ISRAEL JOURNAL OF ENTOMOLOGY, Vol. 53, pp. 93–112 (22 July 2024)

On the liphistiomorph trichobothria and the significance of their structure for tracking the bothria evolution in the order Araneae

Kirill Y. Eskov[1], Sergei L. Zonstein[2] & Yuri M. Marusik[3*]

[1] *Borissiak Paleontological Institute, Russian Academy of Sciences, 123 Profsoyuznaya Str.,*
Moscow, 117647, Russia. E-mail: afranius999@gmail.com
[2] *The Steinhardt Museum of Natural History, 12 Klausner Str.,*
Tel Aviv, 69978, Israel. E-mail: serzon56@gmail.com
[3] *Institute for Biological Problems of the North, 18 Portovaya Str., Magadan, 685000, Russia;*
Department of Zoology & Entomology, University of the Free State,
Bloemfontein, 9300, South Africa;
Altai State University, 61 Lenina Pr., Barnaul, RF-656049, Russia.
E-mail: yurmar@mail.ru
**Corresponding author*

ABSTRACT

Femoral trichobothria in liphistiomorph spiders are re-discovered and described for the first time. Present in both Liphistiidae and Heptathelidae, they turned out to be another synapomorphy of this suborder. The trichobothria of Liphistiomorphae, situated dorsally on the distal leg/palp joints (as usual in spiders), and ventrally on femora, possess sharply dissimilar bothria; two types of trichobothrial bases in the same species are a unique case among Arachnida. The morphology of the bothria in the liphistiomorphs has been compared with those in the mygalomorphs and araneomorphs, as well as those in the tetrapulmonate and non-tetrapulmonate arachnid orders. The evolution of the bothrial types in all three main lineages of the Araneae seems to have been parallel.

KEYWORDS: Aranei, Mesothelae, bothrial evolution, bothrial morphology, femoral trichobothria, trichia.

INTRODUCTION

Trichobothria is a conspicuous type of mechanoreceptive sensilla in terrestrial arthropods. They are straight strongly elongated setae (trichia) set in a deep cup-like socket, the bothrium. Both structures may be modified in some way. For instance, in Acari the bothria are highly uniform simple cups, whereas setae are in some cases strongly transformed, even globular (Alberti & Coons 1999: fig. 348A–D); by contrast, in Araneae trichobothrial setae are quite uniform, whereas trichobothrial bases are very diverse (see Ramírez 2014).

The only particular type of trichobothrial setae known in the spiders is the ‘clavate’, or ‘club-shaped’, trichobothria in some Orthognatha lineages: “The difference between the typical filiform trichobothria of any spider and clavate trichobothria is basically the thicker distal portion, and both have a similar base (bothrium). Therefore, the clavate trichobothria surely derived from typical filiform trichobothria” (Mori & Bertani 2020: 12).

DOI: 10.5281/zenodo.12790018; ISSN (online) 2224-6304
Received: 23 June 2024 / Revised: 3 July 2024 / Accepted: 14 July 2024
urn:lsid:zoobank.org:pub:21CADACD-586B-4C94-BDF2-D13425324C57

In *Liphistius* Schiødte, 1849, the clavate trichobothria (Murphy & Platnick 1981, figs 5, 6) are present in addition to the filiform ones, and have been stated as a genus synapomorphy (Platnick & Sedgwick 1984). In another liphitiomorph genus, *Heptathela* Kishida, 1923 (elevated now up to the subfamily/family level and divided into several genera: Xu *et al*. 2015; Sivayyapram *et al*. 2024), only the filiform trichbothria are recorded (Platnick & Sedgwick 1984). Recently, Wunderlich (2017) described three extinct liphistiomorph families (Burmathelidae, Cretaceothelidae and Parvithelidae) from the mid-Cretaceous Burmese amber, and specially remarked that they all lacked the club-shaped trichobothria, in contrast to the extant monogeneric Liphistiidae.

In Mygalomorphae, the clavate/club-shaped trichobothria are recorded in all Theraphosidae and in the majority of Barychelidae (Guadanucci 2012), in all Ummidiinae (but not in another halonoproctid subfamily, Halonoproctinae: Decae *et al*. 2021), and in a single genus of Idiopidae, *Prothemenops* Schwendinger, 1991 (Schwendinger & Hongpadharakiree 2014). All the paratropidid and nemesiid genera with clavate trichobothria listed by Raven (1985) are relocated now to Theraphosidae or Barychelidae; the indication of clavate trichobothria for Dipluridae by Lehtinen (1980) has never been confirmed (including our own observations) and seems erroneous.

The clavate trichobothria of liphistiomorphs and mygalomorphs are considered usually as parallel autapomorphies in these lineages, being non-homologous (Lehtinen 1980; Goloboff 1993). However, few concrete arguments for this commonplace opinion have been presented:

(1) "None of the mygalomorph clavate trichobothria yet observed with scanning electron microscopy have the circularly arranged rows of tiny spikes typical of the liphistiid forms" (Murphy & Platnick 1981: 51);

(2) "In *Liphistius* [...] there are alternating, distinct rows of clavate and filiform trichobothria [...]. In the theraphosoids and some ctenizids and idiopids, in contrast, the clavate trichobothria are interspersed among the filiform ones" (Goloboff 1993: 14).

In addition, Raven (1985: 22) noted that the clavate trichobothria are recorded in several unrelated advanced lineages, "but are not present in any of the plesiomorphic mygalomorph families".

However, the above-mentioned morphological differences seem overrated. In *Liphistius* the clavate trichobothria, in fact, are "interspersed among the filiform ones" in the same way as in mygalomorphs (Fig. 1A cf. Fig. 1D). In theraphosids and barychelids "rows of tiny spikes" on setal shaft surface clearly differ from the *Liphistius* ones, being sufficiently smaller and arranged in longitudinal (non-oblique) rows (Fig. 1C cf. Fig. 1E; Guadanucci 2012, figs 18, 134), whereas the clavate trichobothria of the halonoproctid genus *Ummidia* Thorell, 1875 (Fig. 1F) and the idiopid genus *Prothemenops* (Schwendinger & Hongpadharakiree 2014, fig. 1C) seem indistinguishable in this respect from the *Liphistius* ones (Fig. 1C).

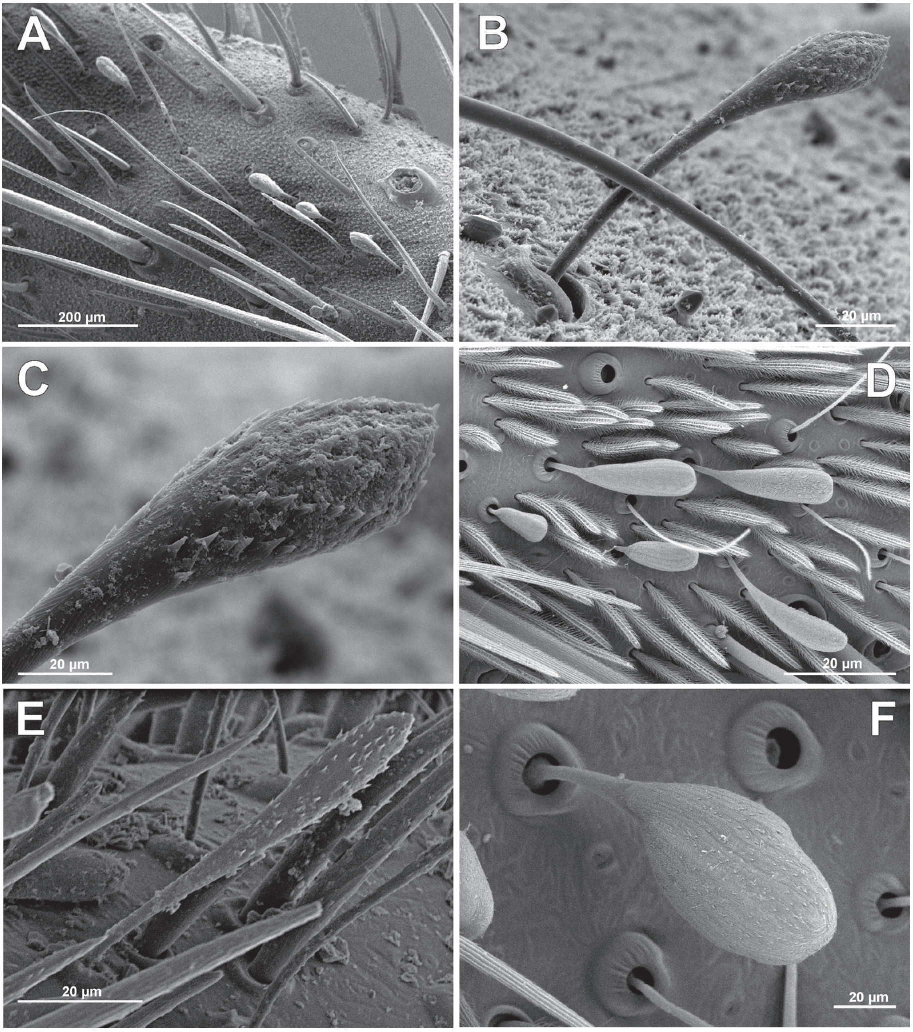

Fig. 1: Clavate trichobothria of Liphistiidae and Myalomorphae on tarsus III (A–C, E, F) and II, showing also filiform trichobothria (D): (A, C) *Liphistius desultor* (Liphistiidae), (C) same, enlarged, (D) *Hapalopus formosus* (Theraphosidae), (E) *Ischnocolus meron* (Theraphosidae), (F) *Ummidia gandjinoi* (Halonoproctidae).

