-3), photo 23-24

Measurements (in mm): Body length 2.0; prosoma: Length 0.9, width ca. 0.7; opisthosomal length ca. 1.0; loose leg I: Femur ca. 1.2, patella 0.24, tibia 1.4; femur IV: Length 0.8, height 0.28; fang 0.2; pedipalpus: tibia ca. 0.23, tarsus ca. 0.38.
Prosoma (fig. 1) dark brown, bearing short dorsal hairs, 6 eyes in a wide field, posterior median eyes close together, posterior row procurved, clypeus short, basal cheliceral articles large and strongly protruding, distally strongly diverging, bearing two strong teeth as well as medially several strong and long hairs. Mouth parts and sternum hidden. - Pedipalpus (fig. 2) with slender articles, tarsal claw existing. - Legs (photo) in an unnatural position, fairly slender, order I/II/IV/III, scopulae, claw tufts and metatarsal preening combs absent, femur IV distinctly thickened, unpaired tarsal claw existing, position of the metatarsal trichobothrium unknown. Bristles difficult to recognize, most femora dorsally 2 but only 1 on femur I, tibia I ventrally at least 2 pairs, metatarsus I ventrally at least 1 pair. - Opisthosoma (photo) deformed, oval, soft, bearing short hairs.

The clutch (or lump) of eggs and offspring (fig. 3, photos 23-24)

The eggs are oval, smooth and light grey, their size is ca. 0.2 x 0.13 mm, the deformed offspring including legs are 0.2–0.3 mm long. Most offspring are only partly free from their cover, light grey, their legs are strongly bent but not stretched.

Discussion, behaviour, ecology

The extinct family Parvosegestriidae is closely related to the family Segestriidae (Cretaceous to extant) whose extant members live in tubes constructed in the ground, under stones or under the bark of trees. In ancient spider families - like Pholcidae, Scytodidae and Segestriidae -, females do not construct a protecting egg sac (cocoon). Members of certain ancient families like Pholcidae and Scytotidae carry their clutch of eggs and offsprings - bound loosely by silk - under their prosoma with the help of their chelicerae. In some other ancient taxa, like in extant Segestriidae, the clutch is fixed by the female to a substrate within the margin of its tube; to my knowledge the clutch is not carried by the mother. The behaviour of members of Cretaceous spiders is unknown. Did the present female actually transport her eggs and hatching offspring - but did not fix them at a substrate? The position of the specimens in question within the amber (the spider holding the clump as well as the special flood of resin, see the paragraph “preservation and syninclusions” above) indicates that the female really carried her clutch. This kind of behaviour may be an old (“primitive”) behaviour of the Cretaceous Parvosegestriidae (as well as of several other spider families, see above), whereas fixing the clutch by extant members of the related family Segestriidae (and other families like Dysderidae) may be regarded as a derived behaviour. Furthermore the “primitive” transporting behaviour may be a diagnostic character of the family Parvosegestriidae, absent in related (extant) Segestriidae.

Finally the present piece of amber and its inclusions document something about the life style of the Parvosegestriidae: at least some members of this extinct family lived on the bark of trees and constructed most probably their silken tubes under bark.

Notes: A protecting carrying of eggs rsp. offspring by their mother evolved convergently in very few advanced families of the RTA-clade, in which an egg sac (cocoon) exists, e. g., in the family Pisauridae (with the help of the chelicerae) and in the family Lycosidae (transported on the back of the opisthosoma). - A fossil female of the family Synotaxidae (superfamily Araneoidea), holding her lump of offspring with the help of her legs (threads of silk are absent) is preserved in Eocene Baltic amber, see WUNDERLICH (2004: 83 and photo 522 p. 532). - Brood care behaviour in Cretaceous Kachin amber has also been reported from spiders (Araneae) of the extinct family Lagonomegopidae. - A questionable brood care behaviour is preserved in a flat “cocoon”, diameter 6-7 mm, in Kachin amber (photos 25-26). The cocoon-shaped molting chamber – or brood chamber? – of a questionable Diplopoda is cut off on two sides, mainly leg articles are observable. A scan study of the object is needed. Brood care is rare in extant Diplopoda; it is known, e. g., from *Polyzenium germanicum.* A fossil report of this behaviour is completely unknown to me.

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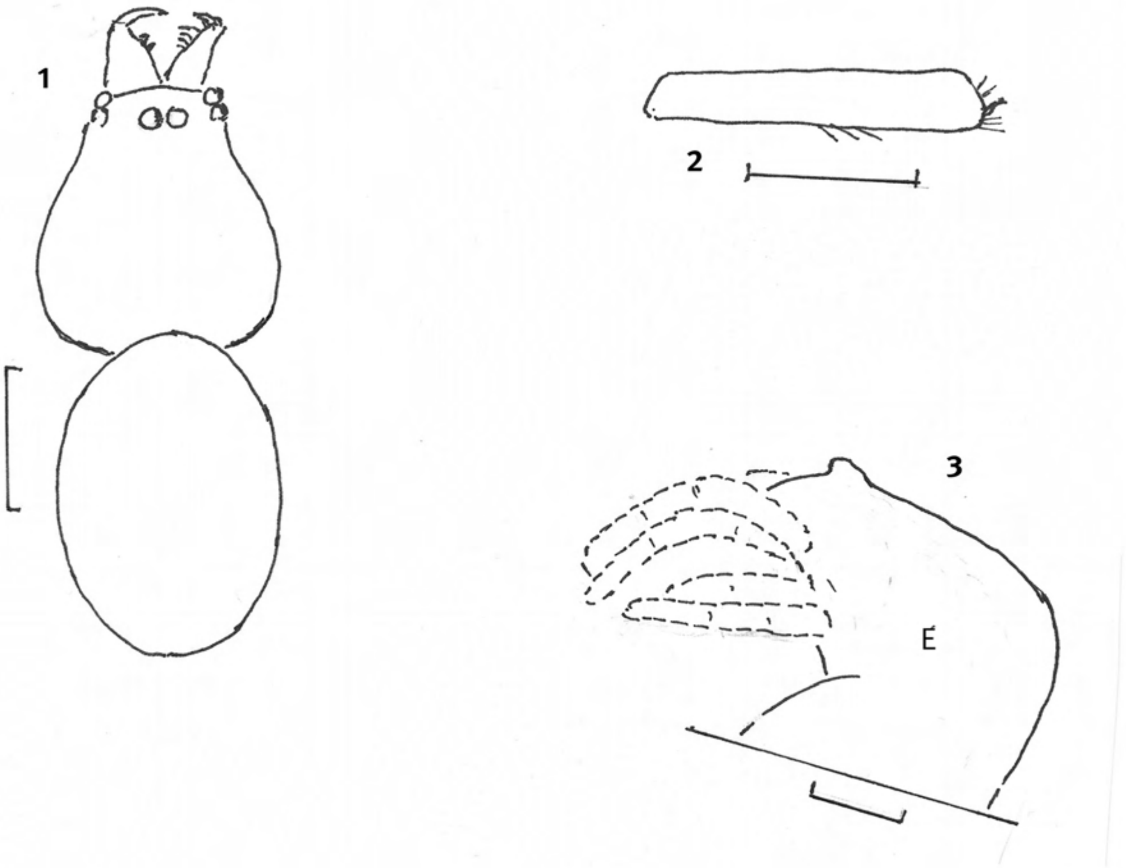
-- & MÜLLER, P. (2020): New and already described fossil spiders (Araneae) of 20 families in Mid Cretaceous Burmese amber with notes on spider phylogeny, evolution and classification. -- Beitr. Araneol., 13: 22-164



Figs. 1-3: ***Parvosegestria*** sp. indet. (Parvosegestriidae) in Cretaceous Kachin amber from Myanmar.

Figs. 1-2: Female. 1) Dorsal aspect of the body; 2) Retrolateral aspect of the tarsus of the left pedipalpus. - Scale = 0.5 and 0.2 mm;

fig. 3) Remains of an offspring, part, outline, lateral aspect. The legs are covered with an emulsion. - E = egg cover. Scale = 0.1 mm.

BEITR. ARANEOL., 18 (2025: 101–105)

NEW FOSSIL SPIDER (ARANEAE) TAXA IN CRETACEOUS KACHIN (BURMESE) AMBER FROM MYANMAR AND NOTES ON FOSSIL NEMATODA

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Abstract: The follwing species are described from Mid Cretaceous Kachin amber from Myanmar (Burma): Eopsilodercidae: *Eopsiloderces* sp. indet, Leptonetidae: *Palaeoleptoneta* sp. indet., *Furczarqua incerta* **n. gen. n. sp**. (Zarqaraneidae). As syninclusions of *Eopsiloderces* rsp. *Palaeoleptoneta* two species of Nematoda indet. are shortly described.

Key words: Araneae, Eopsilodercidae, Leptonetidae, Nematoda, Zarqaraneidae.

I got a part of the material during my visit of Myanmar in the year 2013.

See also above, the paper on the Archaeoid branch.

Notes on fossil Annelida in amber: See WUNDERLICH (2023: 189).

Family LEPTONETIDAE

Palaeoleptoneta sp. indet. (photo 29)

Material: 1♂ in Mid/Upper Cretaceous amber from Myanmar (Burma), F3922/BU/CJW.

Preservation: The spider is badly, incompletely and deformed preserved in a mainly clear piece of amber, the left leg IV is broken off beyond the end of the femur and loose within the amber, both pedipalpi are loose and badly preserved, broken off beyond their coxae. Its body is 1.5 mm long, femur I is 0.9 mm long. The pedipalpi are strongly deformed, the cymbium bears a well developed spine.

Syninclusions are numerous. Of most interest is the part of the body of a specimen of the **Nematoda** near the male of *Plaeoleptoneta* sp. indet. (photo), body length 0.7 mm, width ca. 0.03 mm. It possesses about 70 short “segments” similar to Annelida, their cross section is almost circular; the specimen has been injured near the middle, has been ribbed off at one end, and is narrowed and pointed at the other end. - Further syninclusions are parts of a strong spider leg (mainly the tibia), which bear long and strong bristles, few Acari, 2 Coleoptera, 1 Diptera, parts of questionable Hymenoptera, remains of Blattaria, 1 Myriapoda, insect excrements and particles of detritus.

Close **relationships** are unknown to me.

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

Family EOPSILODERCIDAE

Eopsiloderces sp. indet., photo 28

Material: 1♂ 1♀ in Mid Cretaceous Kachin amber from Myanmar (Burma) F3923/BU/CJW; see also the syninclusions.

The couple of spiders (photos) is strongly deformed preserved in a flattened partly clear yellow-orange piece of amber, the male is complete, some leg articles of the female are missing. The female sex of this family was unknown. Measurements (♂/♀ in mm): Body length ca. 2.0/2.2, tibia I 1.6/1.4. The cymbium of the strongly deformed ♂-pedipalpus bears a strong bristle, the female genital area is strongly deformed.

Syninclusions are: remains of at least one further spider species, probably also Eopsilodercidae:
(1) A *very* long, thin and bristle-less leg (photo), laying quite near the couple of *Eopsiloderces* sp. indet.; measurements (in mm): Femur 5.0 (diameter in the middle 08 <!>), patella 0.3, tibia 4.2, metatarsus 2.6, tarsus: only the basal 1.5 mms are preserved.
(2) Preserved at the margin of the piece of amber above the male *Eopsiloderces* sp. indet. the tarsus and a part of a bristle-less metatarsus (diameter ca. 0.02 mm), a slender and stronly deformed opisthosoma - only almost 0.8 mm of its length is preserved - with long anterior spinnerets, two small chelicerae with teeth on the anterior margin as well as parts of two small ♂-pedipalpi which bear simple small bulbi and a slender straight embolus. - I do not want to exclude - but I can hardly imagine - that these very small spider remains belong to the long-legged specimen (1) described above.
Further syninclusions are parts of some large leaves in few wide layers as well above and below of it several animals: Some Acari, 1 Diptera, 1 Aphidoidea, 1 Psocoptera, 2 questionable Auchenorrhyncha, a questionable seed and remains of a Collembola.
The most interesting syninclusion is the part of a **Nematoda** (fig. 1) similar to an Annelida. It is preserved near the couple of *Eopsiloderces* sp. indet. and is ca. 5 mm long and 0.03 to 0.05 mm wide. The ca 150 “segments” bear tiny hairs; I found no bristles. Its wider end is broken off and shows a circular cross section. Its other end is narrowed and shrunk; probably it has been dried out or it is a regenerate. - See the “annelid” specimen published by WUNDERLICH (2023: 189, photo 46 p. 2409) which actually also is a Nematoda, according to C. Ereseus and R. Schmelz.
The wide layers of leaves as well as the partly dissected or decomposed arthropod bodies indicate that the inclusions were trapped at the bottom of the forest but not on or below the bark of a tree.

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

Family ZARQARANEIDAE

To my knowledge the extinct Cretaceous family Zarqaraneidae is the most diverse spider family on genus, species and specimen level in Kachin (Burmese) amber from Myanmar, see WUNDERLICH (2018). Here I describe a further new taxon:

Furczarqa **n. gen.**

Etymology: The name refers (a) to the furcate distal apophsis of the tegulum, from lat. furca, and (b) to the first part of the family name Zarqaraneidae.

The gender of the name is feminine.

Type species (by monotypy): *Furczarqa incerta* n. sp.

Diagnostic characters (♂; ♀ unknown): Sequence of the dorsal tibial bristles 2/2/1/2, metatarsal bristles absent, tibia I slender; pedipalpus (fig. 2): Paracymbium quite long, slender and slightly bent, tegulum apically with a long, slender and divided apophysis, and with a slender, strongly bent apophysis in a more basal position, embolus unknown.
Further characters: Prosomal length 0.58 mm, clypeus of medium length, legs not annulated.

Close **relationships** are unknown. In *Alteraraneus* WUNDERLICH 2018 chaetotaxy and body length are quite similar but the tibiae are annulated, the shape of the long paracymbium is different and a furcate tegular apophysis is absent.

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

Furczarqa incerta **n. gen. n. sp**. (fig. 2), photo 27

Etymology: The name of the species refers to its uncertain (lat. incertus) taxonomical position.

Material: Holotype (♂) in Upper (Mid) Cretaceous Kachin amber from Myanmar (Burma), F3924/BU/CJW.

Preservation and syninclusion: The spider is completely preserved in a flat and partly clear yellowish piece of amber. - Syninclusions are numerous small air bubbles, few tiny plant hairs and particles of detritus.

Diagnostic characters and distribution: See above.

Description (♂):
Measurements (in mm): Body length 1.1; prosoma: Length 0.58, width 0.47; opisthosoma: Length 0.7, width 0.45; leg I: Femur 0.73, patella 0.24, tibia 0.5, tarsus 0.3.
Colour: Prosoma and legs medium brown, legs not annulated, opisthosoma medium grey.
Prosoma (photo) 1.23 times longer than wide, bearing few dorsal hairs of medium length, fovea well developed, 8 large eyes which bear emulsions, posterior row slightly procurved, posterior median eyes widely spaced, clypeus fairly short, basal cheliceral articles and fangs of medium length, anterior margin of the fang furrow with few teeth. - Legs (photo) only fairly

long, order I/II/IV/III, tibia I not thickened, hairs short, bristles long, existing on femora to tibiae, femora with few dorsal bristles (some may be rubbed off), I with 1 dorsal and 1 prolateral bristle, the left femur IV bears 2 dorsal bristles in the basal half, patellae dorsally 1/1 bristles, sequence of the dorsal tibial bristles 2/2/1/2, tibia I additionally with 1 long prolateral bristle in the middle and with apical bristles. - Opisthosoma oval, 1.55 times longer than wide, slightly flattened, bearing longer hairs and two or three pairs of sigillae; three pairs of short spinnerets. - Pedipalpus (fig. 2, see above): Tibia and patella without bristles, patella slender, cymbium with long hairs.

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-- (2018): Fossil spiders (Araneae) in Cretaceous Burmese amber. -- Beitr. Araneol., 11: 1-177.

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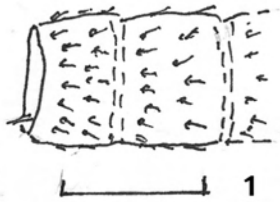

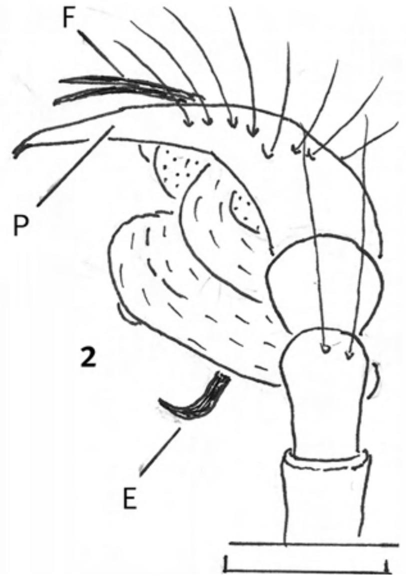

Fig. 1) **Nematoda indet.** with *Eopsiloderces* sp. indet., F3923, broken off at the end (left). Note: The position and the number of the tiny hairs are not exactly drawn. Scale: 0.05 mm;

fig. 2) ***Furczarqa incerta*** **n. gen. n. sp.**, ♂, dorsal-basal aspect of the left pedipalpus. Not all hairs are drawn. - E = embolus, F = furcate tegular apophysis, P = paracymbium. Scale: 0.1 mm.

BEITR. ARANEOL., 18 (2025: 106–110)

FOSSIL SPIDERS IN EOCENE FUSHUN AMBER FROM CHINA (ARANEAE: PALPIMANIDAE, THERIDIIDAE AND *SINODICTYNA* HONG YOUCHONG 1982)

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Abstract: Two fossil spiders (Araneae) in Lower Eocene amber from Fushun (Liaoning, China) are described: *Fushunpalpimanus exuviae* n. gen. n. sp. (Palpimanidae) and Theridiidae indet. A note is given on *Sinodictyna* HONG YOUCHONG 1982, erroneously described as a member of the family Dictynidae. It is regarded by me as a genus of an unsure family of the branch “Dionycha” but surely not a member of the Dictynidae.

