ISRAEL JOURNAL OF ENTOMOLOGY, Vol. 55, pp. 73 – 146 (29 June 2026)

A comparative morphology of trichobothrial bases in mygalomorph spiders and its significance for the phylogeny and system of the infraorder (Arachnida: Araneae: Mygalomorphae)

Kirill Y. Eskov[1], José Paulo L. Guadanucci[2], Rafael P. Indicatti[2,3], Yuri M. Marusik[4,5]* & Sergei L. Zonstein[6]

[1]Borissiak Paleontological Institute, Russian Academy of Sciences, 123 Profsoyuznaya Str., Moscow 117647, Russia. E-mail: afranius999@gmail.com
[2]Department of Biodiversity, São Paulo State University (UNESP), Institute of Biosciences, Rio Claro, Av. 24A, 1515 Rio Claro, SP, 13506-900, Brazil. E-mail: jose.guadanucci@unesp.br
[3]Laboratório de Coleções Zoológicas, Instituto Butantan, São Paulo, Brazil. E-mail: indicatti@gmail.com
[4]Institute of Biological Problems of the North, Far Eastern Branch, Russian Academy of Sciences, 18 Portovaya Str., Magadan 68500, Russia. E-mail: yurmar@mail.ru
[5]Department of Zoology & Entomology, University of the Free State, Bloemfontein 9300, South Africa
[6]The Steinhardt Museum of Natural History, 12 Klausner Str., Tel Aviv 69978, Israel. E-mail: serzon56@gmail.com

*Corresponding author: yurmar@mail.ru

ABSTRACT

The morphology of trichobothrial bases was studied using scanning electron microscopy in 97 genera representing all 31 currently recognized extant families of the Mygalomorphae. The ancestral bothrial type in the infraorder is the 'hooded' bothria, characterized by clearly separated proximal and distal plates (a well-known 'collar-like bothrium' is one of its subtypes). The most advanced type is the solid, usually domed bothria with completely fused initial proximal and distal plates (a well-known 'corrugiform bothrium' is one of its subtypes). Several intermediate types, in which the border between the fused proximal and distal plates is still traceable, are also identified. Bothrial morphology supports general outlines of the Opatova *et al*. (2020) cladogram (e.g., the primary split of infraorder stem to the 'atypoid' and the 'non-atypoid' branches), as well as some of its 'purely molecular-based' to date clades (e.g., the placement of the Atracidae far outside of the Hexathelidae and together with the Actinopodidae). The ancestral hooded bothrial type is exclusive to 'atypoids' and predominant in 'hexatheloids' (both being basal phylogenetic lineages), whereas it is completely absent in 'nemesioids' (the distalmost lineage). The parallel continuous bothrial sequences from the ancestral hooded type to the advanced solid domed one, via intermediate ones, are observed in 'ctenizoids' and 'theraphosoids'. The parallel replacement of the ancestral hooded bothria by the advanced solid ones appears to represent a general evolutionary trend in the infraorder Mygalomorphae. This trend is recognizable as well at the level of particular lineages (e.g., in 'ctenizoids'), families (e.g., in Theraphosidae) and even subfamilies (e.g., in Ummidiinae). Strikingly similar patterns of parallel bothrial transformation have been documented in araneomorphs (e.g., in Dionycha and Araneoidea).

KEYWORDS: Araneae, Mygalomorphae, trichobothrial bases morphology, trichobothrial bases evolution.

DOI: 10.5281/zenodo.20829215; ISSN (online) 2224-6304
Received: 25 December 2025 / Revised: 18 March 2026 / Accepted: 1 April 2026
urn:lsid:zoobank.org:pub:0F7695A6-AFA9-406B-999A-31B4BE1B1ED3

INTRODUCTION

Trichobothria are a specialized type of mechanoreceptive sensilla in terrestrial arthropods. They consist of thin, strongly elongated setae, the trichia, which sit within deep cup-like sockets, the bothria. The morphology of bothria is highly diverse among spiders, and has become a popular subject of investigation almost immediately after the scanning electron microscopy was applied to the study of the order. In mygalomorphs, bothrial characters were used in the diagnosis of supra-generic taxa (e.g., Raven & Platnick 1981; Coyle 1995) as well as in phylogenetic reconstructions (e.g., Raven 1985*a*).