Therefore, the opposite polarity of this character may be proposed. The clavate trichobothria are a synapomorphy of the order Araneae, with its subsequent parallel loss in all liphistiomorphs outside *Liphistius*, in the majority of the mygalomorph lineages (including the same ones as Raven's "plesiomorphic mygalomorph families"), and in all the araneomorphs.

We do not insist on this exact interpretation, especially because under this hypothesis clavate trichobothria are considered a plesiomorphic condition of the order and, in any event, are incapable to confirming a close relationship between the 'club-bearing' taxa. Nevertheless, these unusual trichobothria have been repeatedly discussed, from their discovery in *Liphistius* by Abraham (1930) until now (e.g. Lin & Li 2023). Most likely, just because this exotic structure attracted the entire attention of researchers, the two other, more important in our opinion, features of liphistiomorph trichobothria avoided such attention.

First, only three unrelated spider lineages, i.e. uloborids, some tetragnathids and the aberrant genus of giant linyphids *Orsonwelles* Hormiga, 2002, were reported to possess the femoral trichobothria (Hormiga, 2002: 176). Lehtinen (1980: 497) discovered them in the liphistiomorphs, both liphistiids and heptathelids, but Raven (1985: 21) confidently rejected that record: "Contrary to Lehtinen (1980), no femoral trichobothria occur in any known liphistiid or mygalomorph". However, our data clearly support the Lehtinen's statement.

Second, Platnick and Gertsch (1976: 9–12) found out that the morphology of the bothria radically differs in the liphistiomorphs and all other spiders, and stated that this character was one of the three synapomorphies of the suborder Mesothelae: "The morphology of the trichobothria [...] appears to differ in liphistiids and other spiders. [...] Most [mygalomorphs] have a base consisting of a rounded dome covered on one side by a flattened plate [...]. Other [mygalomorph] genera have a dome only (although it may bear numerous parallel wrinkles or ridges) [...] The Araneomorphae have not yet been surveyed in as great detail but preliminary results [...] show the dome and single plate structure to be widespread in that group. Both *Liphistius* and *Heptathela*, however, show a different structure, involving a dome and two flattened plates [...]. Investigation of an amblypygid trichobothrium [...] shows no dome or plate surrounding the socket; we therefore regard both the two plate (3a) and single plate or simple dome (3b) conditions as being derived."

Unfortunately, these particular liphistiomorph bothria were further mentioned, but once and in passing, only by Raven (1985: 21) in his attempt at the classifying of mygalomorth bothrial types: "The Mesothelae have two short crescentic opposed plates"; after that they completely disappeared from investigators' focus. Surprisingly, a couple of half-a-century-old micrographs by Platnick and Gertsch (1976, figs 9, 11) are still the only images of these structures, despite dozens of modern publications on liphistiomorph taxonomy and phylogeny.

Now it has turned out, in the course of our wide-scale study of spider trichobothria, that liphistiomorphs, in addition to the setal shafts of two dissimilar types, possess bothria of two types as well. They are located dorsally on terminal leg joints and ventrally on femora, and this case seems unique among arachnids. The subject of this study is a comparison of the bothrial morphology in the liphistiomorphs and other spider lineages, as well as in other arachnid orders, with some conclusions on the possible evolution of these structures.

MATERIALS AND METHODS

SEM images were taken on a Tescan Vega2 and a Tescan Vega3 scanning electron microscopes (Brno, Czech Republic) in the Borissiak Palaeontological Institute, Russian Academy of Sciences (Moscow), operated in a high vacuum mode at the accelerating voltages 10–20 kV, using SE and BSE detectors. The specimens were gradually dehydrated in 100 % ethanol, dried, and sputtered with goldpalladium.

The studied specimens are stored in the following institutions:

AMNH – American Museum of Natural History, New York, USA;
MACN – Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina;
MMUE – The Manchester Museum, University of Manchester, UK;
RMCA – Royal Museum for Central Africa, Tervuren, Belgium;
SMNHTAU – Steinhardt Museum of Natural History, Tel Aviv, Israel;
ZMMU – Zoological Museum of the Moscow State University, Moscow, Russia;
ZMTU – Zoological Museum, University of Turku, Finland.

The following material has been examined for this study:

Araneae: Liphistiomorphae
Family Liphistiidae Thorell, 1869
Liphistius desultor Schiødte, 1849

Malaysia: 1♀, Penang, vii.1977, "coll. E.W.C." [N.I. Platnick det., 1983] (MMUE).

Liphistius panching Platnick & Sedgwick, 1984

Malaysia: 1♀, Gua Panching, 31.vii.1982, W. Sedgwick [N.I. Platnick det., 1984] (AMNH).

Family Heptathelidae Kishida, 1923
Heptathela sp.

Japan: *Kyushu Isl.*: 1♀, environs of Beppu, 7.vii.1973, A.G. Ponomarenko, forest litter (ZMMU).

Vinathela sp.

Vietnam: 1♀, central Vietnam, 12°35'39.2"N 108°44'18.3"E, 26.i.2024, Khang Nguyn (ZMMU).

Araneae: Mygalomorphae
Family Dipluridae Simon, 1889
Diplura aff. *sanguinea* (F. O. Pickard-Cambridge, 1896)

Peru: *Junin Region*: 1♀, 10 km SE from Satipo, Paratushali, 22.ix.2017, K. Eskov, webs under logs (SMNHTAU).

Family Halonoproctidae Pocock, 1901
Ummidia gandjinoi (Andreeva, 1968)

Tajikistan: *Khatlon Region*: 1♀, Khovaling, 38°20'N 70°00'E, 11.x.1987, S. Zonstein (SMNHTAU).

Family Macrothelidae Simon, 1892
Macrothele sp.

Vietnam: 1♀, Cat Tien NP, 11.458922°N 107.364657°E, 25.i.2024. D. Osipov (ZMMU).

Family Migidae Simon, 1889
Goloboffia megadeth Ferretti, Ríos-Tamayo & Goloboff, 2019

Chile: *Coquimbo Region*: 1♀, Monte Redondo, 15 km N de Manto de Hornillos, 1.xi.1988, P.A. Goloboff, E.A. Maury & C.L. Szumik [C.J. Grismado det.] (MACN-Ar-36131).

Moggridgea aff. *anactenidia* Griswold, 1987

Cameroon: 1♂, Réserve de faune du Dja, 6.v.2005, I. Deblauwe (RMCA-ARA-219538).

Paramigas perroti (Simon, 1891)

Madagascar: 1♂, without exact locality, date or collector's name [P.L.G. Benoit det., 1962] (RMCA-ARA-122888).

Family Pycnothelidae Chamberlin, 1917

Acanthogonatus confusus Goloboff, 1995

Chile: *La Araucana Region*: 1♀, Temuco, Cerro Nielol National Monument, 21.i.2014, K. Eskov & D. Shcherbakov, *Nothofagus* forest, under logs (SMNHTAU).

Family Theraphosidae Thorell, 1869

Hapalopus formosus Ausserer, 1875

Colombia: 1♀, without exact locality, date or collector's name (ZMMU).

Ischnocolus meron Zonstein, 2023

Israel: *Upper Galilee*: 1♀, Mt Meron, 16.vi.2020, S. Zonstein (SMNHTAU).

Araneae: Araneomorphae

Family Araneidae Clerck, 1757

Argiope bruennichi (Scopoli, 1772)

Azerbaijan: 1♀, Kashkachai, 27.viii.1977, P. Dunin (ZMMU).