Acknowledgement: I thank JASON DUNLOP very much for sending me papers on fossil spiders of China.

Material: I bought the two pieces of Fushun amber referred to here – see directly below - in 1985 from a German dealer who bought them from a Chinese dealer. The two pieces are still kept in my private collection (CJW and will most probably be given later to the Palaeontological Institute of the University of Hamburg (Ulrich Kotthoff).

Only a single fossil spider species has yet been described in Lower Fushun amber, see below. In this paper I describe two further taxa in the same kind of amber which is 50-53 million years old, from China, Liaoning Province, north of Fushun City, see BO WANG et al. (2014).

Family PALPIMANIDAE

These free-living ground spiders feed usually on spiders. Their anterior legs are powerful, their basal cheliceral articles bear "peg teeth" and their fangs are stout. Extant members of this family are very rarely reported from China and from whole South Asia.

Fushunpalpimanus **n. gen.** (figs. 1-3), photo 30

Etymology: The name of the genus refers (1) to the deposit near the city of Fushun in China and (2) to its membership of the family Palpimanidae.

The gender of the name is masculine.

Type species (by monotypy): *Fushunpalpimanus exuviae* n. sp.

Diagnostic characters (female exuvia): Prosoma (peltidium) (figs. 1-3) quite long and low, not granulate, fovea probably absent, 8 large and circular eyes in 2 rows, posterior row straight, anterior median eyes largest, legs (fig. 3, photo) bearing long and partly strong hairs, patellae fairly short, at least tarsi I-III bear a dense claw tuft (the tip of both tarsi IV is cut off).

Relationships: Mainly according to position and size of the eyes, e. g., the contiguous lateral eyes, I regard the new genus most likely to be a member of the subfamily Chediminae. In the extant genus *Sarascelis* SIMON 1887 from South Asia and the tropical Africa the shape of the prosoma (peltidium) is quite different, shorter and higher, and to my knowledge long hairs of the legs are absent.

Distribution: Lower Eocene of Fushun, Liaoning, China.

***Fushunpalpimanus exuviae* n. gen. n. sp**. (figs. 1-3), photo 30

Etymology: The species name refers to the holotype which is preserved as an exuvia.

Material: Holotype ♀ exuviae in Lower Eocene Fushun amber (see above), F3910/FU/ CJW.

Preservation and syninclusions: The exuviae is incompletely and in a deformed state preserved in a 1.5 cm long orange-brown and clear piece of amber. A drilling runs completely through the piece of amber and through articles of both posterior legs, cut off are parts of both anterior legs, the tips of the left leg III, of the right leg II and of both posterior legs; the peltidium is placed right below the sternum, crumpled remains of the opisthosoma are placed posteriorly below the peltidium. - Syninclusions are particles of detritus and remains of a questionable plant (moss?) at one end of the drilling.

Diagnostic characters: See the new genus.

Description (female exuviae):
Measurements (in mm) Body length probably about 6 mm; peltidium: Length 3.0, width 2.0, height 0.55; length of the deformed sternum 1.5; length of the strongly deformed leg IV ca. 8 mm; pedipalpus: Tibia and tarsus each ca. 0.8.
Colour of peltidium and legs light to medium brown, remains of the opisthosoma medium grey.
Prosoma (figs. 1-3, photo) quite long/slender and low, 1.33 times longer than wide, smooth (not granuate), anteriorly relatively wide, fovea apparently absent, 8 large and circular eyes in two rows, posterior row straight, anterior medians largest, basal cheliceral articles deformed, peg teeth existing, fangs stout, gnathocoxae long, labium a free sclerite, sternum long, coxae IV close together, - Pedipalpus long, slender and hairy, tarsal claw apparently absent.- Legs (fig. 3) long, bearing long hairs, order IV/III?/II/III, trochanter I elongated, femur I distinctly thickened, patellae relatively short, metatarsi and tarsi about equal in length, spatulate hairs absent (legs I are only partly existing), bristles absent, claw tufts – at least on I-III - quite dense. - The crumpled remains of the opisthosoma bear short hairs.

Relationships and distribution: See above.

Family THERIDIIDAE: Theridiidae indet. (photo 31)

Material: ?ad. ♀ in Eocene Fushun amber, F3911/FU/CJW.

Preservation and syninclusions: The spider is incompletely in a strongly deformed state preserved in a clear light brown piece of amber which is 0.9 mm long; most leg articles are lost or cut off.

Description (?ad. ♀): Body and legs light brown, legs probably annulated. - Measurements (in mm): Body length ca. 2.2, prosomal length 1.0, opisthosoma: Length ca. 1.4, width 1.3, leg I ca. 4.6, femur II ca. 1.1; prosoma high, 8 eyes in 2 rows, opisthosoma strongly deformed, almost globular; legs long and slender, I longest, hairs short, bristles thin and fairly long, existing on patellae and tibiae, dorsally probably 2/2/2/2 each, position of the metatarsal trichobothrium probably in ca. 0.13.

Relationships: According to the existence of an unpaired tarsal claw, 8 eyes, a globular opisthosoma and the chaetotaxy I regard the species as a member of the family Theridiidae.

Note on *Sinodictyna fushunensis* HONG YOUCHONG 1982

The species is based on a probably adult female, its eyes are unknown, the leg bristles are numerous. It was regarded as a probable or even sure member of the family Dictynidae although neither a cribellum nor a calamistrum nor an unpaired tarsal claw were reported which are typical patterns of the Dictynidae. I regard the taxon as a member of an unsure family of the branch “Dionycha” but surely not of the Dictynidae.

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BO WANG et al. (2014): A Diverse Paleobiota in Early Eocene Fushun Amber from China. -- Current Biology, 24: 1606-1610.

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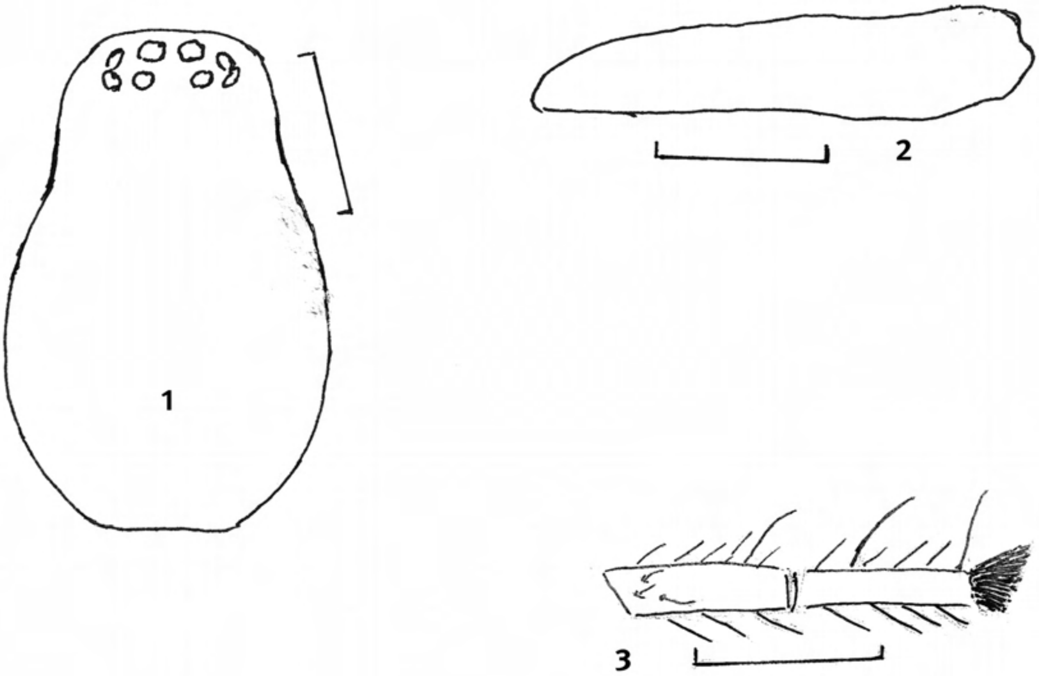

Figs. 1-3: *Fushunpalpimanus exuviae* n. gen. n. sp., exuviae; 1-2) dorsal and lateral aspect of the peltidium; 3) prodistal aspect of the left metatarsus and tarsus II. Not all hairs are drawn. - Scales: 1.0 mm in figs. 1-2, 0.5 mm in fig. 3).

BEITR. ARANEOL., 18 (2025: 111)

NOTE ON THE MESOZOIC SPIDER (ARANEAE) GENUS *CRETADROMUS* CHENG ET AL. 2009 IN STONE FROM LIAONING, CHINA, ERRONEOUSLY DESCRIBED AS A MEMBER OF THE FAMILY PHILODROMIDAE

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Abstract: The mesozoic spider (Araneae) taxon *Cretadromus liaoningensis* CHENG et al. 2009 from China, erroneously described as a member of the Philodromidae, is regarded as a probable member of an unsure family of the branch “Dionycha” but surely not a member of the Philodromidae.

Cretadromus liaoningensis CHENG et al. 2009 has been described from the Late Jurassic – Early Cretaceous Yixian formation of the Liaoning Province in China. It is based on a single probably adult female, body length about 5 mm; its legs are covered with setae, bristles are not mentioned, an unpaired claw is said to be absent; “metatarsi and tarsi with dense setae” may indicate the existence of scopulae. - According to the absence of leg bristles, the equal size of the eyes and the unknown report of mesozoic Philodromidae I exclude that *Cretadromus* belongs to the family Philodromidae. It may be a member of an unsure family of the branch “Dionycha”.

Reference

CHENG, X.-D. et al. (2009): A New Fossil Spider of the Philodromidae from the Yixian Formation of Western Liaoning Province, China (Arachnida, Araneae). -- Acta Arachnologica Sinica, 18 (1): 23-27.

BEITR. ARANEOL., 18 (2025: 112–114)

NOTES ON THREE FUNDAMENTAL HYPOTHESES OF SPIDER (ARANEAE) PHYLOGENY

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Abstract: Three fundamental hypotheses of spider (Aranae) phylogeny are treated: (1) the loss of a “tail” (pygidium, flagellum) by extinct spiders; (2) the origin of a special spinning organ, the cribellum and (3) the origin of a unique kind of capture webs, the orb web.

Key words: Araneae, capture web, Chimerarachne, Chimerarachnida, Cribellatae, cribellum, fossils, Mesothelae, Mesothelida, Mygalomorpha, orb web, phylogeny, “tail” (flagellum, pygidium), spider.

After a long and intensive study of extant and fossil spiders I summarize my ideas regarding difficult questions on spider phylogeny the answers of which have been discussed controversially for several decades. I dare to formulate in short three hypotheses:

(1) The “tail” (pygidium, flagellum) of archaic spiders was probably lost *two* times: (a) by the ancestor of Mesothelae + Mygalomorpha and (b) - a bit later? - by the ancestor of the Cribellatae in the sense of WUNDERLICH (2024), by a taxon related to the extinct family Chimerarachnidae WUNDERLICH 2019. See WUNDERLICH (2024) and fig. A.

(2) The cribellum originated only *a single* time, see WUNDERLICH (2024) and fig. a.

(3) The orb web originated *two* times*:* (a) by the ancestor of the superfamily Deinopoidea and (b) within (!) the superfamily Araneoidea, in the “branch of araneoid orb web weavers”.

See WUNDERLICH (2020) and fig. B.

Notes: (1): Still a sure apomorphic character of the suborder Mesothelida WUNDERLICH 2024 is searched for. Probably the powerful basal cheliceral articles and the existence of a trap door have to be regarded as apomorphic characters of this suborder (fig. A) instead of basal characters of the Araneae, and Chimerarachnida never possessed a tube and a trap door. - (2) I now prefer the widely used name Araneae but not Araneida.

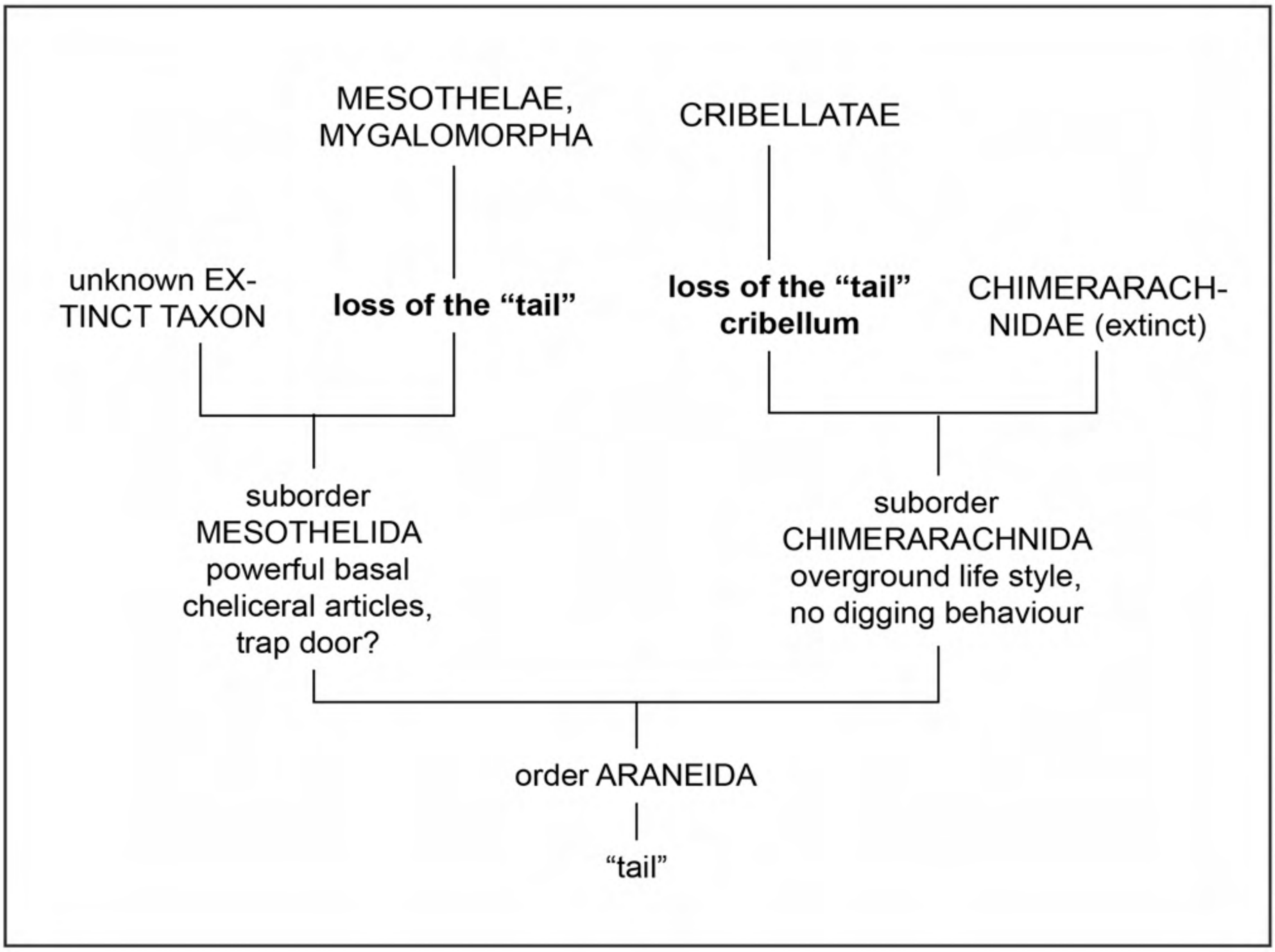

Fig. A. Loss of spider "**tail**" and origin of the **cribellum**, simplified cladogram.

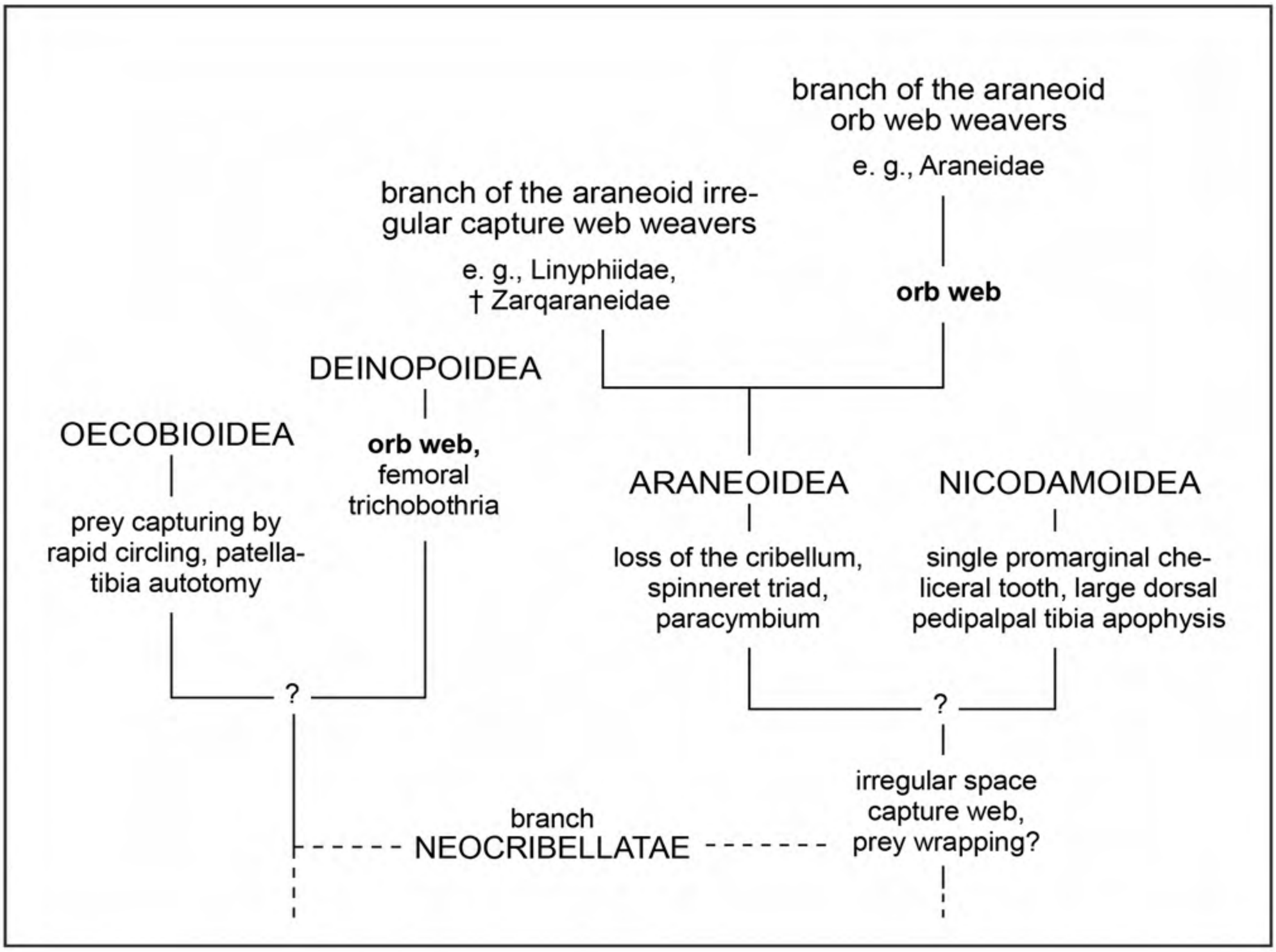

Fig. B. Probably twice origin of the **orb web** within the branch Neocribellatae in the sense of WUNDERLICH (2024), simplified cladogram

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BEITR. ARANEOL., 18 (2025: 115–116)

BRIEF NOTE ON A QUESTIONABLE FOSSIL ARACHNID PRESERVED IN CARBONIFEROUS STONE OF SOUTHERN PORTUGAL (ARACHNIDA: ?TRIGONOTARBIDA)

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Abstract: A badly preserved questionable member of the extinct order Trigonotarbida (Arachnida) is briefly reported in a Carboniferous stone of Southern Portugal.