Raven (1985*a*: 21) distinguished two alternative types of bothria, 'collarlike' and 'corrugiform': "Bothria […] show a number of basic types that are sufficiently consistent in taxa to be useful in estimating group relationships. The antrodiaetids, atypids, hexathelids and mecicobothriids—all plesiomorphic groups—have a collarlike bothria. […] Outgroup comparison with all plesiomorphic mygalomorph families indicates that the corrugiform bothria are synapomorphic for the [distal-most lineage of cladogram] Quadrithelina".

However, the 'big picture' that had been drawn was complicated by numerous reversals and parallelisms (Raven 1985*a*: 21). The actual distribution of the ancestral and derived bothrial types along the branches of the cladogram turned out to be quite chaotic. Moreover, additional, new data on bothria tended to further confuse this 'big picture' rather than clarify it (e.g., Griswold & Ledford 2001).

As a result, the interest in wide-scale comparative studies of the morphology of bothria in mygalomorphs has largely waned. Over the last couple of decades these structures have rarely been discussed. Their morphology is still sometimes used for diagnosing particular taxa (e.g., Passanha & Brescovit 2018), but not for phylogenetic inference. So, in the most fundamental modern study on the phylogeny of the infraorder, bothria were mentioned only once: the "collariform trichobothrial bases" were listed among the characters of the re-ranked Ischnothelinae (Opatova *et al*. 2020: 697).

At the same time, the comparative morphology of bothria in the Araneomorphae appears to be more consistent with the evolution of this infraorder, and evolutionary trends in such distant lineages as Dionycha (Ramírez 2014) and Araneoidea (Eskov & Marusik 2024*a*) are remarkably similar. Moreover, it has been found that the structure of bothria in araneomorphs and mygalomorphs is fundamentally the same and is directly inherited in both infraorders from the basalmost liphistiomorphs (Eskov *et al*. 2024).

Our research shows that previous studies of bothria in Mygalomorphae have missed some important structural details. Therefore, we first refine the classification of mygalomorph bothria based on the material from all currently recognized mygalomorph families. Then we map the newly established bothrial types onto the recent cladogram of Opatova *et al*. (2020: fig. 8).

It is necessary to emphasize that our goal was not to construct yet another artificial classification based on a single character. Instead, we aimed to test the already inferred, primarily molecular phylogeny with respect to variation in a previously neglected morphological character. Specifically, we ask: which molecular phylogenetic innovations are consistent with the new data on the bothria, which are neutral (neither supporting, nor contradicting), and which contradict them? The latter cases, if found, would be of particular interest for further research.

MATERIALS AND METHODS

Trichobothria and leg cuticle of 102 mygalomorph species, representing 97 genera and all 31 currently recognized families, as well as three non-mygalomorph species, are figured. Also, the original images of five mygalomorph bothria were obtained from colleagues. The study is based on specimens listed in Appendix (p. 141).

SEM images were taken with a Tescan Vega2 and a Tescan Vega3 scanning electron microscopes in Borissiak Paleontological Institute, Moscow, and scanning electron microscope LEO 440 in Museu de Zoologia da Universidade de São Paulo, operated in a high vacuum mode at the accelerating voltages of 10–20 kV, using SE and BSE detectors. Specimens were gradually dehydrated in 100% ethanol, dried, and sputter-coated with gold-palladium. All measurements are given in μm.

Chat DeepSeek was used by the authors to edit the original text of the manuscript for English grammar and syntaxis, paragraph by paragraph.

Abbreviations of the leg joints: mt – metatarsus, ta – tarsus, ti – tibia. Terminology of the bothrial parts follows that in Ramírez (2014) and Eskov *et al*. (2024). Abbreviations for trichobothria parts: al – alveolus, dp – distal plate, ff – frontal fold, pp – proximal plate, pp+dp – fused proximal and distal plates, sh – shaft.