Family Malkaridae Davies, 1980

Chilenodes australis Platnick & Forster, 1987

Chile: *Chiloe Isl*.: 1♂, Senda Darwin Biological Station (15 km E of Ancud), 41°52'56'"S 73°40'04"W, 3–4.i.2014, K. Eskov, lowland forest of *Nothofagus* and *Podocarpus*, in litter (ZMMU).

Family Synotaxidae Simon, 1895

Synotaxus sp.

Equador: 1♀, Orellana, Tiputini Biodiversity station, nr Yasuni Nat. Park, Erwin Transect – T/1 Sta.1, 00°37'55"S 76°08'39"W, 8.xi.1999, 220–250 m, T.L. Erwin *et al.* , Lot # 2027 (USNM).

Family Theridiidae Sundewall, 1833

Euryopis flavomaculata (C. L. Koch, 1836).

Russia: *Moscow Region*: 1♀, Prioksko-Terrasny Reserve, Protokskoye Lake, 31.v.2014, R.R. Seifulina (ZMMU).

Amblypygi

Family Charinidae Guintero, 1986

Charinus sp.

Peru: *Junin Region*: 1 subad. (♀?), Pichiquia, 11°23'07"S 74°06'05"W, 500 m, 26.ix.2017, K. Eskov, valley forest, under bark of logs (ZMMU).

Uropygi

Family Thelyphonidae Lucas, 1835

Thelyphonus (?) sp.

Vietnam: 1♀, 5 km N of Ankhe, 21.x.1979, Y.K. Yanushev, under stones (ZMMU).

Schizomida

Family Hubbardiidae Cook, 1899

Trythyreus (?) sp.

Peru: *Junin Region*: 1♀, 16 km NW from Satipo, Rio Venado, 1120 m, 14.ix.2017, K. Eskov, slope forest, in litter (ZMMU).

Scorpiones

Family Buthidae C.L. Koch, 1837

Mesobuthus parthorum (Pocock, 1889)

Turkmenistan: 1♀, Kaplynkyr, 26.vi.1985, L.A. Mitroshina, under *Xylosalsola* bushes [V.Y. Fet det.] (ZMMU).

Pseudoscorpionida

Family Cheliferidae Rosso, 1827

Chernes cimicoides (Fabricius, 1793)

Ukraine: *Cherkassy Region*: 1♀, Kanev State Reserve, 25–29.v.1988, S. Golovatch & L. Penev, *Carpinus* forest [W. Schawaller det.] (ZMMU).

Family Neobissidae Chamberlin, 1930

Neobissium crassifemoratum (Beier, 1928)

Russia: *Krasnodar Province*: 1♀, Caucasian State Reserve, Palukh, ca. 20 km E of Krasnaya Polyana, 18–20.v.1985, S. Golovatch [W. Schawaller] (ZMMU).

RESULTS

Preliminary notes on the bothrial morphology in araneomorphs and mygalomorphs

Before discussing the comparative morphology of bothria in the Liphistiomorphae, it seems necessary to summarize what is known in this respect about bothria in the better studied Mygalomorphae and Araneomorphae. First of all, the used terminology should be unified.

Platnick and Gertsch (1976) distinguished two bothrial types in the Mygalomorphae: ‘a rounded dome covered on one side by a flattened plate’ vs. ‘a dome only, bear numerous parallel [radial] wrinkles’, and recognized two similar bothrial types, named ‘the dome and single plate structure’, in Araneomorphae as well. The two abovementioned mygalomorphae bothrial types perfectly correspond to the ‘collarlike bothria’ and ‘corrugiform bothria’ *sensu* Raven (1985: 21).

The structure of the trichobothria and the naming of their divisions in Araneomorphae are more detailed: “The socket forms a cup or bothrium, with an ample central cavity. The opening of the cup (alveolus) restricts the movement of the setal shaft. The bothrium is usually divided in proximal and distal plates; the proximal plate is often called trichobothrial ‘hood’.” (Ramírez 2014: 124–125). Miller (2007: 30) distinguished two opposite types in the bothria of the Araneoidea: ‘hooded’ and ‘evenly rounded and lack a hood’; these clearly correspond to ‘the dome and single plate structure’ *sensu* Platnick and Gertsch (1976).

A basal (‘hooded’) araneomorph bothrium consists of the following structures: a more or less flattened distal plate with a rounded opening for a setal shaft; a more or less swollen proximal pate (‘hood’) with its distal margin forming a clear transversal ridge; and a cuticular fold that delimits the bothrium from the front, termed here the ‘frontal fold’ (Fig. 2A; see also Ramírez 2014, fig. 84D).

Bothrium transformations were studied in detail and on a large scale in Dionycha by Ramírez (2014: character 176): “Trichobothria proximal and distal plate limit: 0. Well differentiated. The distal margin of the trichobothrial hood is well defined, often overhanging the distal plate and the opening of the socket [...]. 1. Not well differentiated. The distal margin of the hood is tenuous, superficial, not well marked [...]. 2. Homogeneous. The bothrium is smooth, without distinction into proximal and distal plates [...]. States are ordered, as state 1 is intermediate between states 0 and 2”.

Exactly the same regularities were discovered also in Araneoidea by Eskov and Marusik (unpubl. data). The basal type in the superfamily is a ‘hooded’ bothrium with a well-developed transversal ridge dividing its proximal and distal plates (‘*Erigone*-type’; Fig. 2A); the terminal type is a solid dome-shaped bothrium, where proximal and distal plates are completely fused without vestiges of the ridge (‘*Theridion*-type’; Fig. 2D); and there are several intermediate types reflecting various ways and stages of the ridge reduction (united as ‘*Argiope*-type’; Fig. 2B, C).

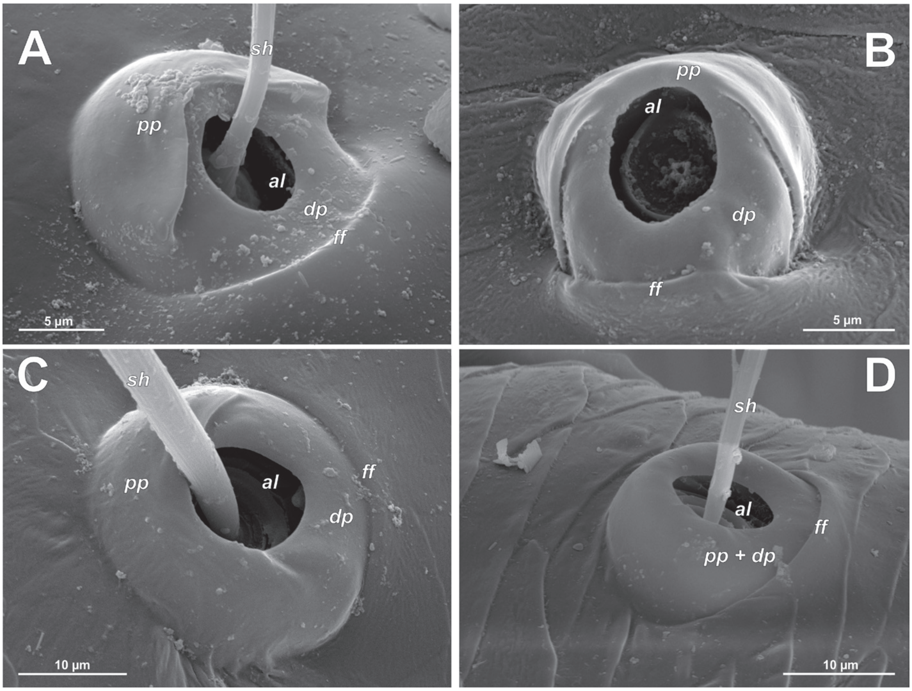

Fig. 2: Bothrial morphology in araneomorph superfamily Araneoidea, showing basal '*Erigone*-type' (A), intermediate '*Argiope*-type' (B, C) and terminal '*Theridion*-type' (D) constructions: (A) *Chilenodes australis* (Malkaridae), (B) *Synotaxus* sp. (Synotaxidae), (C) *Argiope bruennichi* (Araneidae), (D) *Euryopis flavomaculata* (Theridiidae). Abbreviations: al – alveolus, dp – distal plate, dp+pp – completely fused distal and proximal plates, ff – frontal fold, pp – proximal pate ('hood'), sh – setal shaft.

Raven (1985: 21) found that the collarlike bothria are restricted to the basal Mygalomorphae lineages, whereas the distal lineages possess the corrugiform bothria. The principal structure of the mygalomorph collarlike bothria perfectly corresponds to the basal araneomorph hooded bothria: a 'distal plate' with an opening for the shaft, a 'proximal pate' with a deep notch on its distal margin (a 'collar'), and a cuticular 'frontal fold' (cf. Figs 3A and 2A).