In April 2025 I collected a 24x15x5 cm large dark brown stone at a stony slope 8 km N Altura in the SE Algarve, Portugal. The piece is kept in my private collection, no. F3925/CJW, and will most probably be given to the Palaeontological Institute of the University of Hamburg (Ulrich Kotthoff).

According to Stefan Rosendahl (pers. commun.) the present stone is Upper Carboniferous, ca. 320 million years old.

On the surface of the dark brown stone a flat and badly preserved conspicuous object is preserved (photo 32). Its dark brown median part – probably part of the body – is 15 mm long and 11 mm wide and surrounded by an irregular light structure, ca. 2 mm wide. From the apparently frontal half originate four pairs of questionable appendages which may be remains of legs and point sidewards. A sure articulation of these structures is not recognizable.

I suppose that this specimen represents remains of a fossil Trigonotarbida, an extinct arachnid order, see DUNLOP & PENNEY (2012: 100-106): Fossil Archnids. This order has previously been reported by CORREIA in 2013 from the Carboniferous of the Iberian Massif in Portugal. Jason Dunlop who saw a photo of the specimen (pers. commun.) was not sure about the determination of the badly preserved object.

BEITR. ARANEOL., 18 (2025: .117–121)

EVOLUTION AND EVOLVOLUTION - PARTS OF A FIFTH DIMENSION OF THE UNIVERSE?

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ABSTRACT: Evolvolution (in a wide and new sense), including the evolution, is provisionally regarded as part of a wide range which one may call the “fifth dimension” of the universe. In a strict sense it is basically represented by *speciation* (of biota), a diversifying process of adaptation by the mutation of selfish genes and by natural selection. Evolvolution induces the phenomena of the most evolved ”Immaterial Derivates” - e. g., psyche, spirit, emotion, cognition, languages and culture - which well may represent a further range.

Acknowledgments: I thank very much Klaus Scheler for exitations and a wide critical discussion, and my wife Ruthild Schöneich for correcting the English text of most parts of the manuscript.

What is the basic structure of the universe and what are its basic elements, levels, dimensions and ranges? Can theories of physics explain all phenomena *of life*? In this paper I provide some ideas, fragments of thought, and hypotheses that may be of general interest.

Elements and the development of the universe, of galaxies, stars, planets, atoms, species, ecosystems, spirit, cognition, emotions (*), technology, information, languages, cultures, etc., are partly well-known phenomena, see, e. g., URSUL & URSUL (2018). *Stable* may be the laws of nature.

Development and change are connected with movement: The result of a "moving" point (dimension 0, "singularity") is a line (dimension 1); the result of a moving line is a surface (dimension 2) (**); the result of a moving surface is a space (dimension 3, a further orthogonal dimension which is connected with volume, mass and energy); the result of a moving space is time (dimension 4, the "Minkowsky space"), the result of moving space-time is *development*. This may be called a further level or "dimension", the *fifth dimension* in the sense of a mathematical abstraction and may probably be regarded as a real phenomenon as well. The last trinity continuum may be called "space-time-changeability" or "space-time-evolveability", a fifth dimension. The term "dimension" is by far not well defined and possesses various meanings. "Carriers" (bases) of the fifth dimension are the lower dimensions. I would like to discriminate four levels (1 to 4) of this range (or "fifth dimension") as well as two sublevels of the evolvolution:

(1) MOVEMENT in the sense of this paper is the most simple state of this range, the "fifth dimensional space": the *moving* of photons, molecules, waves, organisms, stars etc. Moving an (material) object means (similar to the flow of water) the existence in a different locality and point of time as well, *at least quite slightly differing*. So movement is basicly connected with development; its coordinates are time and change. - Movements exist also in higher levels and provide the existence of change and development in these states.

(2) DEVELOPMENTs in my opinion are inherent changes in the direction of the "arrow of time" to "intermediate phases" or "final states" (e. g. "white dwarfs"). It is the "simple" individual development like the ontogeny of organisms as well as the degradation (growing of entropy) of organic as well as of anorganic structures like molecules, stars and galaxies.

(3) EVOLVOLUTION in the wide sense of this paper is the building of *organic* structures by "capturing/fixing/transforming" energy: growth of negentropy, increase of order. I discriminate at least two sublevels:

(a) *EVOLUTION* in the strict sense of this paper. Originally - in ancient times of the earth – self-organizing and self-reproducing *organic* molecules - replicators (RNAs, DNA and metabolistical structures (proteins)) – evolved as "Praebiota", which were later united in *cell-like complexes*, existing in "swarms" - analogous to simple "*populations*" -, so that mutation and selection could already happen. Such organic structures are already able to "*catch and store" energy and to change it to different kinds* like chemical or kinetical energy. I regard these processes to be a kick-off, a "switch point", providing a new sublevel of evolvolution in the wide sense, in which different reproductive complexes in populations – *species* and speciation - evolved. In my opinion this highly evolved sublevel justifies the term

(b) *EVOLVOLUTION* in the strict sense of this paper is basically represented by *speciation* (of biota), a process of adaptation by the mutation of selfish genes and natural selection. The above (under a) mentioned phenomena provide reproductive complexes, existing in populations (of several or numerous individuals) which are called species, and the phenomenon of *diversification* of species is called speciation. Species were the first structures one can call biota (not praebiota); they show special reactions to the environment like *irritability*. *Evol-*

volution is characterized by long-term self-optimizing adaptative processes of species whose emergent ability is limited by the range of their possibilities (1), provided by numerous innovations like the origin of complicated structures, of organs – e. g., special gills in fish - or the colonisation of continents (mainland) with the help of lungs or innovations in spider evolution (2). Evolvolution in the strict sense represents a new level of evolvability which is quite different from simply reproductive molecules and a chemical level – see I. PRIGOGINE -, and are also different from overlapping physical and chemical disciplines but represent *biological* disciplines. - In my opinion processes of evolvolution give rise to a further quite important "switch point", providing the next range or level, of *immaterial phenomena* which I call ...

(4) *IMMATERIAL DERIVATES* (3) of the Evolvolution. Examples are, e. g., conciousness, psyche, spirit, emotion, cognition, technology, languages, culture, and probably the interactions within ecosystems and information, too. These phenomena are not the matter of this paper. This level (4) may very well be regarded to be only a sublevel of level (3) or even as a further – sixth – range ("dimension") of the universe. Compare the concept of memes like catchphrases or melodies, the spreading of ideas from one mind to another, and cultural phenomena, cultural analogies to (biological) genes which even may be "living structures physically (!) residing in the brain,".

According to my hypothesis "dimensions" are always based on lower "dimensions". Therefore artificial conciousness, artificial thinking, artificial emotions etc. of the "dimension 5" should be based on elements of "dimension 4" which includes *proteins* of *living systems*. (Anorganic) computers - "dimension 4" - cannot directly evolve IMMATERIAL DERIVATES like conciousness which is *a matter of "dimension 5"*. Therefore conciousness cannot be digitalized but only simulized, see CHRISTOF KOCH (2019), and "artificial intelligence" is basically completely different from natural - e. g. human - intelligence.

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(1) Two simple examples: The existence of wings of their body provides the ability to fly but never the ability to understand the meaning of e = mc2. The voluminous and highly organized brain of humans provides the understanding of the meaning of e = mc2 but not the ability to fly with the help of parts of their body.

(2) As is well known all spiders (Araneae) possess spinnerets at the end of their opisthosoma in contrast to all remaining arachnids. Furthermore spiders are *tail-less* in contrast to certain arachnids, e. g., scorpions. A "tail" is an ancient character of arachnids which exists not only in scorpions. Not mentioned in the paper by WUNDERLICH (2015) is the surprising recent discovery of true spiders which possess spinnerets *and* a "tail" as well (!). These *extinct* spiders of the genus *Chimerarachne* have been found in 100 million year- old Burmese amber (Burmit) of Myanmar. Their extinct relatives - which possessed spinnerets *and* tails like *Chimerarachne* - are still unknown and must have lived already more than 300 million years ago (the reasons for the predicted high age of these peculiar, ancient and still unknown spiders are not explained here). - All spiders possess opisthosoma's spinnerets near the tail's base of *Chimerarachne*. Why did spiders lose a tail? We can easily imagine that the existence of a tail hinders a wide use of threads by spinnerets for various purposes, and the loss of a tail has well been an adequate and most important adaptation of spiders, without any reversal - a loss as an innovation of spiders.! This is apparently the reason that we find only a single, rare and unusual group of – ancient and extinct – spider in which spinnerets and a tail are known as well: *Chimerarachne*. - *Note*: As the existence of tail-less 300 million year-old fossil spiders demonstrates the loss of a tail of spiders happened already about 300 million years ago – except of the surviving predecessors of *Chimerarachne.*

(3) "Immaterial Derivates" do not at all mean a "domain" or "kingdom" of its own in the sense of R. DESCARTES – see also SHELDRAKE (2021) - but is more like "descendent" (in German "Abkömmling"), and it probably has to be included as (c) in (3), the Evolvolution in a wide sense.

The kinds - of changes/processes - of the ranges 3-4 in the present sense are numerous and much more diverse than the kinds (diversity) of the levels 1-2. These processes of differentiation and inherent self-organisation happen within the *fifth* dimension (***). The term

Evolvolution, introduced by WUNDERLICH (2015), is modified (restricted) here, see above, and has something in common with the terms “Universal/Global Evolution” or “Global Evolutism” in the sense of URSUL & URSUL (2018) and other Russian authors like BAZALUK and URMANTSEV (2009) as well as with the term “Meta-evolution” in the sense of GRINCHENKO (2004); *but the idea of the existence of a further range, the “fifth dimension” is added in this paper* . - See also the “Evolution of Evolvability” on a higher level in the sense of R. DAWKINS and the “unfolding”, e. g., in the sense of SHELDRAKE.

Self-oganization of *synergetic* natural processes are found, e. g., in crystals (simple), RNA and components of proteins, the amino acids, which fold together by themselves (!) and provide the origin of complicated structures. Hierarchical order in the sense of HERMAN HAKEN (1981: e. g., p. 19) is organized by ORGANIZERS (in German “Ordner”), see also LEE SMOLIN (1999). The simple term “LIFE” – according to our present knowledge – may be regarded as a most important material part of the “fifth dimension” in the sense of this paper although a diversity of definitions of the term life exists, see, e. g., the term autopoietic. Changing by mutability is a genetic program of living systems, combined with selection, adaptation and self-optimizing. Probably selection within almost identical elements of a population can work as a “kick off”. Organisms are characterized by temporary negentropy (decrease of entropy, increase of order), providing the increase of complicated structures, the possibility to change kinds of energy, as pointed out above, and speciation.

(*) A part of the Evolvolution in communcation can probably be regarded as tradition.

(**) similar in some respect to a shadow. Such mathematical abstractions demonstrate that a carrier for the dimensions is always needed. Dimensions are frequently characterized by the existence of space and coordinates. A more exact definition of the term “dimension” - and certain other terms - is a matter of the future.

(***) The fifth dimension in the present sense has nothing to do with mathematical abstractions of hidden dimensions or of a fifth dimension in the sense of T. KALUZA or of a “geometrical dimension” or of dimensions of the string theories.

LEE SMOLIN (1999: 348) listed ALBERT EINSTEIN, NIELS BOHR and CHARLES DARWIN as probably being the most important (modern) thinkers about the principles of order of the universe. In my opinion certain names like RICHARD DAWKINS may have to be added to the short list!

Remarkably, even more often the names of physicists than biologists are listed in this matter – but why? Usually important aspects of the universe like “life” and “spirit” are not explicitly included in the view of physics. Self-organization, to give an example, is not restricted to the field of physics (see above), and the system of mutability, selfish genes - see DAWKINS (1976) -, natural selection, adaptation and other phenomena of evolution and evolvolution - as well as its “derivates”, see above -, are typical phenomena of life which exist *all together* in life and are ignored if only an (an-organic) material world is treated. In contrast to the fourth dimension the “fifth dimension of evolvolution” - e. g. (biological) speciation and adaptation, parasitism, symbiosis or the development of ecosystems - contains various *qualitative* processes – like self-organizing and unfolding - which can only hardly be described mathematically because they are *not or only hardly quantificable*; and *accidents* play an important role, too.

Are life, emotions and culture among the latest – or even final? - “hot spots” of the development of the universe?

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BEITR. ARANEOL., 18 (2025: 122–123)

CORRECTIONS

J. WUNDERLICH,
D-69493 Hirschberg; *e-mail*: joergwunderlich@t-online.de.
Website: joergwunderlich.de. - Here a digital version of this paper can be found.

a) Regarding vol. 17 (2024) of the Beitr. Araneol.

p. 14 below has to be eliminated “as well as in females of *Holocnemus caudatus*, see HUBER (2022: 44)”.

p. 15, key no. 2(1) has to be eliminated “♀-chelicerae according to HUBER (2022: 44) without stridulatory files.”.

p. 59 in the middle and p. 61 line 3: The genus name is *Bararaneus* but not *Baltaraneus*.

p. 76 f: I now accept again the widely used name Araneae but not Araneida.

(b) Regarding earlier volumes of the Beitr. Araneol.

Keith Edkins kindly informed me that three names of spider genera described by me turned out to be junior homonyms and in three spider species the epicthets do not agree in gender with feminine names:

- *Longithorax* WUNDERLICH 2017 (Beitr. Araneol., 10: 133) is a junior homonym of *Longithorax* IHIG 1906: 200 (Malacostraca). Herewith I substitute the name *Longithorax* WUNDERLICH 2017 by the **new name** *Longthorax*.

- *Microlinus* WUNDERLICH 2004 (Beitr. Ananeol., 3B: 1799) is a junior homonym of *Microlinus* CASEY 1906: 372 (Coleptera). Herewith I substitute the name *Microlinus* WUNDERLICH 2004 by the **new name** *Microlininus*.

- *Parvispina* WUNDERLICH 2015 (Beitr. Araneol., 9: 192) is a junior homonym of *Parvispina* KORNICKER & IMRIE 1958: 94 (Holothuroidea). Herewith I substitute the name *Parvispina* WUNDERLICH 2015 by the **new name** *Parvispinina*. Furthermore the subfamily name Parvispinae is substitutet by the **new name** Parvispininae.

* *Intermesothele pulcher* WUNDERLICH 2019 (Beitr. Araneol., 12: 20) = *I. pulchra*.

* *Myannemesis glaber* WUNDERLICH 2020 (Beitr. Araneol, 13: 40) = *M. glabra*.

* *Priscaleclercera liber* WUNDERLICH 2020 (Beitr. Araneol, 13: 102) = *P. libera*.

BEITR. ARANEOL., 18 (2025: 124–160)

Spider templates, sexual selection and the risk of zerogamy: a taxonomist’s view

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Running title: Mate check and the zerogamy risk

Abstract

Sexual selection theory is riddled with incongruities and contradictions due to the many ad hoc explanations. It fails to explain the vast range of secondary sexual characters in templates, the intraspecific stasis of these characters, the synchrony of male action in many leks and others. The assumption that the arms race between sexes drives speciation without new ecological adaptations adds to the confusion. Taxonomic observations lead to an alternative interpretation of these poorly understood phenomena. Low average population densities in combination with avoidance of inbreeding, adds to the problem of mate detection and implies the risk of zerogamy. Sexual selection, to use the present terminology, results in markers, linked genetically by pleiotropy to niche compatible behaviour with as a culmination the correct whereabouts in the mating period. The presence of these markers is checked during courtship and mating. Females prefer unrelated males with the right markers.

Mate check of whereabouts behaviour explains vast ranges of secondary sexual organs, intraspecific stability of copulatory organs and synchronous male activity in leks. It does not drive speciation but facilitates it.