The studied specimens belong to the following institutions:

AMNH – American Museum of Natural History, New York, USA;
CAD – Coleção Aracnológica Diamantina, Rio Claro, Brazil;
CAS – California Academy of Sciences, San Francisco, USA;
CUPC – Charles University, Prague, Czech Republic;
DWC – Private collection D. Weinmann. Stuttgart, Germany;
FMNH – Field Museum of Natural History, Chicago, USA;
IBSP – Instituto Butantan, São Paulo, Brazil;
MACN – Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina;
NHM – Natural History Museum, London, UK
MMUE – The Manchester Museum, University of Manchester, UK;
MPEG – Museu Paraense Emilio Goeldi, Belém, Brazil;
NMBA – National Museum, Bloemfontein, South Africa;
MNHZ – Museum of Nature Hamburg, Zoologie, Hamburg, Germany;
NMSA – KwaZulu-Natal Museum, Pietermaritzburg, South Africa;
QMS – Queensland Museum, Brisbane, Australia;
RMCA – Royal Museum for Central Africa, Tervuren, Belgium;
SDSU – San Diego State University, California, USA;

SMNK – Staatliches Museum für Naturkunde Karlsruhe, Germany;
SMNHTAU – The Steinhardt Museum of Natural History, Tel Aviv, Israel;
WAM – Western Australian Museum, Perth, Australia;
ZMMU – Zoological Museum of the Moscow State University, Russia;
ZMTU – Zoological Museum, University of Turku, Finland;
ZMUC – Zoological Museum, University of Copenhagen, Denmark.

RESULTS

Preliminary notes on the system of the Mygalomorphae

As an infraorder system, we have adopted the cladogram from Opatova *et al*. (2020: fig. 8) which summarizes the phylogenetic relationships of mygalomorph families and based on both molecular and morphological data. However, we have made some terminological clarifications (Fig. 1).

Opatova *et al*. (2020) used a mix of typified names (e.g., 'Atypoidea', 'Theraphosoidina') and descriptive names (e.g., 'Bipectina', 'Venom Clade') for their clades. To standardize the nomenclature, we assigned typified names to all six main lineages recognized by Opatova *et al*. (2020): (1) 'Atypoid lineage' or 'atypoids', (2) 'hexatheloids', (3) 'actinopodoids', (4) 'ctenizoids', (5) 'theraphosoids' and (6) 'nemesioids' (note that Hexatheloid and Actinopodoid lineages are paraphyletic). These names are used here informally, as formal ranking and hierarchical classification of these lineages fall outside the scope of our work.

To avoid nomenclatural confusion, we refrain from using the Simon's (1892) name 'Avicularioidea' for the clade encompassing all mygalomorphs except the basalmost Atypoidea (which clade includes Theraphosidae, i.e. the supratxon of the modern Aviculariinae). Instead, we use the taxonomically neutral term 'non-atypoid clade' (or 'non-atypoids'), following Hedin and Bond (2006: 454, 459).

It should be emphasized that 'orthodox cladistics' rejects the very concept of a 'basal lineage' – a term we use here and below: "In phylogenetic systematics/cladistics there is no reason and no justification to weight clades at all. Sister groups always have the same rank and the same weight or value in the phylogenetic system. […] It makes no sense to call the crocodiles the basal clade of the Archosauria and the speciose Aves the derived group (or the other way round)" (Krell & Cranston 2004: 280).

Nevertheless, the apomorphic and plesiomorphic states of the analyzed characters are not distributed equally between the lineages of a sister pair; the lineage in which plesiomorphies predominate we will consider 'basal'. For example, in the sister pair 'atypoids' and 'non-atypoids', the basal lineage is the former.

Preliminary notes on the evolutionary morphology of bothria and leg cuticle patterns in Mygalomorphae

The unity of the general structure of bothria in Mygalomorphae and Araneomorphae, as well as the homology of their main elements with those of Liphistiomorphae, has