As in araneomorphs, there is a general trend of transforming the basal mygalomorph bothrial type, collarlike (Fig. 3A), to the terminal type, corrugiform, where the proximal and distal plates are completely fused into a single dome (Fig. 3C), via the intermediate types, where the border between fused proximal and distal plates is still traceable (Fig. 3B). Interestingly, this trend, general for the suborder, may sometimes be recognized at the family level as well, e.g. in Migidae (Fig. 3D–F). So, the principal structures of the bothria and the general trends of their transformation in both Mygalomorphae and Araneomorphae seem to be parallel.

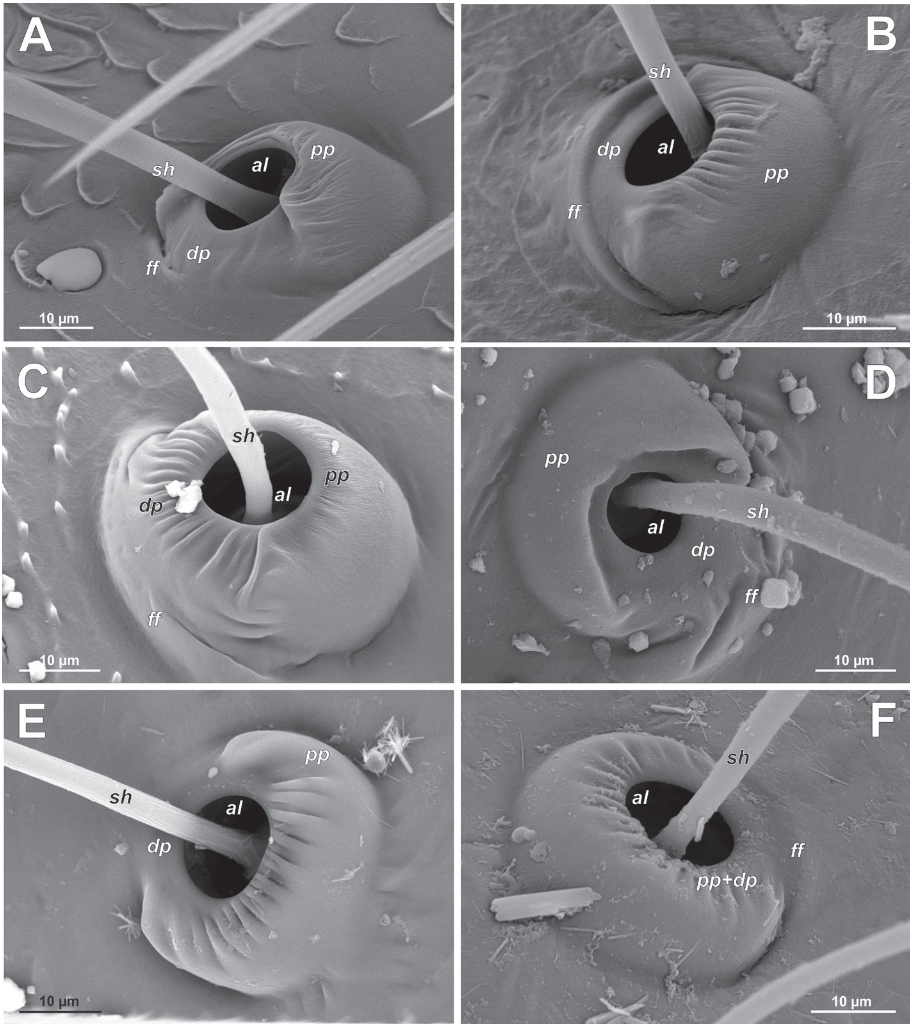

Fig. 3: Bothrial morphology in Mygalomorphae, showing basal collarlike (A, D), intermediate (B, E) and terminal corrugiform (C, F) types of construction: (A) *Macrothele* sp. (Macrothelidae), (B) *Acanthogonatus confusus* (Pycnothelidae), (C) *Diplura* sp. aff. *sanguinea* (Dipluridae), (D) *Goloboffia megadeth* (Migidae), (E) *Moggridgea* sp. aff. *anactenidia* (Migidae), (F) *Paramigas perroti* (Migidae). Abbreviations: al – alveolus, dp – distal plate, dp+pp – completely fused distal and proximal plates, ff – frontal fold, pp – proximal pate (a 'collar'), sh – setal shaft.

Two dissimilar types of bothria in Liphistiomorphae

Platnick and Gertsch (1976: 12) described a unique and autapomorphic, in their opinion, bothrial morphology of liphistiomorphs in this way: "Both *Liphistius* and

Heptathela, however, show a different [from all Opisthothelae] structure, involving a dome and two flattened plates (figs 9, 11); in the latter genus the dome is recessed considerably below the plates". Raven (1985: 21) laconically noted that "The Mesothelae have two short crescentic opposed plates."

First of all, these descriptions refer only to the trichobothria arranged on the dorsal surface of the distal joints of the legs and palps, as usual in spiders (Fig. 4A, see also Fig. 1A). However, the Liphistiomorphae have also another, previously undescribed, type of trichobothria arranged in two longitudinal rows on the ventral surface of the femora (Fig. 4C) and represented by drastically different bothria. Let us therefore homologize the parts of these dissimilar liphistiomorph bothria (termed 'dorsal' and 'ventral' in this study) with each other, as well as with the mygalomorph and araneomorph ones.

The starting point in our interpretation of the 'dorsal bothria' structure is the recognition of the central diaphragm, or 'dome' according to Platnick and Gertsch (1976), due to its opening for the setal shaft, as the distal plate of both the 'hooded' araneomorph and 'collarlike' mygalomorph bothria (Fig. 4B cf. Figs 2A, 3A). If this is correct, the 'two crescentic opposed plates' (after Raven 1985), posterior and anterior, correspond to the proximal plate ('hood'/'collar') and to the 'frontal fold', respectively. So, the 'dorsal bothria' type of Mesothelae is nothing more than the basal bothrial type ('hooded'/'collarlike') of both Opisthothelae lineages *in statu nascendi*.

At the same time, the 'ventral bothria' of liphistiomorphs perfectly correspond to the terminal types of the solid dome-shaped bothria in both araneomorphs and mygalomorphs, and the distal and proximal plates, forming a dome, are distinguishable in at least some genera (Fig. 4D).

Thus, the case of Liphistiomorphae is twice as interesting in this respect. First, the presence of two types of bothria in the same spider is a unique case within the entire order (and, as it is known, in the entire class Arachnida). Second, exactly these two bothrial types reflects the entire sequence in the development of this structure in the Araneae.

Evolution of the bothria in the suborder Liphistiomorphae may be traceable through the comparison of representatives of both families, Liphistiidae (*Liphistius*) and Heptathelidae (*Heptathela* and *Vinathela* Ono, 2000).

The basal type of the 'dorsal bothria' is obviously the bothria of *Heptathela*, in which both 'crescentic opposed plates' arising on the posterior and anterior edges of the primary bothrial cup are almost equal in shape and size (Fig. 5A, B). In *Liphistius*, the posterior plate is relatively upsized, whereas the anterior one is somewhat downsized (Fig. 5C, D). Finally, in *Vinathela* the posterior plate is enlarged and modified into an actual 'hood', whereas the anterior one is downsized to the very 'frontal fold' of the Opistothelae (Fig. 5E, F).

Ramírez (2014), following Forster *et al*. (1987), paid special attention to the shape of the opening for the setal shaft in the araneomorph distal plate: regularly rounded or notched. “Trichobothria alveolus distal margin: 0. Entire. The margin of the alveolus is smooth [...]. 1. Notched. The distal margin of the alveolus has a well-defined notch […] COMMENTS: *Hypochilus*: from Forster *et al*. (1987: fig. 377) [alveolus entire], but metatarsal trichobothria alveoli of immature notched! (fig. 94A) (scored 0).” Ramírez (2014: 145, character 179).

However, the distal margin of the alveolus is notched in both liphistiids (Fig. 5C) and heptathelids (Fig. 5B, F), as well as in the basal ‘hypochiloid’ araneomorphs (Hypochilidae and Austrochilidae), figured by Forster *et al*. (1987, figs 103, 105) and Ramírez (2014, fig. 94A–B). Thus, the polarity of this character is rather opposite, and the notched alveolus margin could be plesiomorphic in Araneomorphae. The presence of the notched alveoli only in immature hypochilids (see above) indicates that this is an ancestral character.