Keywords

Araneae, inbreeding, mate check, population density, singletons, whereabouts

Abbreviations

CFC: cryptic female choice

CHC: cuticular hydrocarbon

SAC: sexually antagonistic coevolution

SSC: secondary sexual characters

Introduction

The core of the evolution theory as proposed by Darwin (1859) is genius by its simplicity. Its essence can be summarized in a single sentence: "Small variations are sieved by natural selection which is the result of the struggle for life and survival of the fittest". The appearance of black morphs in the peppered moth (*Biston betularia*) as an implication of changes in tree stem color due to air pollution is a perfect example, as it illustrates how natural selection operates.

How different is the topic of 'sexual selection' invoked by Darwin (1871) to reply to criticisms questioning the development of grotesque forms of sexual dimorphism? The controversy with natural selection that implies parsimony, has provoked an avalanche of papers concerning sexual selection summarized in temporary overviews as those by Anderson (1994) and Eberhard (1985, 1996) and intermediary considerations (Hosken & Stockley 2004), even a project for a metastudy of metastudies on the subject (Pollo *et al.* preview). The rationalizations in this connection are so numerous, so varied and often contradictory, that it has become impossible to explain sexual selection in concise terms as it is for natural selection. The approach of the problems from a human standpoint leading to anthropomorphic explanations (Kokko 2017) has certainly not contributed to such a formulation. The plea of Jones & Ratterman (2009) therefore remains relevant: "… a review of the literature shows that key aspects of sexual selection are still plagued by
confusion and disagreement. Many of these areas are complex and
will require new theory and empirical data for complete resolution."

The present paper shortly highlights the many concepts that are used in the theory of sexual selection, which is mainly the field of ethologists and ecologists, confronts them with views and statements in taxonomy, and investigates a possible alternative.

The concepts of 'sexual selection'

In contrast with that of natural selection, the theory of sexual selection is composed of several concepts: male-male and sperm competition, female choice, cryptic female choice and arms race between the sexes. But before these terms became commonly used and the subjects widely studied, species differences were studied in terms of the so-called 'lock and key' hypothesis.

The ‘Lock and key’ hypothesis

The ‘lock and key’ hypothesis describing the matching of female (lock) and male (key) genitalia prevailed for a long time (Paterson 1980,1982, 1985, Ferguson 1990) in an attempt to explain the ubiquitous differences between species. It assumed that the purpose of these differences preclude reproduction between partners lacking the precise key for the particular lock, avoiding interspecific mating thus reducing the risk for sterile hybrids (Paterson 1988, Gabrys *et al.* 2021) often referred to as satyrization (Ribeiro & Spielman 1986; Reiskind et al, 2018)

After almost 200 years of discussion about the importance of the ‘lock and key’ theory (Paterson 1982, Masly 2012), there is still no clear conclusion about its role in evolution. The origin of the discussion is the undeniable observation that species, even closely related taxa, obviously have different genitalia or SSC. The idea of the lock and key mechanism remained acceptable and prominent until it became obvious that not only vertebrates, but even invertebrates, in the first place arthropods, recognize conspecificity of possible mates. In the latter taxonomic group they even distinguish the relationship of kin simply by recognition of the hydrocarbons in their tegument (Coyne & Orr 1997; Hemptinne *et al.* 1998; Sullivan 2009; Xue *et al.* 2016). There is no doubt that the theory has survived such a long time because of the puzzling species specificity of genitalia and SSC. Even closely related species exhibit differences that can apparently not be explained by the lock and key theory. But the alternatives formulated under the umbrella of ‘sexual selection’ do not really provide an answer to the ubiquity of interspecific differences (Kelly & Moore, 2016). On the contrary, if a particular morphology or behavior is ‘sexy’ or provides an answer to intersex competition one would expect an ideal optimum at least for those species belonging to a template (see below). Because of this lack of a general frame explaining interspecific differences, the lock and key hypothesis keeps popping up (e.g. Masly 2012, Simmons 2014).

Male-male and sperm competition

Probably the most straightforward and understandable observations are those that concern the competition between males in their struggle to secure fatherhood. Most of the actions in this respect are self-explaining. Pick a fight and leave the insemination of a nearby waiting female or a herd to the strongest, hold the female until she lays eggs, plug the entrance of the female copulatory organ (Fig. 1) are all logical activities that hardly need explanation. Some male spiders even sever their own copulatory organs after copulation to become eunuchs (Kuntner *et al.* 2015) in order to increase their mobility and shield off the female against competing males. This behavioral range easily explains the development of particular morphological modifications such as the huge mandibles in stag beetles (*Lucanus cervus* L., 1785) or antlers in deer (*Cervus elaphus* L., 1785). The observation that less well-equipped males may succeed in inseminating females without a preliminary fight by using a stealthy approach, has given rise to the term ‘cheaters’.

Fig. 1. In this female spider (*Diores godfreyi* Hewitt, 1919) one of the two copulation openings, on the venter of the abdomen, is closed with a sticky dark brown plug.

Parker (2020) makes a clear difference between male-male competition and sperm competition, the latter describing the rivalry between sperm cells. This approach bears a certain similarity with the difference made between ‘female choice’ and ‘cryptic female choice’ in which choice is made respectively before and after mating.

It should be questioned why this type of competition is qualified as an aspect of sexual selection. It is not because a particular selection only affects one sex it is to be understood as 'sexual'. In many birds, the females exhibit camouflage colors often contrasting with brightly colored males. The color pattern of the females has to be interpreted as an answer to risks of predation when they are immobile on their nest and is thus not the result of what is usually understood as sexual selection. In the same line of reasoning, the adaptations of males in their contest during courtship are to be seen as the result of intraspecific competition for a resource that can be qualified as 'eggs' or 'offspring carrier' which may be scant as explained further.

Female choice

The core of sexual selection is the concept 'female choice' already used by Darwin (1871) in his book 'The descent of Man, selection in relation to sex'. It was developed in the first place to explain the often grotesque male forms of secondary sexual characters, which was one of the major phenomena, questioning the validity of the evolution theory. Since struggle for life implies parsimony, itself at the base of ecological theories like optimal foraging (Werner & Hall 1974, Pulliam 1974), a concept had to be invented to counter the apparent exceptions to natural selection.

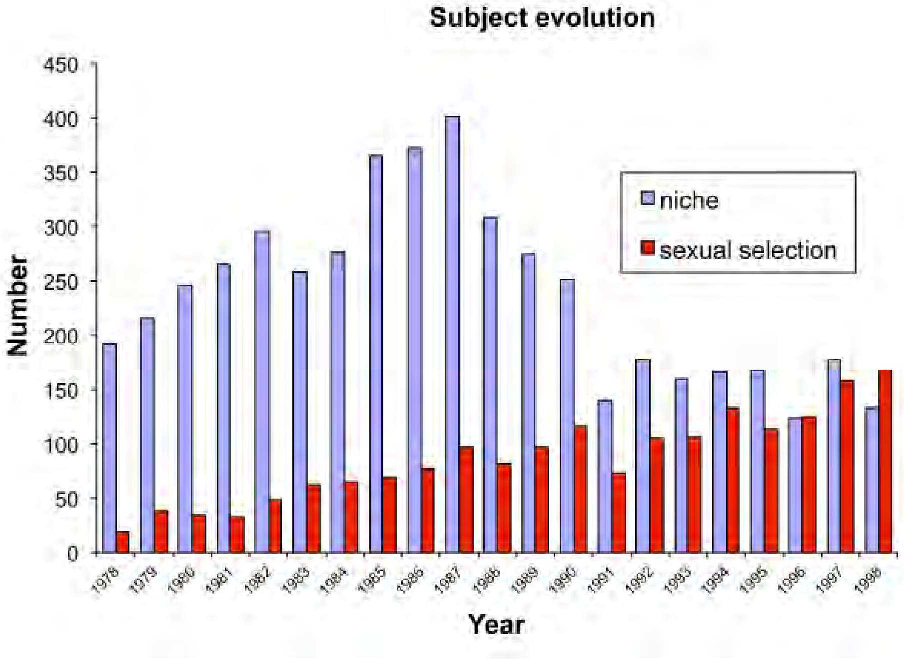

Fig. 2. Number of titles with the terms 'niche' and 'sexual selection' in the years 1978 to 1998 in the online version of 'zoological record', accessed in May 2000.

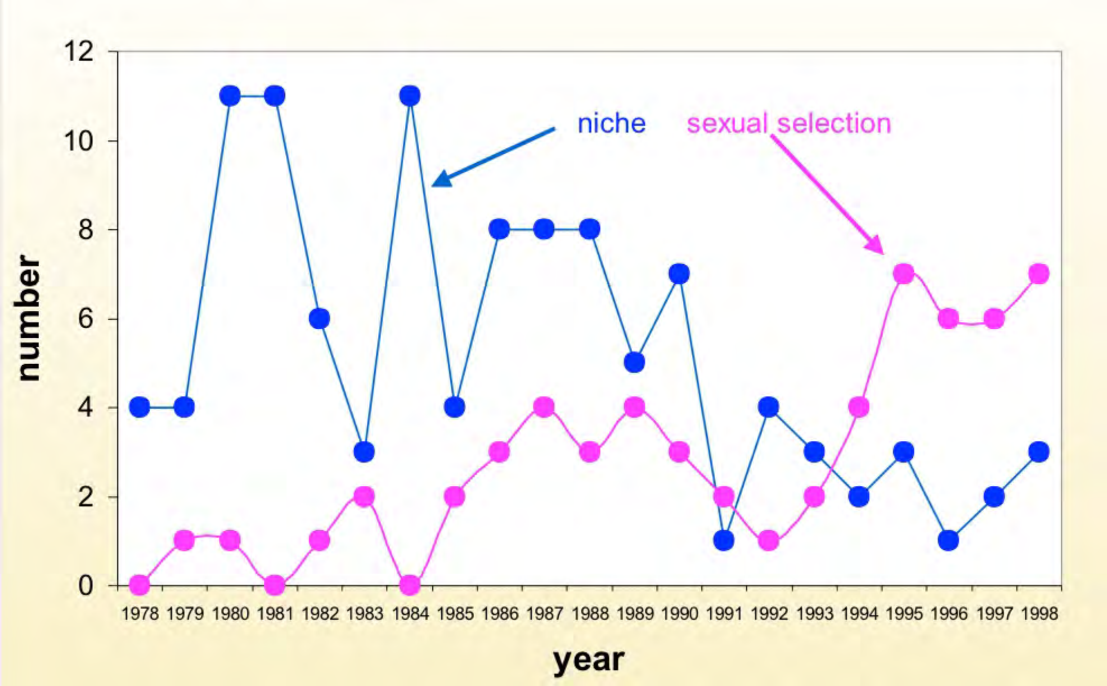

Fig. 3. Number of titles with combinations of the terms ‘speciation and niche’ and ‘speciation and sexual selection’ in the years 1978 to 1998 in the online version of the ‘zoological record’, accessed in May 2000.

The idea remained somewhat under the radar until the second half of the previous century (Fig. 2) during which a sudden interest in the phenomenon grew, resulting in a flood of studies, summarized in Eberhard (1985) and Anderson (1994). Although ‘female choice’ is widely accepted it remains a source of discussion what precisely females choose for. Among the most often mentioned criteria is the ‘Fisherian runaway’ concept (Fisher 1915, 1958, Pomiankovski *et al.* 1991) also referred to as ‘sexy sons’ hypothesis (Dawkins 1976, Weatherhead & Robertson 1979), assuming that females choose the sexiest male guaranteeing that the males in the offspring will also be sexy and will easily find a partner. All these possibilities suppose that the special structures of males vary to a certain extent to allow the females to choose.

It assumes that male ornaments tend to be amplified by persistent female choice. Dependent on this idea is the handicap theory (Zahavi 1975, Iwasa *et al.* 1991). Males develop structures which imply a high energy cost, proving that they have ‘good genes’ but Flintham *et al.* (2023) found that this type of sexual selection may even be detrimental to the survival of the population in certain circumstances.

Quite similar to this is the hypothesis that males can only develop the handicap when they are immune for a series of parasites (Zuk 1992).

Female choice is evidently not only based on ‘sexual dimorphism’ and visual cues, it may also imply activity (mating dances), auditory (stridulation) or chemical (pheromones, gustatorial) types of courtship. The whole of all the aspects that are involved in courtship have been referred to as the mating module (Jocqué & Szüts 2001, Jocqué 2002, Henrard & Jocqué 2012) a concept elaborated from the 'copulatory module' coined by Danielopol *et al.* (1990) and Martens (2000).

Cryptic female choice

Female choice is somewhat difficult to understand in animals without sexual dimorphism other than genitalia or copulatory organs. The females of such organisms are assumed to choose in a postcopulatory process whether they will allow sperm of a particular male to fertilize their eggs after copulation, a phenomenon defined as 'cryptic female choice' (CFC) (Eberhard 1991, 1996, Baer 2015) sometimes considered 'the last piece of Darwin's puzzle (Firman *et al.* 2017). Apart from animals in which apparent external sexual dimorphism is the rule (many vertebrates e. g. Pilastro *et al.* 2004), the male genitalia are assumed to be the main criteria used by females to make the decision. The assumption is that the chosen male is the one that best stimulates the female sensory system during copulation.

In view of studies supporting convergence of morphological structures with similar function (Conway Morris 2009, MacGhee 2011, Stern 2013), it is surprising that there is not such an evolution for genitalia that are supposed to stimulate the female. It is the more puzzling that even in animal species from templates with very similar somatic morphology, the genitalia tend to differ to a large extent as shown in Figs. 4-7. CFC further suffers from the difficulty to separate its effect from sperm competition (Firman *et al.* 2017) and from the observations that it does not seem to contribute to the quality of the next generation (Slatyer *et al.* 2012, Lumley *et al.* 2017).

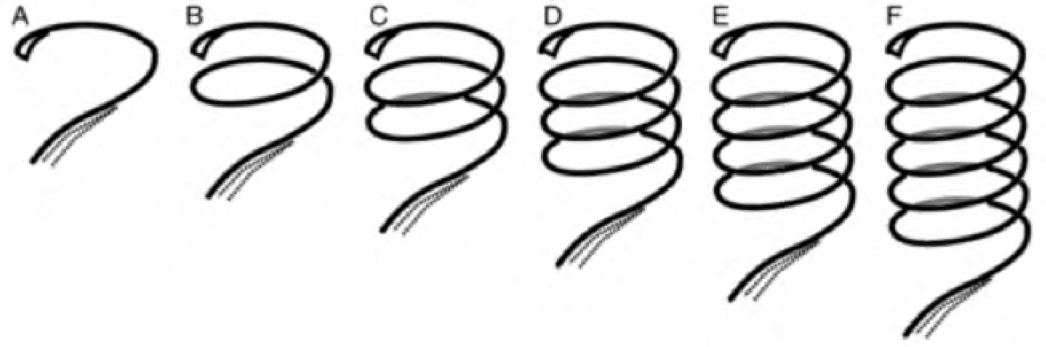

Fig. 4. Spires in the copulatory organs of six closely related species of group 2 in the flatworm genus *Trichonostoma* Schmidt, 1852 (from Willems *et al.* 2004).

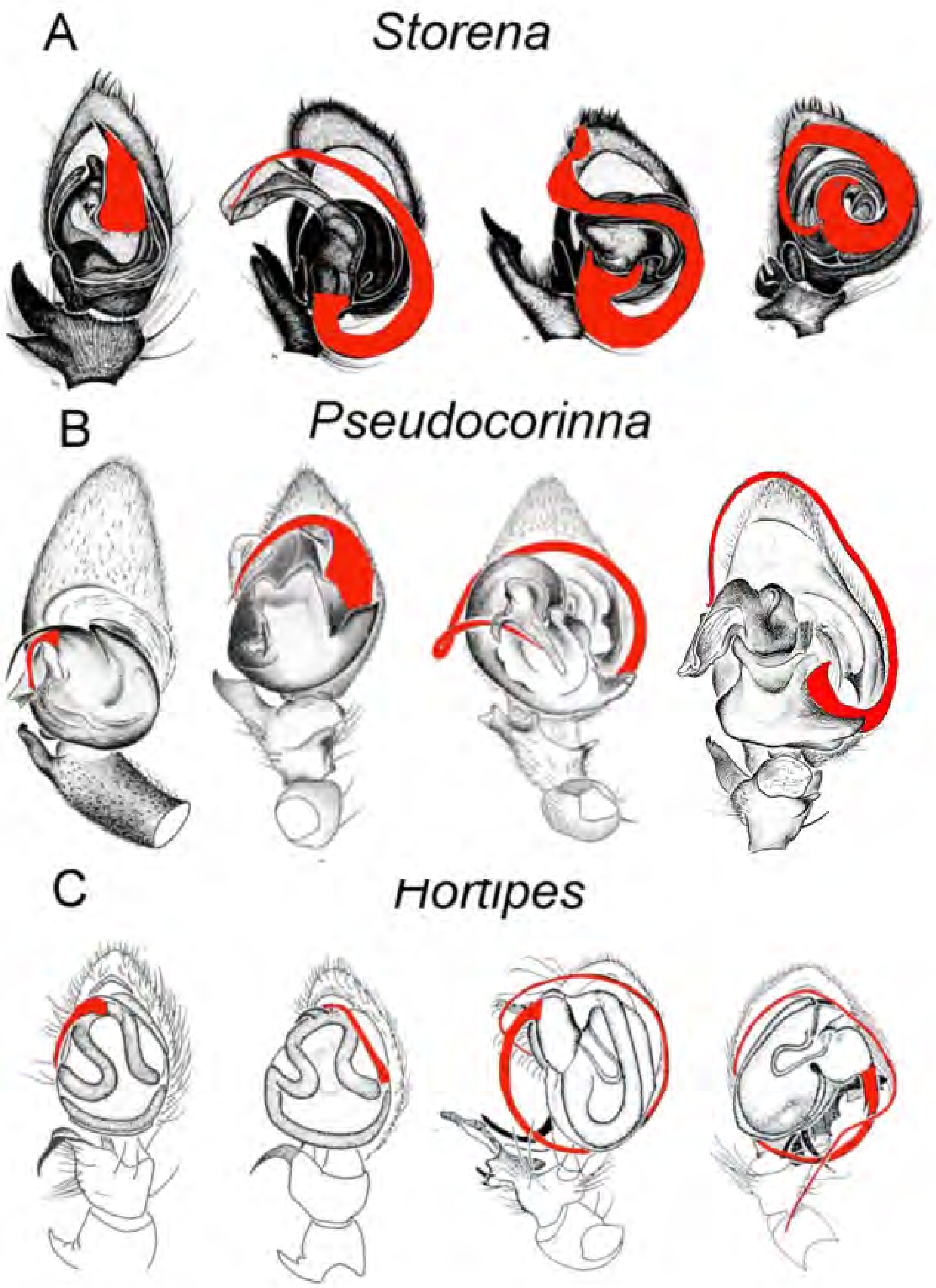

Fig. 5. Ventral views of male copulatory organs of a selection from three spider genera: A. *Storena* Walckenaer, 1805 (29 species, Zodariidae), B. *Pseudocorinna* Simon, 1909 (29 species, Corinnidae) and C. *Hortipes* Bosselaers & Ledoux, 1998 (70 species, Corinnidae) showing the size range of the intromittent organ (embolus in red). (resp. from Jocqué & Baehr 1992, Jocqué & Bosselaers 2011, Bosselaers & Jocqué 2000). The similarity of the simple organs with a short curved embolus and the difference of the complex ones support the assumption that the mating module of templates increases in complexity with increasing specialization. (from left to right: A. *Storena harveyi* Jocqué & Baehr, 1995; *S. fungina* Jocqué & Baehr, 1992; *S. formosa* Thorell, 1870; *S. mainae* Jocqué & Baehr, 1995; **B**. *Pseudocorinna banco* Jocqué &

Bosselaers, 2011; *P. rutila* Simon, 1909; *P. perplexa* Jocqué & Bosselaers, 2011; *P. ubicki* Jocqué & Bosselaers, 2011; **C.** *Hortipes pollux* Bosselaers & Jocqué, 2000; *H. castor* Bosselaers & Jocqué, 2000; *H. terminator* Bosselaers & Jocqué, 2000; *H. tarachodes* Bosselaers & Jocqué, 2000.)