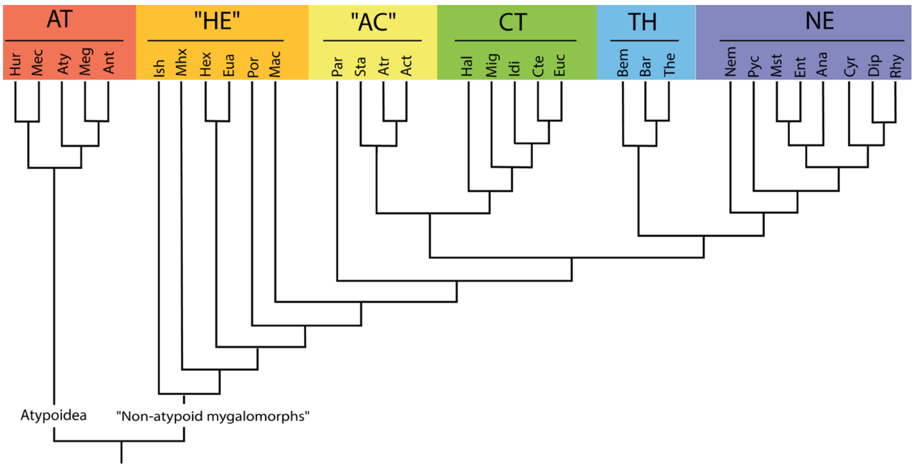

Fig. 1. Accepted classification of the infraorder Mygalomorphae to the family level, based on the cladogram from Opatova *et al*. (2020: fig. 8). (N.B.: The clades in the Nemesioid and Atypoid lineages are rearranged here according to Montes de Oca *et al*. (2022: fig. 7) and the observations of M. Hedin (letter dated 26.viii.2024). Abbreviations: **"AC"** – Actinopodoid lineage, paraphyletic (Act – Actinopodidae, Atr – Atracidae, Par – Paratropididae, Sta – Stasimopidae); **AT** – Atypoid lineage (Ant – Antrodiaetidae, Aty – Atypidae, Hur – Hexurellidae, Mec – Mecicobothriidae, Meg – Megahexuridae); **CT** – Ctenizoid lineage (Cte – Ctenizidae, Euc – Euctenizidae, Hal – Halonoproctidae, Idi – Idiopidae, Mig – Migidae); **"HE"** – Hexatheloid lineage, paraphyletic (Eua – Euagridae, Hex – Hexathelidae, Ish – Ischnothelidae, Mac – Macrothelidae, Mhx – Microhexuridae, Por – Porrhothelidae); **NE** – Nemesioid lineage (Ana – Anamidae, Cyr – Cyrtaucheniidae, Dip – Dipluridae, Ent – Entypesidae, Mst – Microstigmatidae, Nem – Nemesiidae, Pyc – Pycnothelidae, Rhy – Rhytidicolidae); **TH** – Theraphosoid lineage (Bar – Barychelidae, Bem – Bemmeridae, The – Theraphosidae).

been substantiated in detail by Eskov *et al*. (2024). The terminology for bothrial divisions has been unified here following the Araneomorphae standard, as it is the most detailed (Ramírez 2014: 124–125; Eskov & Marusik 2024*a*: 8–9).

An ancestral ('hooded') araneomorph bothrium consists of the following structures: (1) a more or less flattened distal plate with a rounded opening (alveolus) for a setal shaft; (2) a more or less swollen proximal plate ('hood') with its distal margin forming a distinct transversal ridge; and (3) a cuticular frontal fold that delimits the bothrium anteriorly (Fig. 2A; Eskov & Marusik 2024*a*: fig. 3A–D). In advanced araneomorph bothria proximal and distal plates are fused, completely (Fig. 2B; Eskov & Marusik 2024*a*: fig. 3E, F) or partially (Eskov *et al*. 2024: fig. 2B, C; Eskov & Marusik 2024*a*: fig. 4A–F).

Raven (1985*a*: 21) observed that in Mygalomorphae 'collarlike bothria' are restricted to basal lineages, whereas more distal lineages possess 'corrugiform bothria'. The principal structure of the ancestral mygalomorph 'collarlike bothria' closely corresponds to that of the ancestral araneomorph 'hooded bothria': a distal plate with an opening for the shaft, a proximal plate ('collar') with a notch on its anterior