Regarding the ‘ventral bothria’, their basal type is obviously again the bothria of *Heptathela*, where the border between the distal and proximal plates is traceable most clearly: the distal plate with an opening for the setal shaft is more flattened

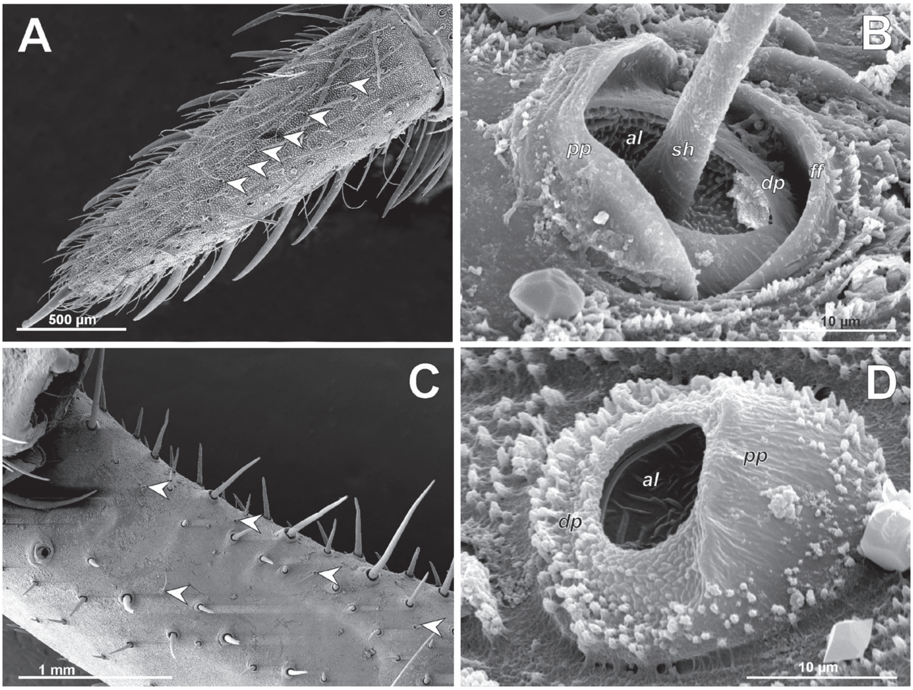

Fig. 4: Bothrial arrangement (A, C) and morphology of an individual bothrium (B, D) in females of the Liphistiomorphae, ‘dorsal’ (A, B) and ‘ventral’ (C, D) types on palpal tarsus (A), tarsus III (B), and femur III (C, D): (A, D) *Heptathela* sp. (Heptathelidae), (B) *Liphistius desultor* (Liphistiidae), (C) *Vinathela* sp. (Heptathelidae). Abbreviations: al – alveolus, dp – distal plate, ff – frontal fold, pp – proximal pate, sh – setal shaft.

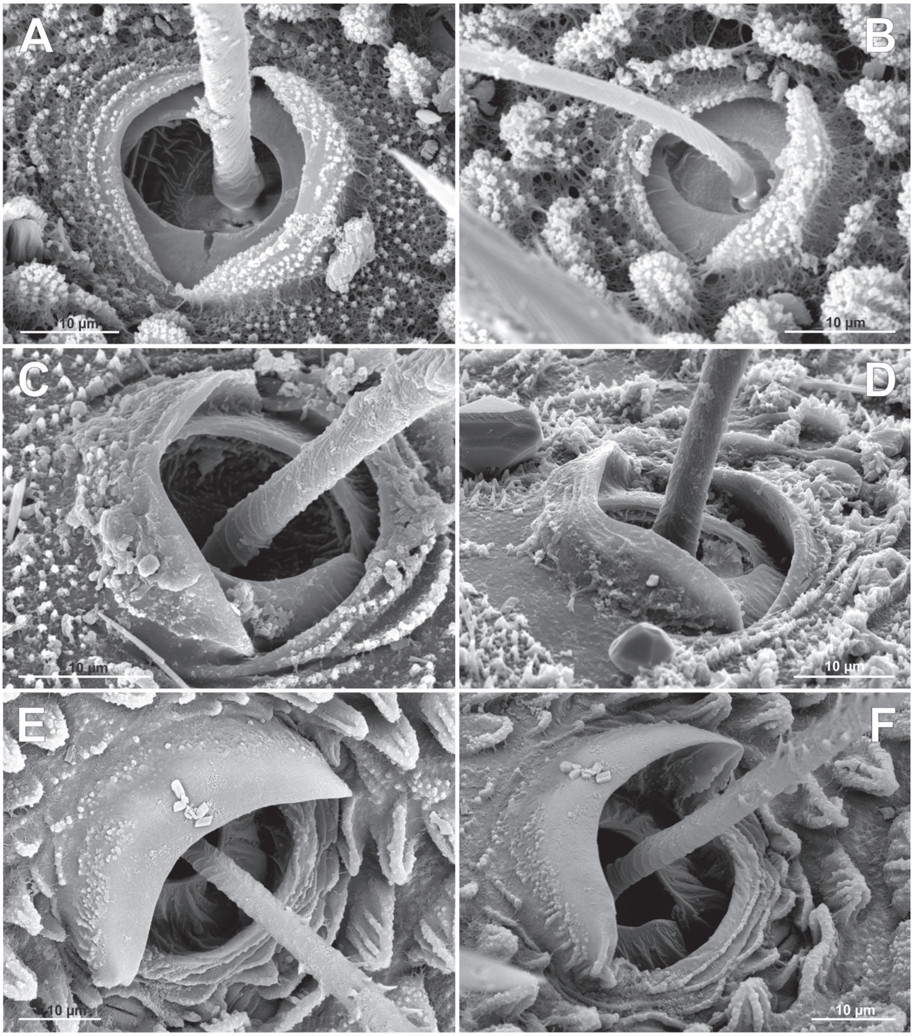

Fig. 5: Diversity of the 'dorsal bothria' in females of the Liphistiomorphae, palpal tarsus (A, B), tarsus III (C, D) and metatarsus III (E, F): (A, B) *Heptathela* sp. (Heptathelidae), (C, D) *Liphistius desultor* (Liphistiidae), (E, F) *Vinathela* sp. (Heptathelidae).

and differs in its sculpture (Figs 4D, 6A, B). In *Vinathela* the distal plate can be distinguished only by its sculpture (Fig. 6C, D). Finally, in *Liphistius* the bothrium is transformed into a regular dome without any vestiges of the border between the distal and proximal plates (Fig. 6E, F), as in the terminal types of the Opisthothelae (e.g. Fig. 2D).

Thus, the general trend of bothrial transformations in the Mesothelae seems to be the same as in the Opisthothelae, and the two liphistiomorph families do not differ from each other in this character.

Bothrial morphology in Araneae and in other arachnid orders

Trichobothria are recorded in all arachnid orders except Solifugae, Ricinulei and Opiliones. The typical arachnid trichobothrial base (bothrium) is a cup-like setal socket with its bottom lined by the membranous wrinkled cuticle ('joint membrane' *sensu* Messlinger 1987, fig. 15); "Just above the thin articulation [of a setal shaft] with the socket there is a basal expansion that may be variously sculptured" (Ramírez 2014: 124).

Simple cup-shaped bothria are characteristic of all non-tetrapulmonate arachnids: Scorpiones (Fig. 7A; Messlinger 1987, figs 2–4), Pseudoscorpiones (Fig. 7B, C), Palpigradi (Fig. 7E, F), and Acari (Fig. 7D; Krantz & Walter 2009, fig. 3.23); the last is the only arachnid group that has trichobothria not only on the appendages, but also all over the body. The inner margin of the cup is sometimes provided with a horizontal rim, either solid, as in pseudoscorpions (Fig. 7C), or presenting a palisade of cuticular spikes, as in Palpigradi (Fig. 7F).

The bothria of the closest spider relatives of the clade Tetrapulmonata are much more diverse. Only Amblypygi retain the initial, simple cup-shaped bothrial structure (Fig. 8E, F; Platnick & Gertsch 1976, fig. 7), whereas it is transformed in one way or another in the remaining three orders, i.e. Araneae, Uropygi and Schizomida. The basal bothrial type of Araneae arises in its most archaic clade, Mesothelae, as two short crescentic outgrowths of the bothrial cup margin, anterior and posterior, framing a horizontal diaphragm with an opening for the setal shaft, which overlaps the central alveolus of the bothrium (Fig. 4B); this diaphragm (the 'dome' of Platnick & Gertsch 1976) is homologous, in our opinion, to the 'distal plate' of the Opisthothelae (see above).