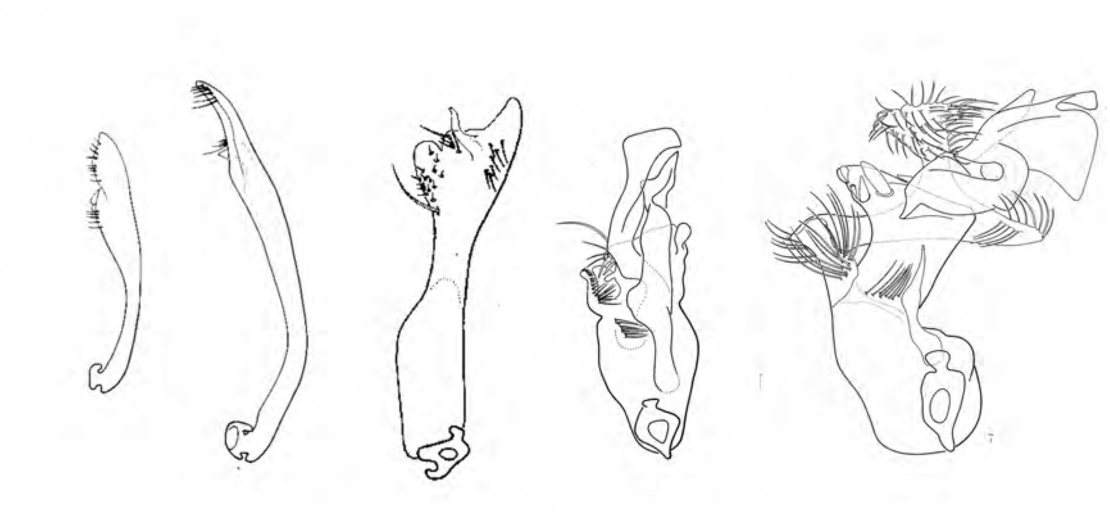

Fig. 6. Ventral views of the aedeagus of a selection of the water beetles *Limnebius* Leach, 1815 (91 holarctic species; Coleoptera: Hydraenidae). (from Jäch 1993)

Arms race

Yet another explanation for the evolution of dimorphism and/or complex courtship and genitalia is the arms race between the sexes, based on the statement that interests between sexes differ. This hypothesis, often referred to as ‘sexually antagonistic coevolution‘ (SAC), has been assumed to be responsible for rapid evolution and hence speciation (Arnquist *et al.* 2000, Arnquist & Rowe 2005). Eberhard (2004), Aisenberg & Eberhard (20069) already countered the idea and found no confirmation of male – female conflict in insects and spiders.

It is mainly this last assumption, that speciation is often largely due to sexual selection (Masta & Maddison 2002, Boul *et al.* 2007), which has raised skepticism. It completely passes the basic ecological idea that species cannot co-exist when they share the same niche (Hutchinson 1959, May 1974, Pianka 1974). In the last part of the previous century it became apparently fashionable to make abstraction of the niche theory and explain biological phenomena from a standpoint linked to sexual selection. (Fig. 3)

However, Ritchie (2007) relativizes these standpoints and even mentions that sexual selection can slow down speciation and writes:” Models confirm that the process can occur, but is strongest in conjunction with ecological or niche specialization. Some models also show that strong sexual selection can act against speciation.” The recognition that sexual selection alone is not sufficient to drive speciation has been detailed in studies like these of Bush (1992) and Boughman & Svanbäck (2016).

Much of the huge literature on the subject, which became fashionable in the last part of the previous century (Fig. 2), is devoted to the contradictions between sexually antagonistic coevolution, female choice and cryptic female choice (e.g. Eberhard 2009). Cornwallis & Uller (2010) state: “studies of sexual traits fail to encompass three important features of evolution”. It culminates in the report of Carleial *et al.* (2023), which reveals some of the major shortcomings in many studies on the subject, their main conclusion being that the opportunity for sexual selection varies substantially in the course of the mating season. Since most studies have short observation times, the real importance of sexual selection as presently understood tends to be overestimated.

The importance of male-male competition may similarly be influenced by the length of the period over which observations are spread. Male-male competition is often largely influenced by the size of the individuals (e. g. Whitehouse 1997, McGinley *et al.* 2015). However, it has been shown that there is an inverse relationship between the quantity of food available and the time gap between two moults but also of the size of the individuals in the adult phase (Turnbull 1965). The size of the adult males of temperate spiders may decrease in time, sometimes spread over up to four months (Jocqué 1981). In order to study the contribution of small males to the next generation, a long observation period would be needed to test this.

So far, the input of systematicians and taxonomists in these discussions has been rather restricted. Their main contribution has been describing the remarkable genitalia and sexual dimorphic features, that have puzzled ethologists and ecologists to such an extent that they have formulated several hypotheses, often contradictory, to explain the existence of these structures. Conclusions of taxonomists in this connection are most often restricted to general remarks in which the decision as to what type of sexual selection is responsible is left open. A few examples reveal the indecision about which mechanism plays the crucial role in sexual selection: “The hypotheses of sexual selection are not mutually exclusive, and different processes may together affect the evolution of genital complexity” (Azevedo at al. 2018); “Nephilid coevolution appears to be driven at least in part by sexual conflict” (Kuntner *et al.* 2009); “Our analysis showed that a variety of male prosomal modifications have evolved multiple times in parallel, which indicates that sexual selection has played an important role in the evolution of these sexually dimorphic features, as well as in species diversification of erigonine spiders.” (Lin *et al.* 2022).

However, the multitude of particular observations by taxonomists has prompted the present contribution. More precisely the existence of 'templates' in the animal world adds an important argument to the discussion. The term 'templates' was introduced by Jocqué & Bosselaers (2011) in a revision of the Afrotropical spider genus *Pseudocorinna* Simon, 1909. A template is a group of animals with extremely similar somatic morphology in which the species can only be identified by the morphology of their genitalia or secondary sexual characters. These groups of animals have apparently a very successful somatic morphology that allows them to thrive in a wide range of microhabitats. Very often these animals are put together in a genus. There are quite a few examples of such templates in spiders: *Bacelarella* Berland & Millot, 1941 (Szüts & Jocqué 2001), *Diores* Simon, 1893 (Jocqué 1990), *Draconarius* Ovtchinnikov, 1999 (Wang *et al.* 2010), *Hortipes* Bosselaers & Ledoux (Bosselaers & Jocqué 2000), *Pseudocorinna* (Jocqué & Bosselaers 2000), *Storena* Walckenaer, 1805 (Jocqué & Baehr 1992), Australian Sparassidae (Jäger 2005) and in many insects of which the water beetles *Limnebius* Leach, 1815 (Jäch 1993, Rudoy *et al.* 2016) is a perfect example (Fig.6). So is the case of the intromittent part of the copulatory organ in flatworms of the genus *Trigonostomum* Schmidt, 1852 (Willems *et al.* 2004)(Fig. 4).

But in other animal groups where sexual selection is common, many templates go unnoticed because their taxon is split up on the base of the wide range of genitalic characters (see Jocqué *et al.* 2013, fig. 12). It is exactly because of this range of genitalic traits that the phenomenon is mentioned here. Splitting up genera because of the variation in the genitalia impedes the important observations linked with templates. The remark that the range of genitalia is puzzling or surprising is an understatement. It is indeed difficult if not impossible, to explain why the secondary sexual characters (SSC) or the copulatory organs vary with an important factor. A few examples (Figs. 5-6) illustrate this variation. The obvious questions these observations raise are the following: are the species with very simple copulatory organs and SSC not subject to the same degree of sexual selection? And if it is a question of stimulating the female, why does the morphology of these genitalia and SSC vary to such an extent and why are they different in every species? One of the hypotheses is that the environment plays a crucial role in the effect of sexual selection (Eberhard 1985, Anderson 1994). However, there are cases where a template with such a range is observed of animals living in the same habitat. Not less than six species of very similar salticids spiders of the genus *Bacelarella* Berland & Millot, 1941 co-occur in Ivory Coast rainforests (Jocqué & Szüts, 2001). Their genitalia show a very large range of complexity (Fig. 7) refuting the idea that the differences are a result of environmental constraints.

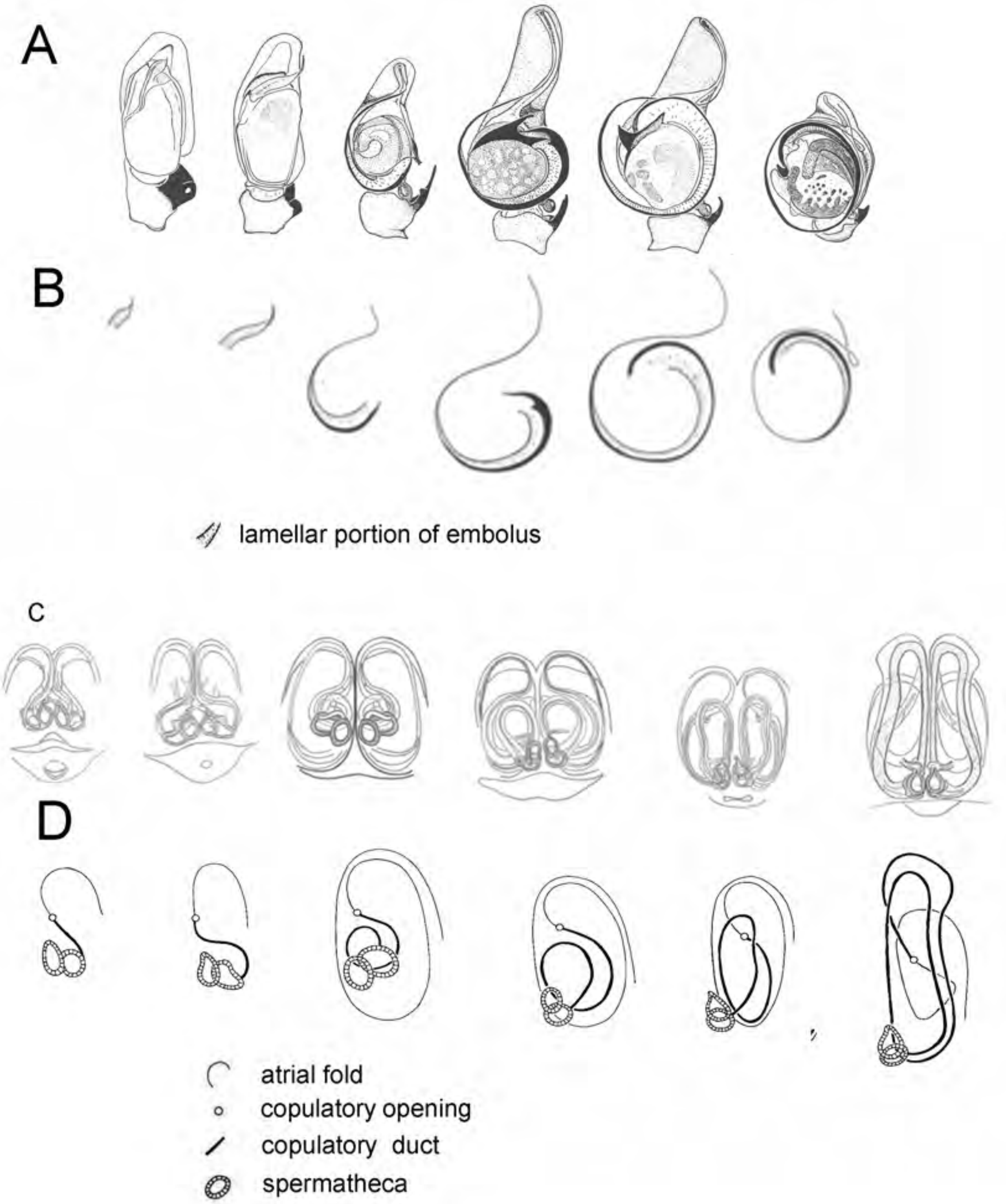

Fig.7. Copulatory organs in six co-occurring species of the spider genus *Bacelarella*. (Araneae, Salticidae). A. Ventral view of male palps; B. details of the embolus, the intromittent organ; C. dorsal view of cleared epigyne; D. details of internal structure of epigyne (from Jocqué & Szüts 2001). Since the shape of the cymbium, the sclerite housing the bulbus of the palp, is an important character for the definition of genera in this subfamily of Salticidae, the species ended up in different genera (Wesołowska & Wiśniewski 2023) obscuring the template.

The distribution of sexual selection

Since sexual selection is very common in the largest animal groups, Arthropoda, Mollusca and birds for the terrestrial vertebrates, the impression exists that the phenomenon with appearance of SSC is ubiquitous. However, it appears that the majority of the animal phyla (88%) do not present sexual dimorphism (Wiens & Tuschhoff 2020). But even in the phyla where sexual dimorphism is common, certain taxa do without it. In molluscs, the aquatic Bivalvia use mass production of gametes similar to what occurs in a multitude of marine broadcast spawners from other phyla. One of the most striking examples in terrestrial arthropods, the phylum in which sexual selection tends to be the rule, are the termites which are devoid of complex genitalia or secondary sexual characters (Grassé 1937). Therefore, the taxonomy of termites makes abstraction of the genitalia (e.g. Uys 2002). Attempts to do it (Belyaeva & Dovgobrod 2006) had to be restricted to small differences in the female genitalia linked with their general somatic structure. In termite males the copulatory organ is membranous and there is no sign of a tendency towards complexity. It is probably not a coincidence that mating in termites follows an unusual course, depending on the swarming of huge numbers of reproductive forms. This behaviour bears a resemblance with the strategy of many marine and freshwater animals producing swarms of gametes.

Another example of animals in which the copulatory organs remain simple are the intertidal barnacles. In these sessile hermaphrodite animals the penis is simple but long, meant to inseminate nearby conspecifics. Here again, finding a partner is not a problem. The animals are fixed and can only mate with the nearby neighbours occurring in dense mats of individuals.

Why these animal groups do not rely on sexual selection for reproduction is an important question. The answer to this question might throw light on the many unexplained issues of sexual selection.

Population density

The core of the present contribution has to do with the observation that many organisms live in very low-density populations. Examples of large-scale inventories of invertebrates illustrate the phenomenon (e.g. Novotny & Basset 2000). Coddington *et al.* (2009) mention a large array of studies and state “frequency of singletons – species represented by single individuals – is anomalously high in most large tropical arthropod surveys”. They add, “The four common hypotheses (small body size, male-biased sex ratio, cryptic habits, clumped distributions) failed to explain singleton frequency”. This is in accordance with the broken stick model developed by MacArthur (1957; 1961). It assumes that speciation implies ecological specialization resulting in large numbers of species, each utilizing a small amount of the available resources. This hypothesis is among the influential contributions MacArthur further developed in the island biogeography theory (MacArthur & Wilson 1963, 1967), which emphasized the importance of population density for the survival of species on islands. According to that theory, populations reach a critical lower density when activities become 'non-convex', an idea already developed by MacArthur (1951). It implies that with increasing specialization, hence less dense populations, densities become so low as to prevent meeting of the sexes within acceptable energetic limits. In other words the risk of 'zerogamy', impossibility to find a mate, increases with the degree of ecological specialization.

The study of deRivera *et al.* (2003) on a fiddler crab recognized the importance of population density for the mate searching behaviour of males and females. So did Kokko & Rankin (2006) in their review on the importance of population density for sexual selection but in which they conclude that the impact of the parameter may vary to a large extent. Rhainds (2010) found that male density is among the main factors causing zerogamy. McCullough *et al.* (2018) recognized that the importance of pre- and post-copulatory sexual selection changes with population density.

Although these studies recognize that population density plays a role for sexual selection, they certainly do not consider sexual selection to be a consequence of the risk of zerogamy in thin populations.