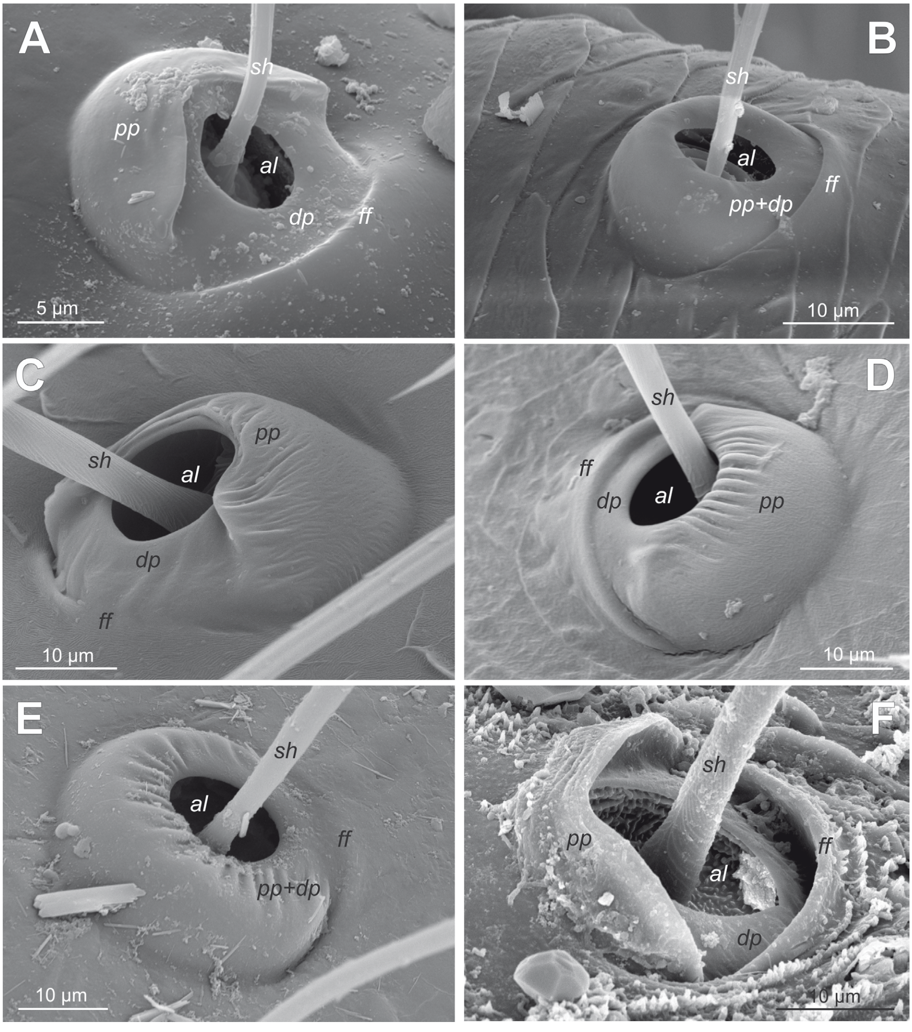

Fig. 2. Bothrial morphology in Araneomorphae (A, B), Mygalomorphae (C–E) and Liphistiomorphae (F): (A) *Chilenodes australis* (Malkaridae), ti3 (ancestral hooded bothrium); (B) *Euryopis flavomaculata* (Theridiidae), ti3 (advanced solid domed bothrium); (C) *Macrothele* sp. (Macrothelidae), ti4 (ancestral hooded 'collar-like' bothrium); (D) *Acanthogonatus confusus* (Pycnothelidae), ti3 (intermediate bothrium); (E) *Paramigas perroti* (Migidae), ti2 (advanced solid domed 'corrugated' bothrium); (F) *Liphistius desultor* (Liphistiidae), mt3 (hooded bothrium *in statu nascendi*). Abbreviations: al – alveolus, dp – distal plate, dp+pp – completely fused distal and proximal plates, ff – frontal fold, pp – proximal plate, sh – setal shaft.