The bothria of Uropygi and Schizomida (Fig. 8A–D) have never been studied earlier. They both possess a unique trichobothrial pattern, considered as one of the synapomorphies of this sister pair (Shultz 1990: character 48): a couple of trichobothria on the dorsodistal end of tibia I, and a single one on the dorsodistal ends of all other tibiae (Fig. 8A, C). However, the bothria of these two orders are rather different (Fig. 8B, D), and those in Schizomida are of special interest.

The schizomid bothria possess a horizontal diaphragm, overlapping the central alveolus of the bothrium, similar to the liphistiomorph 'distal plate' (Fig. 8B cf. Fig. 4B). The liphistiomorph and schizomid diaphragms differ from each other in their surface sculpture and the size of the opening, but they are similar in general structure: in both cases the basal extension of the setal shaft is under the diaphragm plane at the depth of the alveolus. Conversely, in Uropygi such a diaphragm is absent, and the basal extension of the setal shaft is disposed openly on the membranous bothrial bottom (Fig. 8D).

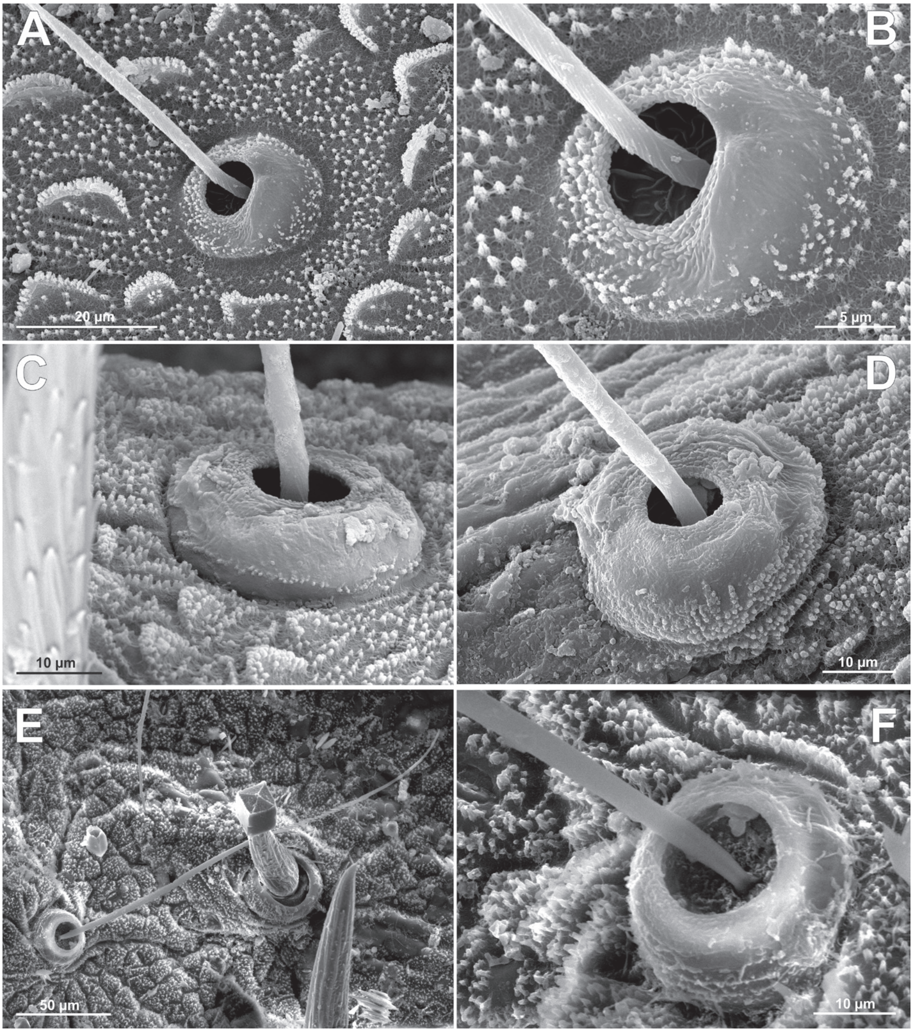

Fig. 6: Diversity of the 'ventral bothria' in females of the Liphistiomorphae, femur III: (A, B) *Heptathela* sp. (Heptathelidae), (C, D) *Vinathela* sp. (Heptathelidae), (E, F) *Liphistius panching* (Liphistiidae).

As regards the origin of this structure, the concentrically arranged 'bothrial lamellae' of Scorpiones (Fig. 7A; Messlinger 1987, figs 2–4, 7, 15) may be proposed as its probable homologues. "One characteristic feature of scorpion trichobothria is the lamellated interior wall of the bothrium. The innermost lamellae which surround the basal opening like a collar […], are supposed to limit (unphysiological) movements of the hair" (Messlinger 1987: 55). The tetrapulmonate 'diaphragm' seems to

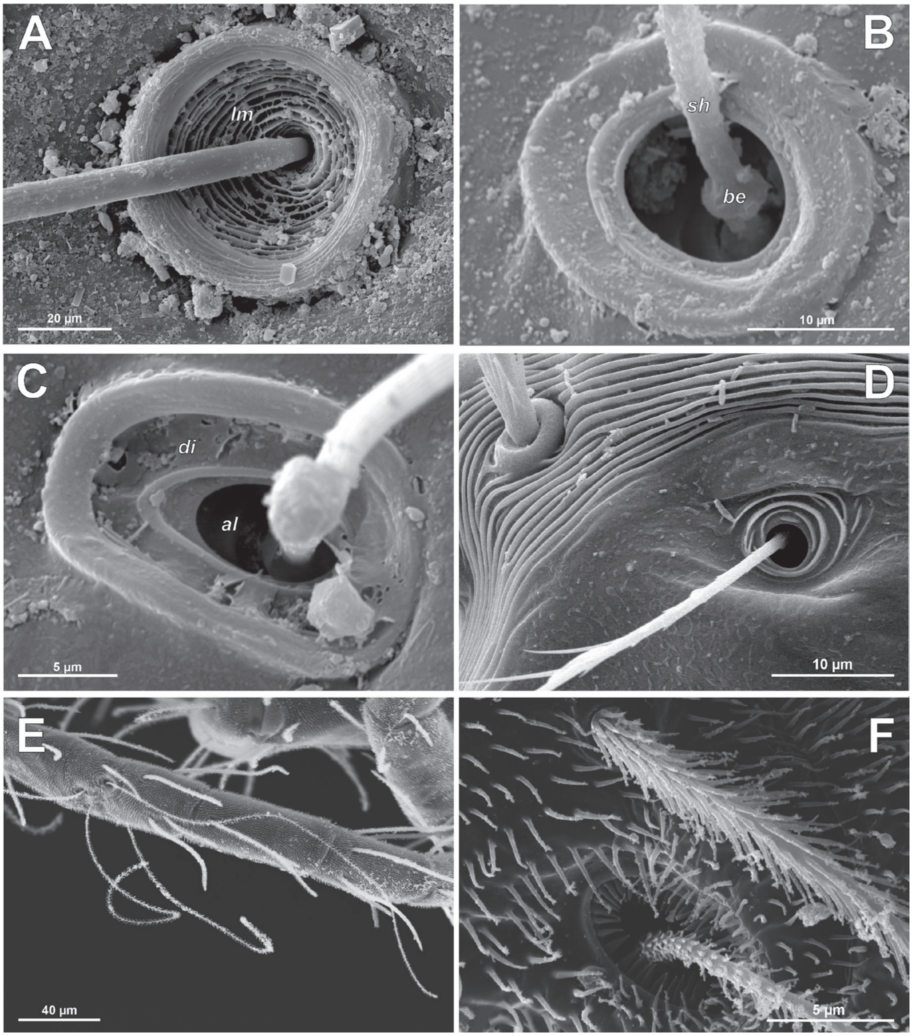

Fig. 7: Bothria of non-tetrapulmonate arachnids: (A) *Mesobuthus parthorum* (Scorpiones), palp; (B) *Neobissium crassifemoratum* (Pseudoscorpionida: Neobissidae), palp; (C) *Chernes cimicoides* (Pseudoscorpionida: Chernetidae), palp; (D) *Hirsutiella zachvatkini* (Schluger, 1948) (Acari: Trombiculidae), prosoma of nymph (micrograph courtesy A.B. Shatrov, unpubl.); (E, F) *Eukoenenia spelaea* (Peyerimhoff, 1902) (Palpigradi: Eukoeneniidae) (Franz-Guess & Starck 2020, fig. 9A, B). Abbreviations: al – alveolus, be – basal expansion of a setal shaft, di – diaphragm, lm – bothrial lamellae, sh – setal shaft.

have arisen as a broadened ancestral bothrial lamella (not the innermost, but rather one of the outer lamellae).