The hazard of inbreeding

Is there a real problem for highly specialized animals to find a partner? Although these organisms have a very patchy distribution due to the scattered mosaic microhabitats they live in, it might be assumed that they can easily find a partner when they grow up in the correct microhabitat where they were born, together with conspecifics. However, an extra problem arises due to inbreeding. The risk of incest has been clearly shown, not only by the occurrence of physical shortcomings (Madsen *et al.* 1996, van de Kerk *et al*. 2019, Wilmer *et al.* 1993, Cristescu *et al.*2009, Johnson *et al.* 2018, Schulz *et al.* 2020) but also by the risk of inbreeding depression (Lande 1993, Pusey & Wolf 1996, Charlesworth & Charlesworth 1999). Several field studies mention the detrimental effect on survivorship leading to extinction of metapopulations (Jimenez *et al.* 1994, Saccheri *et al.* 1998 and Van Oosterhout *et al.* 2000, Keller & Waller 2002). Yet, in a theorethical study, Kokko & Ots (2006) claim that inbreeding may be advantageous, considering the choice between mating with kin immediately on the one hand or waiting for another potential mate to appear on the other hand. According to their model, the latter strategy, called the sequential choice scenario, could be less advantageous when mates are rare. However, they admit that there is a mismatch between theory and data: the almost complete lack of cases where individuals prefer to mate incestuously. More recent fieldwork using genomics (Hoffman *et al.* 2014; Huisman *et al.* 2016; Kardos *et al.* 2016) continues to confirm that inbreeding depression is important in natural populations. Although de Boer *et al.* (2021) consider that inbreeding avoidance has been overestimated, supporting the model of Kokko & Ots (2006), their observation emphasize the risk of remaining unmated, here referred to as zerogamy.

Fairly few studies have been carried out concerning the influence of kinship for female choice. Welke & Schneider (2009) and Chen *et al.* (2018) are among the few studies for spiders. The first study found that females of the large web-spider *Argiope lobata* (Pallas, 1772) were able to avoid inbreeding by polyandry in combination with cryptic female choice. Chen *et al.* (2018) studied prolonged milk provision in a salticid spider, which is remarkable in itself, but observed that males were no longer accepted to be fed by the mother as soon as they were adult, whereas adult females were allowed to continue. Harper *et al.* (2016) found that females of a sawfly preferred to mate with non-siblings rather than with siblings. Tuni *et al.* (2013) found that female crickets choose the sperm of unrelated males in postcopulatory selection. These studies demonstrate that at least some invertebrates are able to recognize siblings and are thus able to avoid inbreeding depression. It seems acceptable that this is the rule rather than the exception.

The effect of inbreeding avoidance is likely to be overlooked. The influence of the sexual selection paradigm is so strong that some observations apparently showing avoidance of kin partners are interpreted in terms of female choice. The fact that *Drosophila* females preferred males with an allopatric cuticular hydrocarbon (CHC) pattern, was interpreted as sexual selection and not as avoidance of kin partners with their own CHC pattern (Higgie & Blows 2008). It may even be questioned whether the observations concerning CFC are not rather avoidance of inbreeding than choosing in an anthropomorphic manner for 'beautiful' mates as in the guppy's studied by Pilastro *et al.* (2004). This would provide an answer as to why CFC does apparently not contribute to the quality of offspring (Slatyer *et al.* 2012, Lumley *et al.* 2017).

For highly specialized animals, avoiding inbreeding implies migrating towards other parts of their mosaic microhabitat. The observation that animals, mainly males (Henry *et al.* 2016) are often found as 'stragglers' outside their habitat must be regarded as the result of these adults crossing unsuitable environment migrating to another 'tile' of their niche mosaic where they might find unrelated conspecific females.

The lek paradox

Although considered exceptional behaviour, lekking has been among the preferred subjects of ethologists. The significance of lekking remains problematic for several reasons (Rathore *et al.* 2023), not in the least for the so-called lek-paradox (Miller & Moore 2007) a phenomenon describing the difficulty to explain that female choice in leks does not erode the variation of males (Lank *et al.* 1995). Another problematic singularity of some leks is synchronicity of the male action. It has been observed in fireflies (Lampyridae) in which lekking males flash synchronously (De Meyer *et al.* 2004: 274; Moiseff & Copeland 2010), in groups of fiddler crabs waving together (Blackwell 2018) and in insects, mainly cicadas, which stridulate in choruses (Greenfield 2018). These activities in animal leks have elicited many studies but without clear answers about why males would drown their individual performance in synchronous activity. One of the most puzzling observations is synchronous waving of male fiddler crabs in the absence of females (Blackwell 2018: 4) but cicada choruses and flashing male fireflies do exactly the same.

The alternative

In this overview, which only scratches the surface of the enormous literature on the subject, we detected many incongruities among the opinions presented in this vast array of studies. The existential problems with finding a partner as a result of low population densities and the risk of zerogamy, the enormous range of complexity in copulatory organs of species belonging in templates, the intraspecific stability of these copulatory organs, the lek paradox, all prompt an alternative explanation for the phenomena that have been addressed under the common denominator ‘sexual selection’.

In the same chain of arguments, the remarkable hypothesis that female choice and arms race drive speciation making abstraction of the niche theory, requires an alternative view. The paper by Boughman & Svanbäck (2016) already presented a hypothesis with speciation resulting from synergistic effects between mate preference and ecological niche, but without genetic link (magic trait) between them. A magic trait is a trait subject to divergent selection and a trait contributing to non-random mating that are pleiotropic expressions of the same gene(s).

The mate check hypothesis already made the assumption that pleiotropy was involved (Jocqué 1998). It was an answer to the idea stipulating that sexual selection stimulates speciation. Although this line of thinking has not yet taken over the reasoning in this context, some authors found a reasonable explanation in the importance of ‘magic genes’. Cornwallis & Uller (2006) already paved the way: “A move from purely gene-focused theories of sexual selection towards research that explicitly integrates development, ecology and evolution is necessary to break the stasis in research on sexual traits." Thibert-Plante & Gavrilets (2013) wrote: "The presence of magic traits may suggest that ecological selection was acting during the origin of new species."

The hypothesis presented here elaborates on the idea of 'mate check' (Jocqué 1998, 2002), which assumes that there is a genetic link between aspects of the genitalia (or the mating module) and behavioural adaptations. The idea was formulated in 'tempore non suspecto', before the concept of 'magic genes' (Servedio *et al.* 2011, Maan & Seehausen 2012) was cornered. In a later study Servedio & Burger (2020) recognized that 'pseudomagic traits' in which the genetic link is less strong, might have the same effect.

In the original formulation of the hypothesis it was left open about what type of 'behavioural adaptation' should be linked to the mating module although it was assumed to be one or more aspects of the many adaptations required to survive in the unique niche the 'new species' would occupy. Eberhard (pers. comm. 2000) countered the idea, postulating that the new aspect in the mating module might easily be imitated by cheating males lacking the correct adaptation. In the present hypothesis at least one necessary condition is specified: behaviour that guarantees the presence of males in the vicinity of fertile females, ready to mate, a behaviour we will call 'correct whereabouts'. The main difference with the previous version is that, lacking the correct whereabouts behaviour, male offspring will run a major risk of 'zerogamy", as explained above; and find their genes lost for the following generation.

Correct whereabouts may involve a large set of possibilities and implies at least three area levels: landscape, habitat and microhabitat. A general landscape dependent mating locality is mediated by hilltopping behaviour occurring in many insects. The many studies on the subject (e.g. Alcock & Gwynne 1988, Opdam 1990, Grof-Tisza *et al.* 2017, Pepi *et al.* 2022, Cannon 2023) reveal that the phenomenon is not only common, but plays an important role in the survival of species living in thin populations (Scott 1968). The link of mating locality to particular landscape characteristics is also illustrated by the reproduction behaviour of *Apis mellifera* L. (Ruttner & Ruttner 1966) and other species of *Apis* (Koeniger & Koeniger 2004). Drones from many hives congregate at a particular locality at a large distance from their hives apparently dependent on specific landscape features, which are still unknown. Queens later fly in and are mated in flight. Swarming is also common in many fly species and has been explained as: 'males swarm, enabling them to be more visible for females' (Mc Alister 2019: 181). The swarming localities are evidently species dependent but may include trees, other plants, rocks and many other landscape features. Some fly species are attracted to smoke and will find a mate in the wake of a fire (Chandler 1978). That the presence in the correct habitat is a prerequisite for mate detection is not particularly surprising and can be understood as part of the habitat preference of a species. But for the majority of small species, the presence in a particular habitat alone will not be sufficient to encounter a possible mate and will require preference for a precise microhabitat. The importance of microhabitat preference and its consequences does not have to be emphasized and is subject of a huge amount of studies (e.g. Vives-Ingla *et al.* 2023). It has been shown that many herbivores find a mate near, or on their host plant (Prokopy 1967, Bush 1992), which seems like a simple solution. However, the observations of Whittier *et al.* (1992) show that the meeting place is not as straightforward as expected: the flies only used a few trees out of a plethora of conspecific trees in an orchard.

Perhaps the most straightforward is the example provided by Hawthorne & Via (2001), who found that resource use and mate choice in a species of aphids are linked by pleiotropy. For species that rely on pheromones to find a partner (Fischer *et al.* 2022), being at a perfect spot to pick up the signal is paramount. The equipment of some male webbing spiders with thousands of sensilla (Talukder *et al.* 2025) illustrates the importance of this strategy for mate detection. For small animals living in the litter layer it will be crucial to be in the vicinity of a possible partner, most likely in the correct microhabitat, to hear a stridulating sound emitted by a conspecific of the other sex. Larger animals may depend on the registration of other types of sound production. It hardly needs explanation that finding a partner on the base of visual signals requires animals to be in the correct habitat to come close enough to a possible partner. For some insects the habit of hill topping is an excellent method to reduce the risk of searching in vain. Lek behaviour should be considered as a method to facilitate the search for a partner. Synchronous waving, singing in choruses and other mass activity doubtlessly decrease the risk of zerogamy.

The requirement of correct whereabouts at the mating season may seem superfluous for many species that occur in dense populations and certainly for the male or males, which are courting a female. Why would a female need confirmation of correct male behaviour when he has already found her?

1. It should not be forgotten that all species resulting from sympatric speciation (Bush 1992, Dieckmann & Doebeli 1999, Kondrashov & Kondrashov 1999) go through a history starting with a tiny population in which finding a partner which is not kin can be a problem. Sympatric speciation is assumed to be a result of sinks (parts of a species' habitat where natality exceeds mortality) and sources (parts where it is the other way round) (Pulliam 1988, Dias 1996), with parts of the source population overflowing into a sink. Acquiring new characters and behaviour that allow survival in the sink with consequent assortative mating is the main mechanism (Jocqué 1998, Janicke *et al.* 2019). In this context the acquisition of behavior to correct whereabouts is primordial not only in function of the habitat but certainly also for the detection and encounter of a mate. With increasing

specialization and the splitting of the habitat into a mosaic, the problem becomes more prominent. The term 'double jeopardy' coined by Gaston (1998) in a comment on Johnson's (1998) hypothesis about the relation between density and geographic range size, confirms the importance of the species' history.

2. Population density fluctuations are the rule rather than the exception; when the population is at a high it may be easy to find a mate whereas at a low it may create a risk for extinction in the absence of whereabouts mate check (e.g. Barraquand et al. 2017, Reder *et al.* 2024).
3. Negative mutation bias is widely observed (Pomiankovski *et al.* 1991) and apparently occurs more often in males than in females (Sharp & Agrawal 2013, Grieshop 2016); it would mean that their attraction to female partners remains but it will greatly depend on stochasticity to find a mate in the absence of whereabouts mate check.

Complexity of genitalia in templates

When the copulatory organs and by extension the mating module of template members have to provide the crucial information about the whereabouts behaviour, it should not be surprising that its complexity increases in the course of the evolution. However, the few phylogenetic studies on the evolution of the complexity of copulatory organs, Rudoy *et al.* (2016) on the species in a template of water beetles, Azevedo *et al.* (2018) on an entire spider family and Li *et al.* (2025) on a large tribe of Salticidae, do not find unidirectional changes in complexity of the male copulatory organs. Yet, both Rudoy *et al.* (2016) and Li *et al.* (2025) describe a large range of complexity in the copulatory organs and detect the simplest organs in the species with ancestral characters. The second study finds intermediate complexity as the ancestral condition. However, the evolution shows a mixture of the direction towards complexity or towards simplification in the three clades.

The information about the male‘s crucial behaviour does not necessarily need to evolve towards increased complexity. In his review on the subject, Wiens (2001) clearly states that SSC often evolve in different directions with loss of sexually selected remotely signalling traits.
It is plausible that the sum of information in the mating module may shrink as long as it is informative enough to convey the message. But once a certain path has been taken, increased complexity is to be expected as witnessed in the dramatic quote of Dawkins & Wong (2004 p. 317) "Sexual selection produces quirky, whimsical evolution that runs away in apparently arbitrary directions, feeding on itself to produce wild flights of evolutionary fancy".

Stability of copulatory organs

Probably the most puzzling phenomenon in connection with sexual selection is the stability of copulatory organs. Whereas they vary to a large extent between species in the same genus/template, they tend to be very stable within the species. In fact, taxonomy is based on the observation that there is hardly any intraspecific variation of copulatory organs. The most common and practicable species concept is based on that statement: "...the smallest aggregation of (sexual) populations or (asexual) lineages diagnosable by a unique combination of character states" (Wheeler & Platnick 2000). In many large animal groups, not in the least those in which sexual selection has been studied (see above), copulatory organs are the 'diagnosable characters' to which Wheeler and Platnick (2000) allude. This species concept implies that even tiny recurring differences in the structure of the copulatory organs will have taxonomic consequences. Specimens with differences in their copulatory organs will be considered as different species, even when the deviations are tiny but stable. McPeek *et al.* (2008) provided a perfect illustration of the discrepancy between intraspecific stasis and rapid interspecific evolution in a large genus of Odonata.

The phenomenon was already observed by Coyle (1985) and a few other taxonomists (Wheeler *et al.* 1993, Johnson 1995) and was formalized by Eberhard *et al.* (1998) and Eberhard (2009) in the influential papers 'One size fits all' and 'static allometry of genitalia'. But these could not render a general explanation solving the many contradictions as stated in the final comments of the latter paper: "Many questions remain to be answered".

It remains particularly difficult to match the stability of copulatory organs with sexual selection, more precisely with the phenomenon which is described as cryptic female choice. If females have to choose between males with different stimulating potential, what is the criterion they will use to select?

What then do females choose?

As explained in the 'mate check' hypothesis (Jocqué 1998), during courtship and mating, the female receives information from the markers of the male's behavioural adaptations guaranteeing survival in a particular niche as seconded by Maan & Seehausen (2012): "Magic traits' affect both ecological fitness and assortative mating". I here argue that it rather concerns the behaviour that ensures the male will be at the right place in the reproduction period. In many cases the ecological fitness will imply choosing the right (micro)habitat. Whereas in the majority of the species the female tends to stay put in the right habitat, males rather move around to avoid inbreeding, which complicates their whereabouts in the breeding period. This does not exclude that in many species, females take the initiative and enter a male swarm or a lek initiated by males, sometimes even search for males emitting a pheromone produced after acquisition of orchid synomones (Clarke *et al.* 2002, Nishida *et al.* 2022).

But even then, females check the quality of the male through the presence of the character(s), which are markers for whereabouts behaviour. Apparently this is not the only criterion used by the female. As mentioned above, avoiding inbreeding has been shown to influence the female's choice. Rejection of sperm or preference for the sperm of a particular male should thus be regarded as depending on these criteria. The bottom line is that females do not choose a 'superior' male but one that is not akin and fulfils the whereabouts criterion.

Hermaphrodites

The existence of simultaneous hermaphrodites evidently complicates the explanations based on female choice. It has been shown that in some organisms being male and female at the same time, there are several possible mechanisms that can influence the acceptation and selection of the sperm by the partner: transfer of seminal fluid proteins (Nakadera *et al.* 2014 *et al.*) decreasing the success of posterior matings in a pond snail, injection of a dart mediated allohormone inhibiting the digestion of sperm by the partner in large land snails (Koene & Schulenberg 2005). But there is no similar justification for a plethora of land snails with shells of all kinds of sizes and shapes. Schilthuizen (2005) proposed sexual selection as an explanation for the enormous diversity of conchological characters. The observation that these, most often small molluscs mount each other before mating (Lipton & Murray 1979, Schilthuizen 2005), is a strong argument for the importance of the shape and ornamentation of their shells as a prerequisite for their approval as partners. Here again, different ad hoc explanations for the extremely different types of behaviour and morphology are paramount for the sexual selection discourse.

The hypothesis that these are different methods to reach the same goal, be at the right place in the reproduction period, is a simple explanation for the many different markers, dependent on the physical possibilities of different organisms.

Implications

In great contrast with the sexual selection concepts female choice, cryptic female choice and arms race, 'mate check' expects an interspecific range of complexity of which the extremes may become astounding, certainly in templates occupying a large area with many species (e.g. *Hortipes*

Bosselaers & Jocqué, 2000). At each speciation event with the implementation of new niche adaptations, the whereabouts requirements and their linked characters change. Once a certain direction has been taken it is plausible that simple increment of a certain structure is the shortest way at a new marker for mate check: a longer embolus in spiders (Figs 5, 7), an extra group hairs on the aedeagus of a water beetle (Fig. 6), a different set of teeth on the aperture or a different ornamentation of the snail shell, a more complex stridulating sound in many insects, a longer and elaborate tail fan in birds etc. Looking at the individual cases may appear fanciful but in the context of increased specialisation the range of complexity of the mating module and as an example, of copulatory organs, is no longer surprising. The necessary changes of secondary sexual characters therefore do not drive speciation but facilitate it. Without such changes, the meeting of unrelated partners is no longer guaranteed in highly specialised species as already found by MacArthur & MacArthur (1961) and MacArthur & Wilson (1963).

Within the species on the other hand, the marker has to be stable to fulfil its function as a proof for the whereabouts behaviour. The intraspecific structural stability of secondary sexual characters and/or copulatory organs is a *conditio sine qua non* for successful tracing of a partner and reproduction. It is exactly this stability that provides the taxonomist with characters that can be trusted in the majority of the species as elegantly shown in the study of McPeek *et al.* (2008).