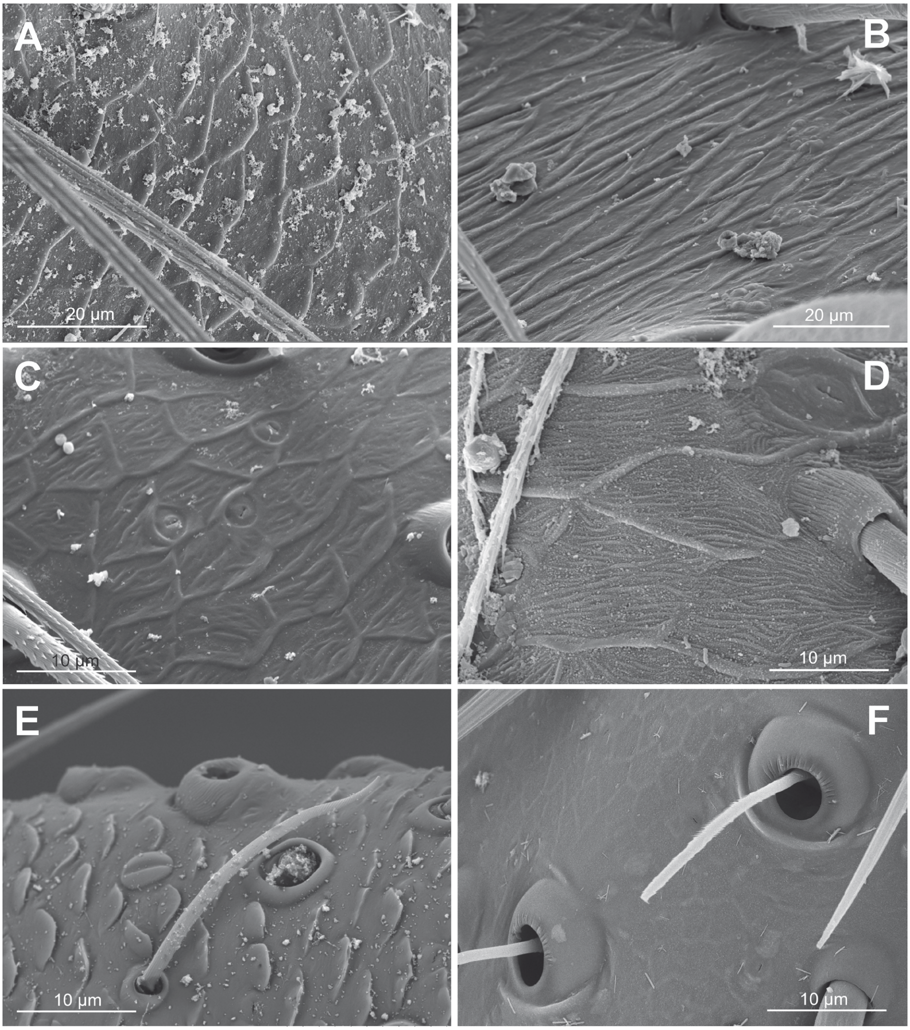

Fig. 3. Ancestral scaly cuticular pattern and its modifications: (A) *Megahexura fulva* (Megahexuridae), mt3 ('typically scaly' cuticle); (B) *Antrodiaetus montanus* (Antrodiaetidae), ti3 ('transversely imbricate' cuticle); (C) *Mecicobothrium thorelli* (Mecicobothriidae), ti2 ('ornamented imbricate' cuticle); (D) *Microhexura montivaga* (Microhexuridae) ti3 ('fingerprint imbricate' cuticle); (E) *Pseudonemesia tabiskey* (Microstigmatidae), leg1 ('pseudoscale' cuticle); (F) *Damarchus* sp. (Bemmeridae), ta3 ('smoothed imbricate' cuticle).

margin, and a cuticular frontal fold (cf. Figs 2C and 2A). As in Araneomorphae, the proximal and distal plates in advanced 'corrugiform bothria' are completely fused into a single dome (Fig. 2E), with intermediate forms in which the boundary between the fused plates remains discernible (Fig. 2D).