The diaphragm-like structure probably emerged in the bothria of some Pseudoscorpiones (Fig. 8C) in a similar way. Thus, the diaphragms of Mesothelae and

Schizomida, being both homologues of the bothrial lamellae, are rather parallelisms than a synapomorphy of these arachnid lineages.

Shultz (1990: 21) noted a similarity of trichobothrial patterns in the extraordinarily preserved fossils of the extinct order Trigonotarbida from the mid-Devonian deposits of New York (Gilboa) and of the extant Uropygi. The unique preservation of these fossils allows distinguishing, in some cases (e.g. Shear *et al*. 1987, figs 119, 120), the bothrial morphology, and it appears to be actually similar to the dome-shaped bothria of the Uropygi (cf. Fig. 8D). Unfortunately, nothing is known about the bothria of Chimerarachnida from the mid-Cretaceous Burmese amber (Wunderlich 2023), whereas it should be an important piece of information, which would clarify the relations of these controversial arachnids with other tetrapulmonate lineages.

CONCLUSIONS

(1) Liphistiomorphs possess two types of trichobothria, termed ‘dorsal’ and ‘ventral’ in this study. The former is situated, as usually in spiders, dorsally on the distal leg/palp joints, whereas the latter, previously unknown, is arranged in two longitudinal rows on the ventral surface of the femora. Their bothria drastically differ; the presence of two types of trichobothrial bases in one spider specimen is a unique case within Arachnida. The femoral trichobothria are present in both Liphistiidae and Heptathelidae and stated here as another synapomorphy of the suborder.

(2) The principal structures of the bothria and the general trends of their transformation in both Araneomorphae and Mygalomorphae seem parallel. The basal type in both lineages is a bothrium that consists of a more or less flattened distal plate with a rounded opening for the setal shaft and a more or less swollen proximal pate (a ‘hood’) with its distal margin forming a clear transversal ridge: the ‘hooded’ and the ‘collarlike’ bothria, respectively. The terminal type in both lineages is a solid dome-shaped bothrium, where the proximal and distal plates are completely fused without vestiges of the ridge: the ‘domed’ and the ‘corrugiform’ bothria, respectively. Moreover, there are several intermediate types reflecting various ways and stages of the fusion of plates and reduction of the ridge.

(3) The ‘dorsal bothrium’ of Liphistiomorphae consists of two opposite crescentic outgrowths of the bothrial margin, anterior and posterior, framing a horizontal diaphragm with an opening for the setal shaft, which overlaps the central alveolus of the bothrium. This diaphragm (the ‘dome’ of Platnick & Gertsch 1976) is homologous, in our opinion, to the distal plate of araneomorphs and mygalomorphs; the distal margin of the alveolus is notched in both liphistiids and heptathelids, as well as in the most archaic araneomorphs (Hypochilidae and Austrochilidae). Therefore, the posterior crescentic outgrowth should be recognized as homologous to the proximal plate (‘hood’/‘collar’), while the anterior one corresponds to a cuticular fold delimiting the bothrium from the front in araneomorphs and mygalomorphs. Thus, the ‘dorsal bothria’ of Mesothelae is nothing more than the basal bothrial type (‘hooded’/‘collarlike’) of both Opisthothelae lineages.

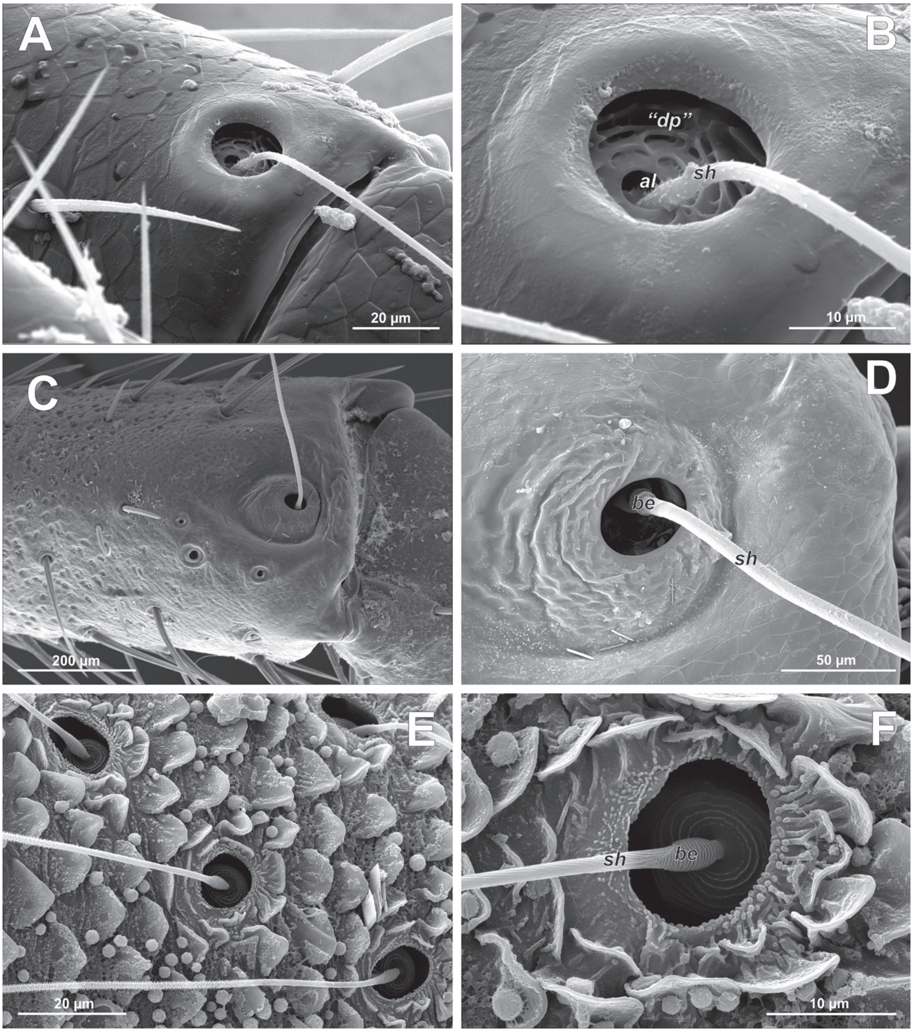

Fig. 8: Bothria of Tetrapulmonata arachnids; dorsodistal end of tibia II, dorsal (A), same, enlarged (B), dorsodistal portion of tibia II, dorsal (C), same, enlarged (D); tibia IV, dorsal (E), same, enlarged (F): (A, B) *Trythyreus* (?) sp. (Schizomida), (C, D) *Thelyphonus* (?) sp. (Uropygi), (E, F) *Charinus* sp. (Amblypygi). Abbreviations: al – alveolus; be – basal expansion of a setal shaft; "dp" – diaphragm, a probable homologue of a distal plate of Araneae; sh – setal shaft.

(4) The 'dorsal bothria' of *Heptathela* should be recognized as basal for Mesothelae: both crescentic opposed outgrowths, which arise on the posterior and anterior edges of the primary bothrial cup, are almost equal in shape and size. In *Liphistius* the posterior outgrowth is relatively upsized, whereas the anterior one is somewhat

reduced. Finally, in *Vinathela* the posterior outgrowth is enlarged and modified into a factual 'hood', whereas the anterior one is downsized to the very 'frontal fold' of Opistothelae.

(5) The 'ventral bothria' of liphistiomorphs perfectly correspond to the exactly terminal types of the solid dome-shaped bothria in both araneomorphs and mygalomorphs. Their basal type is obviously the bothria of *Heptathela*, where the border between the distal and proximal plates is traceable most clearly: the distal plate with an opening for the setal shaft is more flattened and differs in its sculpture. In *Vinathela* the distal plate can be distinguished only by its sculpture. Finally, in *Liphistius* the bothrium is transformed into a regular dome without vestiges of the border between the distal and proximal plates, as well as in the terminal types of Opisthothelae.

(6) All non-tetrapulmonate arachnids have simple cup-shaped bothria. Within Tetrapulmonata, only Amblypygi retain this initial bothrial type, whereas the bothria are transformed in some way in the remaining three orders (Araneae, Uropygi and Schizomida). The bothrium of Schizomida is of special interest: it possesses a horizontal diaphragm overlapping the central alveolus, similar to the liphistiomorph 'distal plate'. These tetrapulmonate diaphragms probably originated from the concentrically arranged 'bothrial lamellae' of Scorpiones (Messlinger 1987) as a broadened version of one such lamella. However, the diaphragms of Mesothelae and Schizomida, even being both homologues of the bothrial lamellae, are rather parallelisms than a synapomorphy of these arachnid lineages.