However, there are cases of similar species in which there are apparently no such dissimilarities (e.g. Huber *et al.* 2005) although they exhibit large size differences. Polymorph species for which the mate check hypothesis fails to provide an explanation so far (e.g. Wirtz-Ocana *et al.* 2014; Hendrickx *et al.* 2015, 2022),
appear slightly more frequent (Jocqué 2002) but seem to occur in particular circumstances. They are apparently common species occurring in high densities (e.g. *Pelecopsis janus* Jocqué, 1984) and with a long activity period.

The presence of discrete intraspecific differences may throw a light on how sudden a different morph may develop in the course of speciation.

Predictions

We did not yet propose a formal model here but simply formulate a frame, which creates room for discussion about the many as yet unexplained observations summarized above. The whereabouts mate check hypothesis implies that the complexity of the mating module increases with ecological specialisation. Smaller species are therefore expected to develop on average more complex genitalia than larger ones. In a continuum from simple to complex genitalia or the mating module, the extremes, very simple and very complex systems, are expected to be less common than the intermediates as explained in Jocqué & Szüts (2001).

Future work

The main challenge to support the mate check-whereabouts hypothesis remains the definition of the genetic link between morphology and behaviour as shown by Hawthorn & Via (2001). This type of research is clearly still in its infancy but may prove to be most rewarding. Detailed information on requirements of mating localities will be crucial in this context but is lacking for the majority of small animals.

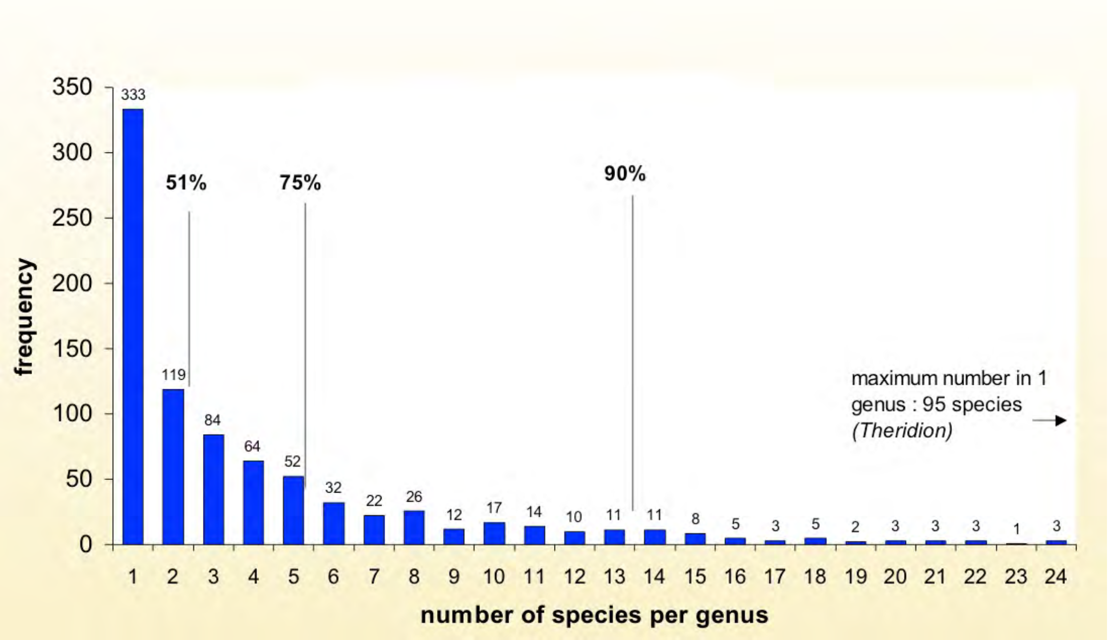

Fig. 8. Number of species per genus in 886 genera of African spiders as mentioned in Dippenaar-Schoeman & Jocqué (1997). The number of monotypic genera reveals the tendency of splitting genera mainly based on secondary sexual characters and copulatory organs, obscuring the templates. (from Jocqué *et al.* 2013)

Avoid the splitting of templates (Fig. 8) and resolve their phylogeny will be another important step for understanding the hypothesis. Morphological analyses often suffered from circular reasoning because simple genitalia were often considered plesiomorphic (e.g. Bosselaers & Jocqué 2000).

It will also be necessary to estimate the encounter time for a male searching a female, calculating the difference between random searching and searching with whereabouts guidelines.

This type of model will need detailed knowledge on the species' niche, on locomotor speed, and population density, most of which are particularly scant.

In a first phase it will therefore be easier to test whether the predictions of the mate check-whereabouts hypothesis tend to be fulfilled.

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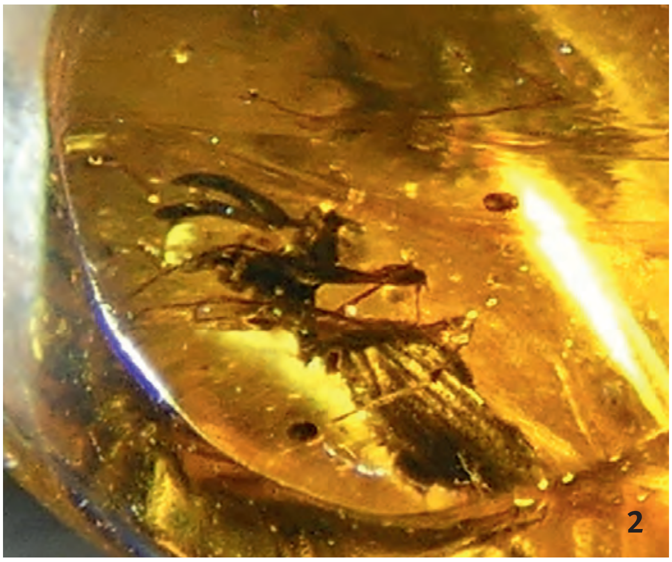
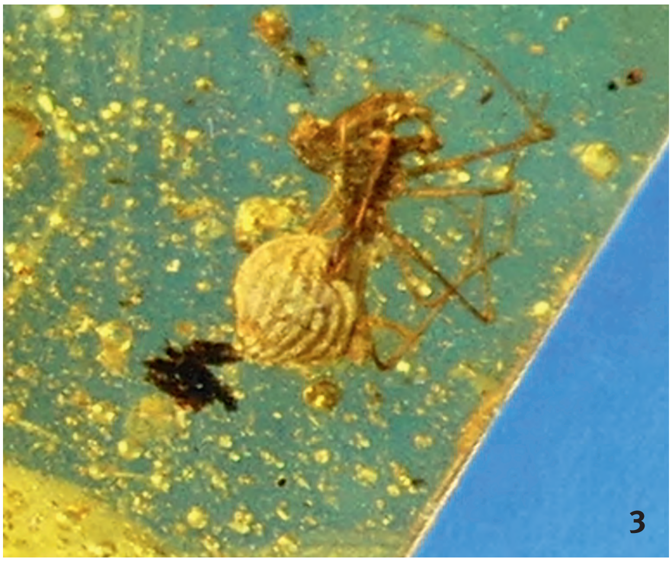
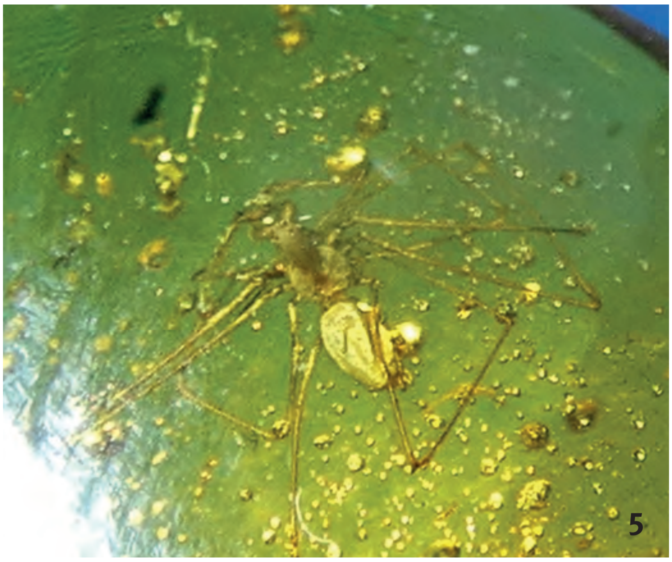
The PHOTOS







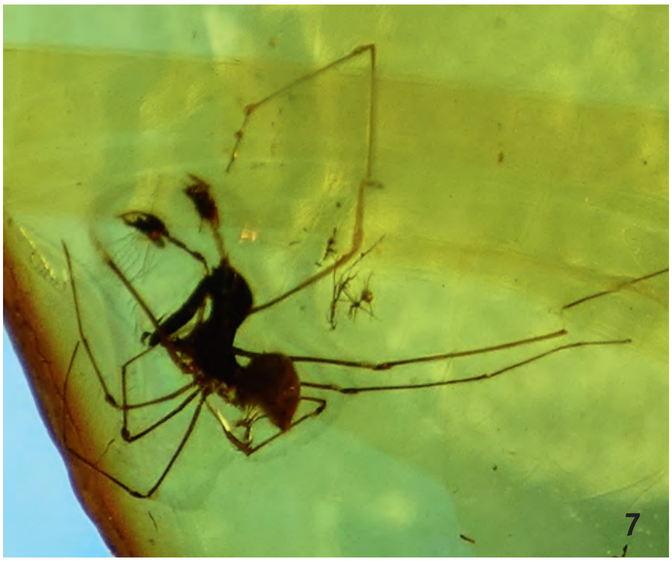
1) ?*Ebrechtella patellamaculata* WUNDERLICH 2023 (Thomisidae), ♂, body length 3.2 mm, extant, Portugal, dorsal aspect.

2) *Burmesarchaea caudata* WUNDERLICH 2015 (Archaeidae), ♂, holotype, body length 2.8 mm, Burmese (Kachin) amber, dorsal aspect.

3) *Burmearchaea spinicaput* **n. sp.** (Archaeidae), ♂, body length 1.9 mm, Kachin amber, lateral aspect.

4) *Lacunauchenius* sp. indet. (Lacunaucheniidae), ♀ F3886/CJW, body length 1.7 mm, Kachin amber, lat. aspect. Note the tiny clypeal horn. Foto: P. Müller.

5) *Planarchaea humilis* **n. sp.** (Planarchaeidae), ♂, body length 1.9 mm, Kachin amber, dorsal aspect.



6) *Planarchaea longipalpitibia* **n. sp.** (Planarchaeidae), ♂, body length 1.5 mm, Kachin amber, lateral aspect.

7) *Planarchaea petersi* **n. sp.** (Planarchaeidae), ♂, body length 1.6 mm, Kachin amber, lateral aspect.

8) *Planarchaea quinquespinae* **n. sp.** (Planarchaeidae), ♂, body length 1.7 mm, Kachin amber, lateral aspect.

9) *Baltplanarchaea oblonga* (WUNDERLICH 2017) (**n. gen.**) (Planarchaeidae), ♀ holotype, F2939/CJW, body length 3.4 mm, Baltic amber, lateral aspect.

10) *Myrmecarchaea sp. indet.* (Archaeidae), ♀, F3885/CJW, body length 2.5 mm, Baltic amber, lateral aspect.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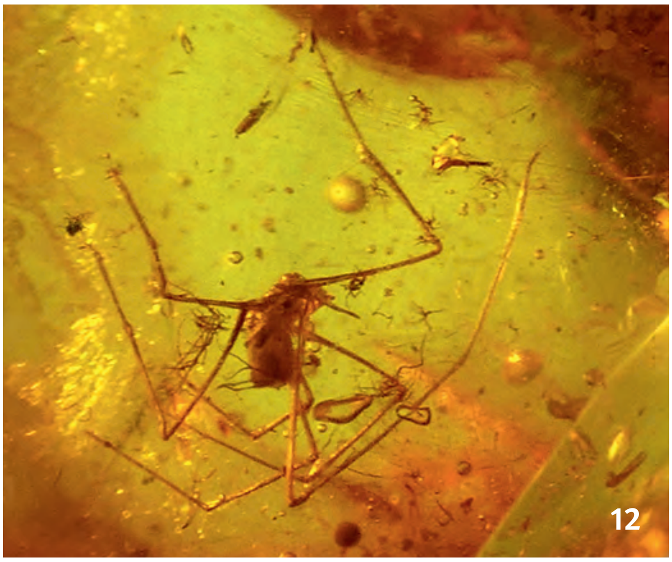
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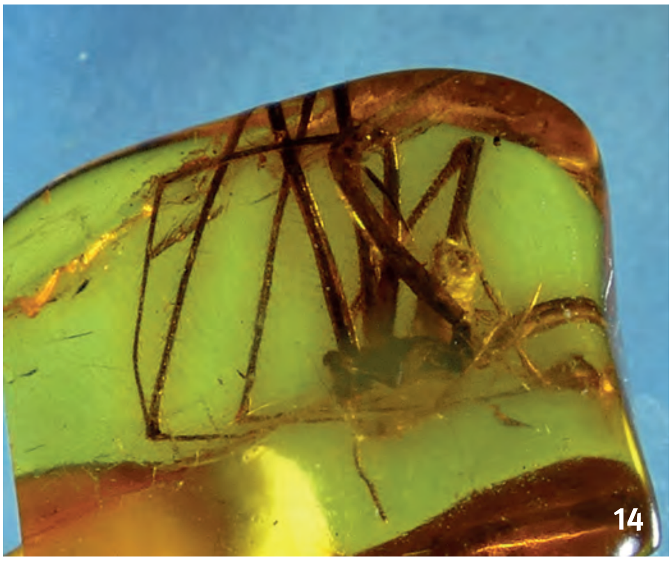
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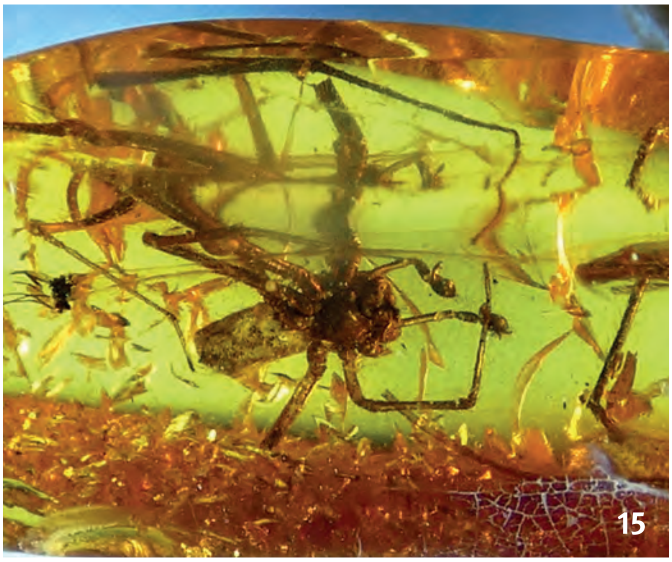
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11) *Cornuanandrus scutatus* **n. sp.** (Synotaxidae), ♂, body length ca. 3.0 mm, Baltic amber, lateral aspect.

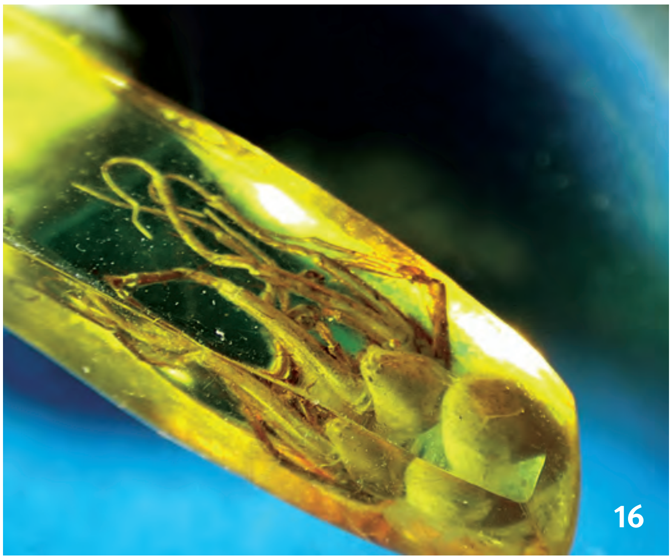
12) *Pseudoacrometa gracilipes* WUNDERLICH 1986 (Synotaxidae), ♀ 3895/CJW, body length ca. 2.5 mm, Baltic amber, lateral aspect.

13) *Balticonesticus acuminatus* **n. sp.** (Nesticidae), ♂, body length 2.0 mm, Baltic amber, anterior-lateral aspect.

14) *Balticonesticus rectus* **n. sp.** (Nesticidae), ♂ holotype, body length ca. 2.7 mm, Baltic amber, lateral aspect.

15) *Heteronesticus rectus* **n. sp.** (Nesticidae), ♂ paratype, F3916/CJW, body length 3.0 mm, Baltic amber, lateral aspect.