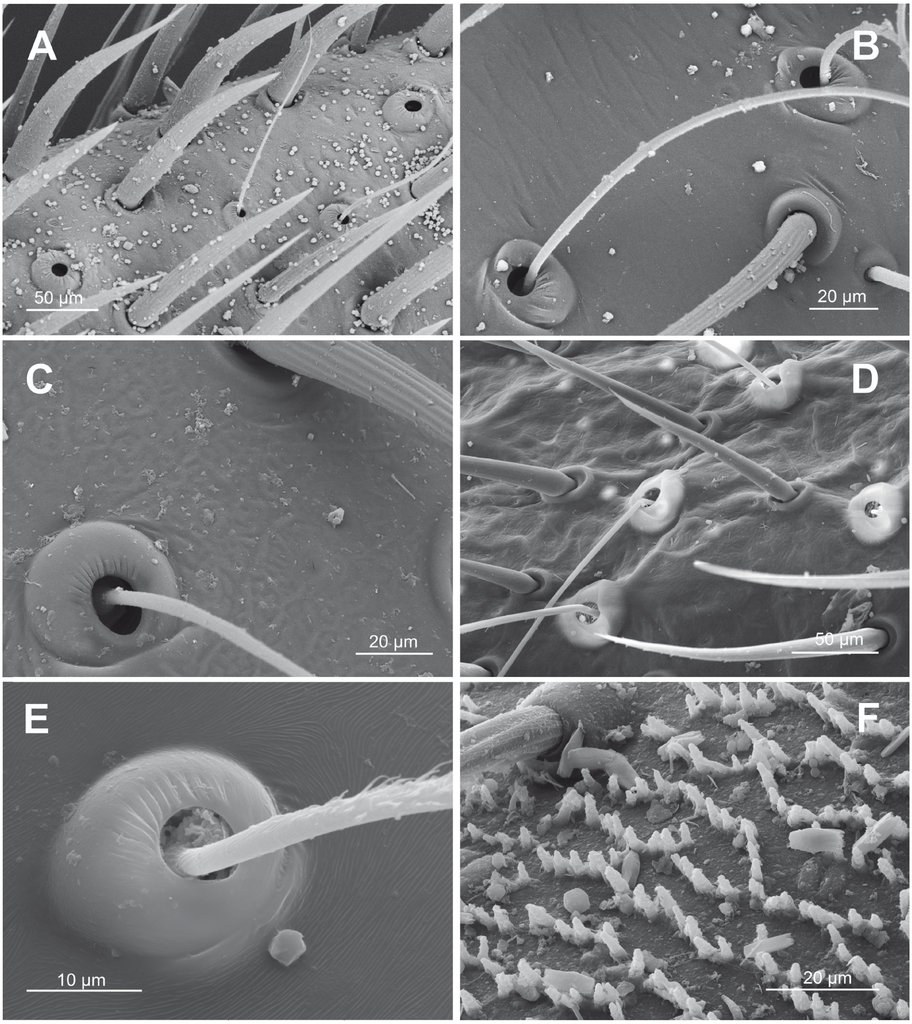

Fig. 4. Advanced, non-scaly, cuticular patterns: (A) *Heteromigas dovei* (Migidae), mt3 (typically smooth cuticle); (B) *Migas nitens* (Migidae), ti3 (smooth cuticle with vestiges of borders between initial scales); (C) *Myrmekiaphila torreya* (Euctenizidae), mt3 ('weakly rugose' cuticle); (D) *Actinopus* sp. (Actinopodidae), ta3 ('strongly rugose' cuticle); (E) *Sason* aff. *sundaicum* (Barychelidae), ta3 ('fingerprint-like' cuticle); (F) *Microstigmata longipes* (Microstigmatidae), ti3 ('pustulose' cuticle).

The bothrial morphology of Liphistiomorphae was long considered unique and autapomorphic: "Both *Liphistius* and *Heptathela*, however, show a different [from all Opisthothelae] structure, involving a dome and two flattened plates [...] The dome is recessed considerably below the plates" (Platnick & Gertsch 1976: 12); "The Mesothelae have two short crescentic opposed plates" (Raven 1985*a*: 21).

However, these liphistiomorph bothrial structures (Fig. 2F) have now been reinterpreted: "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 [...] The 'two crescentic opposed plates' (after Raven 1985*a*), posterior and anterior, correspond to the proximal plate ('hood'/'collar') and to the 'frontal fold', respectively. So, the [dorsal] bothria of Mesothelae is nothing more than the ancestral bothrial type ('hooded'/'collarlike') of both Opisthothelae lineages *in statu nascendi*" (Eskov *et al*. 2024: 102).

The leg cuticular patterns in mygalomorphs are largely the same as in araneomorphs; thus, they are named here following Lopardo and Hormiga (2015: 735–736). The evolutionary trends in the development of cuticular microsculpture in spiders have been widely discussed, but have not found a consensus solution.