(7) As regards the clavate trichobothria of liphistiomorphs and mygalomorphs, considered usually as parallel autapomorphies in these lineages, their dissimilarity is overrated. Mutually arranged clavate and filiform trichobothria and the morphology of setal shafts in *Liphistius* and in at least halonoproctid *Ummidia* seem indistinguishable. Thus, the clavate trichobothria may also be supposed as a synapomorphy of the order Araneae, with their subsequent parallel loss in the non-liphistiid liphistiomorphs, in the majority of the mygalomorph lineages, and in all the araneomorphs. However, even if this interpretation is correct, the presence of clavate trichobothria should be considered a plesiomorphic condition in this order, and it does not confirm any close relationships between the 'club-bearing' taxa.

ACKNOWLEDGEMENTS

We are grateful to Roman A. Rakitov (Borissiak Paleontological Institute, Moscow, Russia) for his help during the preparation of SEM images. Our thanks go to the museum curators for the material under their care: Seppo Koponen (ZMTU, Turku, Finland), Dmitri V. Logunov (MMUE, Manchester, UK), Ivan L.F. Magalhaes (MACN, Buenos Aires, Argentina), Kirill G. Mikhailov (ZMMU, Moscow, Russia) and Daniil V. Osipov (Moscow Zoo Insectarium, Moscow, Russia). We also are thankful to J. Matthias Starck (Ludwig-Maximilians-University Munich, Germany) and Andrey B. Shatrov (Zoological Institute, St Petersburg, Russia) for the kindly provided original micrographs of the trichobothria in Palpigradi and Acari, respectively; and to Pyotr N. Petrov (Moscow, Russia) for improving the English of our manuscript.

REFERENCES

ABRAHAM, H.C. 1930 [1929]. The male of the spider *Liphistius malayanus* H. C. Abr., with further notes on the female and on its habits. *Proceedings of the Zoological Society of London* **99** (4): 671–677.
https://doi.org/10.1111/j.1096-3642.1929.tb01450.x

ALBERTI, G. & COONS, L.B. 1999. Acari: Mites. *In*: Harrison, F.W. & Foelix, R.F. (Eds), *Microscopic Anatomy of Invertebrates.* Vol. 8C, Chelicerate Arthropoda. Wiley, pp. 515–1231.

DECAE, A.E., SCHWENDINGER, P.J. & HONGPADHARAKIREE, K. 2021. Descriptions of four new trapdoor spider species in the subfamily Ummidiinae from Thailand (Araneae, Mygalomorphae, Halonoproctidae). *Zootaxa* **4984** (1): 300–323.
https://doi.org/10.11646/zootaxa.4984.1.22

FORSTER, R.R., PLATNICK, N.I. & GRAY, M.R. 1987. A review of the spider superfamilies Hypochiloidea and Austrochiloidea (Araneae, Araneomorphae). *Bulletin of the American Museum of Natural History* **185** (1): 1–116.
http://hdl.handle.net/2246/969

FRANZ-GUESS, S. & STARCK, J.M. 2020. Microscopic anatomy of *Eukoenenia spelaea* (Peyerimhoff, 1902) (Arachnida: Palpigradi: Eukoeneniidae). *Bonn Zoological Bulletin, Supplementum* **65**: 1–125.
https://doi.org/10.20363/BZB-S-2020.65

GOLOBOFF, P.A. 1993. A reanalysis of mygalomorph spider families (Araneae). *American Museum Novitates* **3056**: 1–32.
http://hdl.handle.net/2246/5017

GUADANUCCI, J.P.L. 2012. Trichobothrial morphology of Theraphosidae and Barychelidae spiders (Araneae, Mygalomorphae). *Zootaxa* **3439** (1): 1–42.
https://doi.org/10.11646/zootaxa.3439.1.1

HORMIGA, G. 2002. *Orsonwelles*, a new genus of giant linyphiid spiders (Araneae) from the Hawaiian Islands. *Invertebrate Systematics* **16** (3): 369–448.
https://doi.org/10.1071/IT01026

KRANTZ, G.W. & WALTER, D.E. (Eds) 2009. *A manual of acarology.* 3rd ed. Texas Tech University Press, Lubbock, USA, 807 pp.
https://doi.org/10.1653/024.092.0323

LEHTINEN, P.T. 1980. Trichobothrial patterns in high level taxonomy of spiders. *In*: *Proceedings of the 8th International Arachnological Congress, Vienna, 7–12 July 1980*, pp. 493–498.

LIN, Y.J. & LI, S.Q. 2023. A new species of *Liphistius* Schiødte, 1849 (Araneae, Liphistiidae) from Yunnan, China. *Biodiversity Data Journal* **11**: Art. e113290.
https://doi.org/10.3897/BDJ.11.e113290

MESSLINGER, K. 1987. Fine structure of scorpion trichobothria (Arachnida, Scorpiones). *Zoomorphology* **107**: 49–57.
https://doi.org/10.1007/BF00312129

MILLER, J.A. 2007. Synaphridae of Madagascar (Araneae: Araneoidea): a new family record for the Afrotropical region. *Proceedings of the California Academy of Sciences* (4) **58** (3): 21–48.
https://archive.org/details/proceedings-california-academy-sciences-58-021-048

MORI, A. & BERTANI, R. 2020. Revision and cladistic analysis of *Psalistops* Simon, 1889, *Trichopelma* Simon, 1888 and *Cyrtogrammomma* Pocock, 1895 (Araneae: Theraphosidae) based on a cladistic analysis of relationships of Theraphosidae, Barychelidae and Paratropididae. *Zootaxa* **4873** (1): 1–132.
https://doi.org/10.11646/zootaxa.4873.1.1

MURPHY, J.A. & PLATNICK, N.I. 1981. On *Liphistius desultor* Schiødte (Araneae, Liphistiidae). *Bulletin of the American Museum of Natural History* **170**: 46–56.
https://wsc.nmbe.ch/reference/5486

PLATNICK, N.I. & GERTSCH, W.J. 1976. The suborders of spiders: a cladistics analysis (Arachnida, Araneae). *American Museum Novitates* **2607**: 1–15.
http://hdl.handle.net/2246/5468

PLATNICK, N.I. & SEDGWICK, W.C. 1984. A revision of the spider genus *Liphistius* (Araneae, Mesothelae). *American Museum Novitates* **2781**: 1–31.
http://hdl.handle.net/2246/5262

Ramírez, M.J. 2014. The morphology and phylogeny of dionychan spiders (Araneae: Araneomorphae). *Bulletin of the American Museum of Natural History* **390**: 1–374. https://doi.org/10.1206/821.1

Raven, R.J. 1985. The spider infraorder Mygalomorphae (Araneae): cladistics and systematics. *Bulletin of the American Museum of Natural History* **182**: 1–180. http://hdl.handle.net/2246/955

Schwendinger, P.J. & Hongpadharakiree, K. 2014. Three new *Prothemenops* species (Araneae: Idiopidae) from central Thailand. *Zootaxa* **3893** (4): 530–550. https://doi.org/10.11646/zootaxa.3893.4.3

Shear, W.A., Selden, P.A., Rolfe, W.D.I., Bonamo, P.M. & Grierson, J.D. 1987. New terrestrial arachnids from the Devonian of Gilboa, New York. *American Museum Novitates* **2901**: 1–74. http://hdl.handle.net/2246/5166

Shultz, J.W. 1990. Evolutionary morphology and phylogeny of Arachnida. *Cladistics* **6** (1): 1–38. https://doi.org/10.1111/j.1096-0031.1990.tb00523.x

Wunderlich, J. 2017. New and rare fossil spiders (Araneae) in Mid Cretaceous Amber from Myanmar (Burma), including the description of new extinct families of the suborders Mesothelae and Opisthothelae, as well as notes on the taxonomy, the evolution and the biogeography of the Mesothelae. *Beiträge zur Araneologie* **10**: 72–279, 333–354. http://www.joergwunderlich.de/Downloads/Beitr._Araneol._Band_10_(2017).pdf

Wunderlich, J. 2023. Contribution to the spider (Araneida: Araneae and Chimerarachnida) fauna in upper (mid) Cretaceous Burmese (Kachin) amber. *Beiträge zur Araneologie* **16**: 162–215. http://www.joergwunderlich.de/Downloads/Beitr._Araneol._Band_16_(2023).pdf

Xu, X., Liu, F.X., Chen, J., Ono, H., Li, D.Q. & Kuntner, M. 2015. A genus-level taxonomic review of primitively segmented spiders (Mesothelae, Liphistiidae). *ZooKeys* **488**: 121–151. https://doi.org/10.3897/zookeys.488.8726