15a



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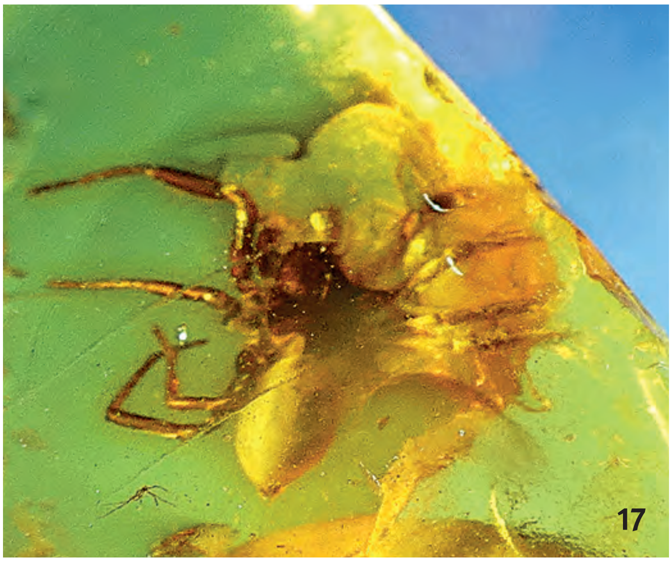

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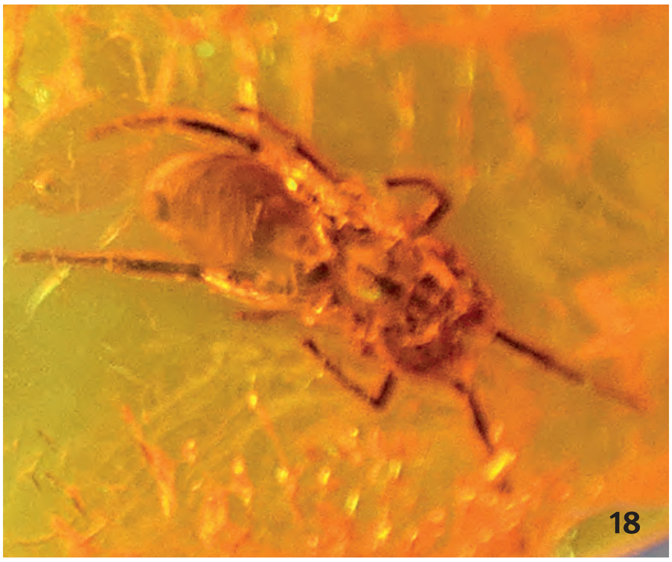

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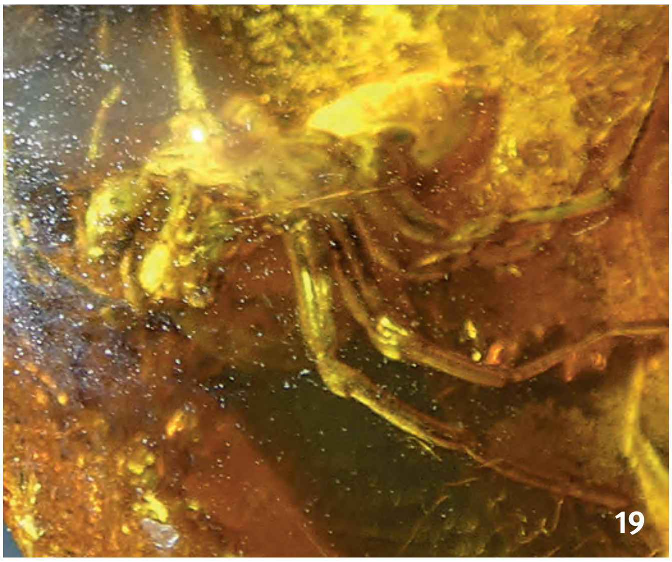

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15a) Heteronesticus sp. indet. 1 (Nesticidae), ♂ F3920/CJW, body length 2.0 mm, Baltic amber, dorsal aspect. – Note the large and erect paracymbium.

16) ?*Mimetus flexuosus* **n. sp.** (Mimetidae), ♂, body length 4.0 mm, Baltic amber, dorsal aspect.

17) *Angusdarion humilis* WUNDERLICH 2004 (Zodariidae), ♂ F3893/CJW, body length ca. 3.3 mm, Baltic amber, dorsal aspect.

18) *Pectenzodarion unicum* **n. sp.** (Zodariidae), ♂, body length 4.3 mm, Baltic amber, ventral aspect.

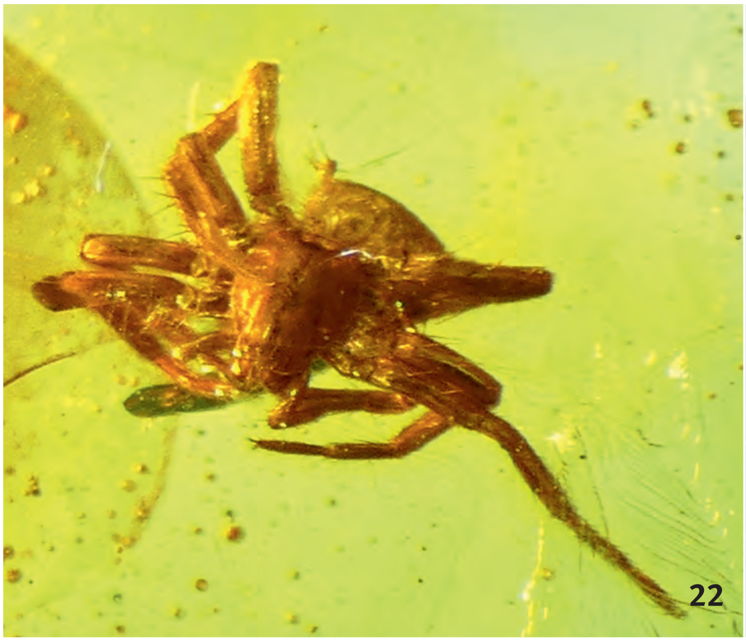
19) Zodariidae indet., ♂, body length ca. 8 mm, Baltic amber, ventral aspect.

20

21

20-21) *Phoresy and parasitism by arachnids on the surface of the same beetle* (Elateridae, body length 8 mm), F3928/CJW, Baltic amber. The long arrow points to the phoretic spider, the short arrow points to the two parasitic mites. See p. 91f. – Photos: Jonas Damzen.

22) Parasitic juv. Acari indet., body length 0.13 mm, sucking blood from a juv. spider of the family Insecutoridae, body length ca. 2.8 mm, F2421/CJW, Baltic amber, anterior-dorsal aspect.



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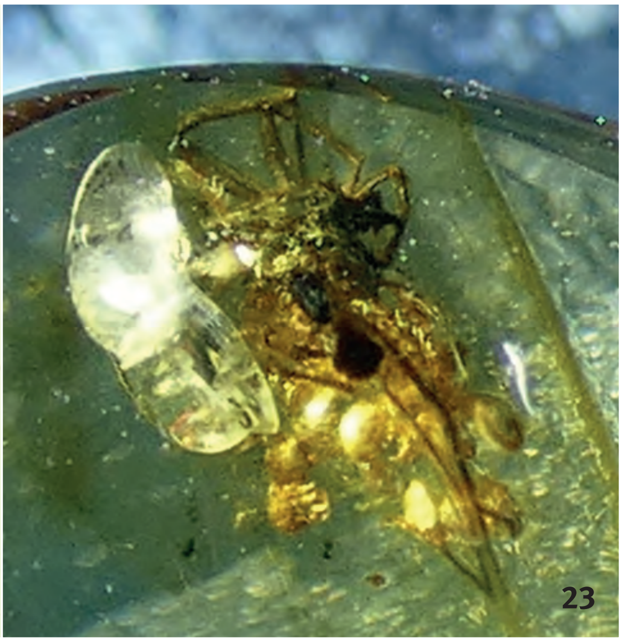

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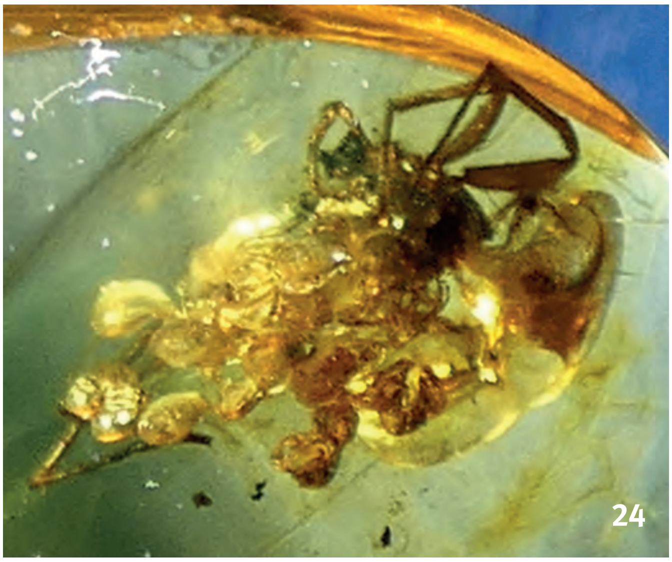
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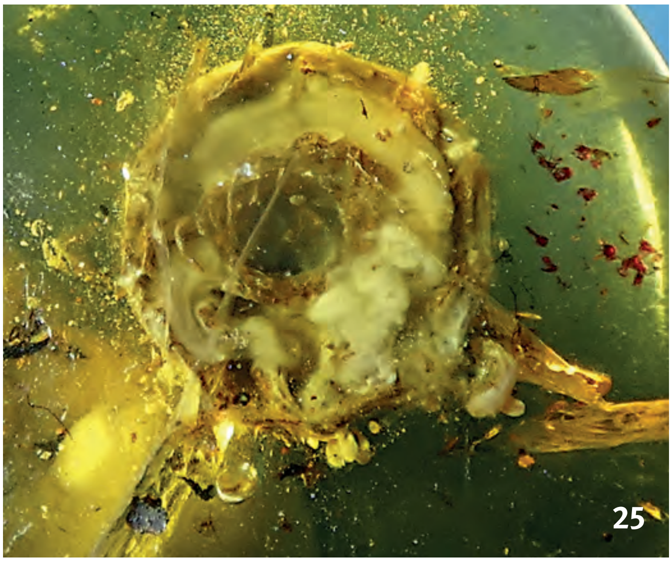
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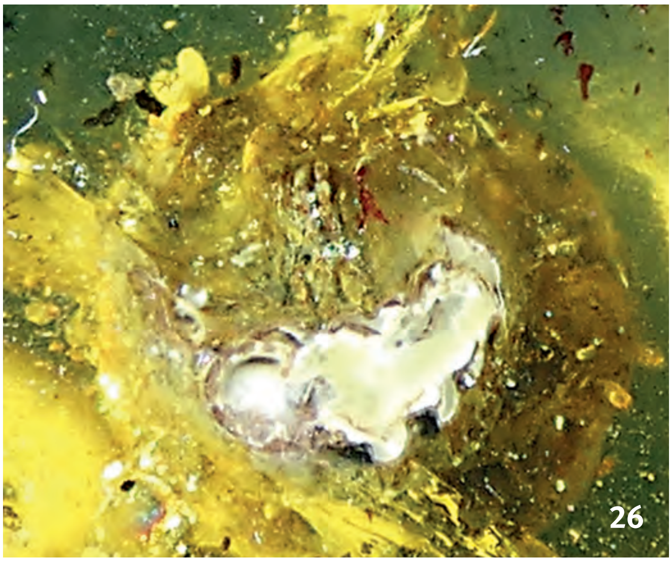
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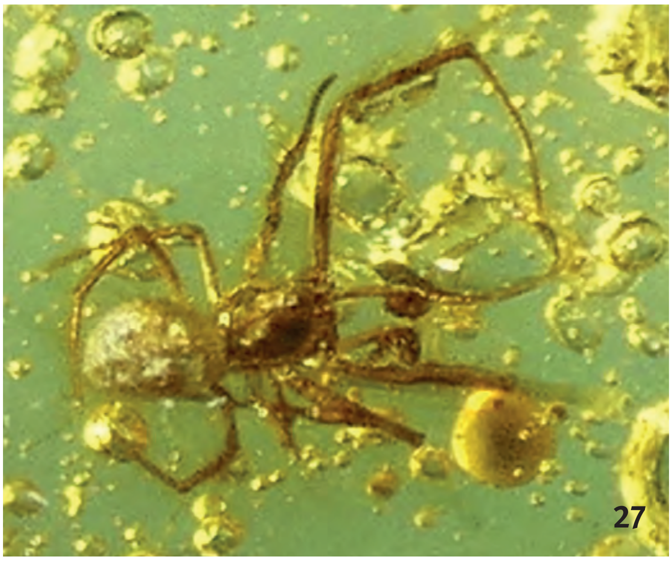
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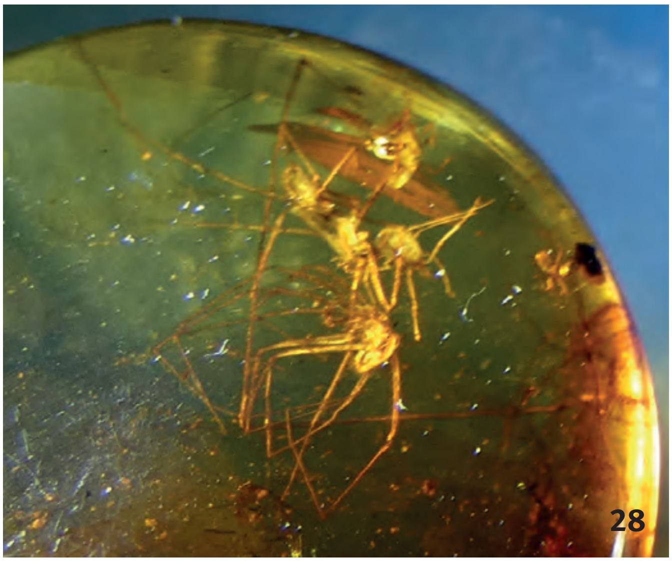
23-24) Parvosegestria sp. indet. (Segestriidae, body length ca. 2 mm) carrying eggs and hatching offspring, F3940/CJW, Kachin amber, dorsal and ventral aspect.

25-26) Questionable moulting chamber of a Diplopoda which is partly cut off, diameter 6-7 mm, F3941/CJW, Kachin amber, two aspects.

27) *Furzarqa incerta* **n. sp.** (Zarqaraneidae), ♂, body length 1.1 mm, Kachin amber, dorsal aspect.

28) *Eopsiloderces* sp. indet. (Eopsilodercidae), deformed male and female, body length ca. 2.3 mm, F3923/CJW, Kachin amber.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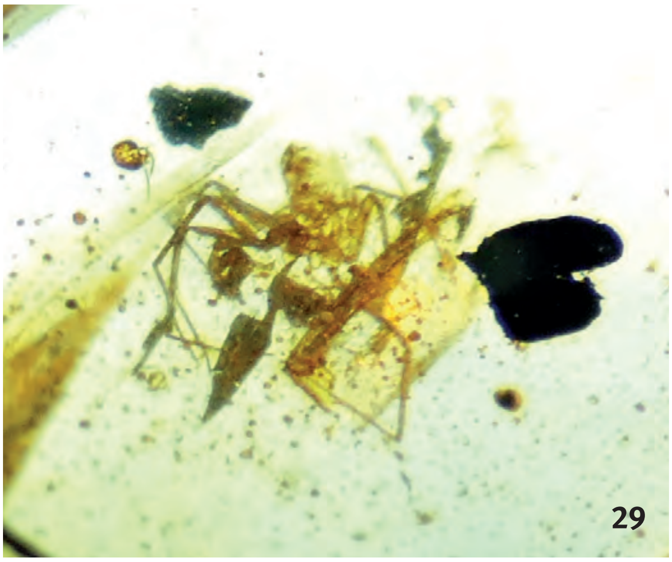

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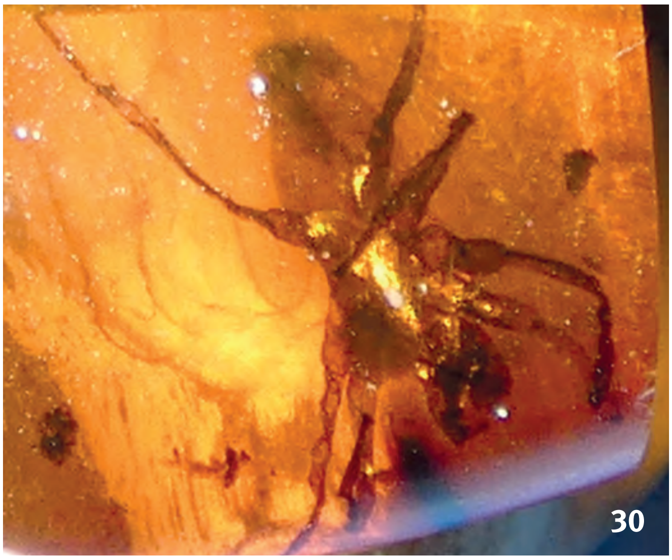

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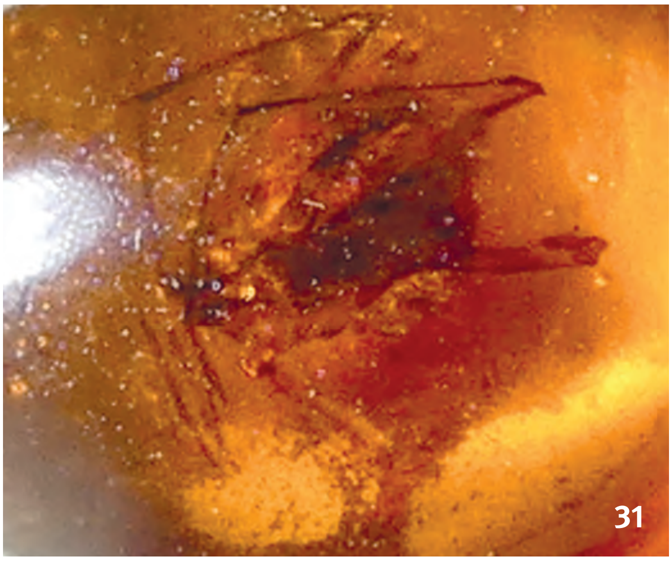

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29) *Palaeoleptoneta* sp. indet. (Leptonetidae), deformed ♂, F3922/CJW, body length 0.7 mm, and a larger arthopod leg, Kachin amber, dorsal aspect.

30) *Fushunpalpimanus exuviae* **n. gen. n. sp.** (Palpimanidae), exuviae, ♀, length of the peltidium (above) 3.0 mm, Fushun amber, ventral aspect.

31) Theridiidae indet. (Theridiidae), probably adult ♀, F3911/CJW, body length ca. 2.2 mm, dark Fushun amber, dorsal aspect.

32) Impression of a questionable member of the extinct arachnid order Trigogotarbida in a stone, Upper Carboniferous, ca. 320 million years old, F3925/CJW, body length ca. 2 cm, S-Portugal.