Lehtinen (1996: 403) correctly identified the main phylogenetic challenge as one of character coding, i.e., establishing the polarity of traits: "Attempts to use leg skin characters for phylogenetic analysis of the main groups of spiders have failed due to incorrect coding. For example, Coddington (1990) [...] coded smooth cuticle plesiomorphic and ridged cuticle as synapomorphy for Gradungulidae, Austrochilidae and Araneoclada. Similarly, Raven (1985*a*) coded smooth cuticle as plesiomorphic in some Mygalomorph groups".

However, Lehtinen's (1996) own coding does not seem more convincing than that of the authors he criticized. We therefore adopt very different assumptions regarding the plesiomorphic versus apomorphic states of leg cuticular patterns.

The scaly (imbricate) cuticle occurs in all orders of Tetrapulmonata (Eskov *et al*. 2024: fig. 8A, C, E), as well as in some other arachnids (e.g., ixodid ticks (Lehtinen 1996: fig. 29)). It is likely the ancestral cuticular type for at least the tetrapulmonate lineage (Eskov & Marusik 2024*b*). As Hinton and Wilson (1970: 483) concluded, the primitive arthropod cuticle consists of polygonal (usually hexagonal) units, each corresponding to the shape of an epidermal cell during epicuticle secretion (see also Moretto *et al*. 2015).

(1) *Scaly* (*imbricate*, *squamate*) *cuticle*. The typical scaly cuticle consists of overlapping, more or less polygonal 'scales' with a relatively smooth surface (Fig. 3A). In some cases, the scales are widened and shortened, appearing as transversal cuticular strips (Fig. 3B); in other cases, their surface additionally sculptured (Fig. 3C). These variations are here designated as 'transversely imbricate' and 'ornamented imbricate', respectively.

A special case of the 'ornamented imbricate' type is the 'imbricate-fingerprint' pattern (Fig. 3D), characterized by ridged scales (Lopardo & Hormiga 2015: 735). Occasionally, the frontal edges of scales extend into rounded protrusions (Fig. 3E), a pattern termed 'pseudoscale' by Eskov and Marusik (2024*b*: 377). In some instances, the scales are nearly fused, with vestigial borders barely visible (Fig. 3F); this condition is here referred to as 'smoothed imbricate'.

Among mygalomorphs, the scaly pattern, including its variations, is the most widespread and common cuticular type (Lehtinen 1996: 402).

(2) *Smooth cuticle*. A smooth, unsculpted surface lacking evident ridges or other structures (Lopardo & Hormiga 2015: 735). This condition is likely evolved through the fusion of ancestral scales into a continuous surface (Fig. 4A), with vestigial borders sometimes still discernible (Fig. 4B). The ‘smoothed imbricate’ pattern (Fig. 3F) may represent an intermediate stage between the ancestral scaly and the fully smooth cuticle.

Although Raven (1985*a*: 46) stated that most mygalomorphs have smooth leg cuticle, our own observations indicate that this advanced condition is relatively rare, occurring only in certain distal lineages of Opatova *et al*. (2020) cladogram – particularly in Ctenizoid and Theraphosoid lineages.

(3) *Rugose* (*irregular*, *asperous*, *bumpy*) *cuticle*. An irregular ‘crumpled sheet’ pattern with folds and bumps of this varying prominence (Lopardo & Hormiga 2015: 736). The ‘weakly rugose’ form (Fig. 4C) may result from the fusion of ‘ornamented imbricate’ scales, while the ‘strongly rugose’ type (Fig. 4D) appears to be a further elaboration of this unite surface.

This pattern is uncommon in mygalomorphs and occurs only in few unrelated distal lineages.

(4) *Fingerprint-like* (*ridged*, *finely strigulate*) *cuticle*. A smooth surface covered with parallel thin ridges resembling a fingerprint (Lopardo & Hormiga 2015: 735). This pattern likely arises from the fusion of individual ‘imbricate-fingerprint’ scales (i.e., ‘ornamented imbricate’ scales with a ridged surface, as in Figs 3D, 12A) into a continuous surface (Figs 4E, 9B).

Previously, the ‘fingerprint-like’ cuticle was considered absent in basal spider lineages (Liphistiomorphae, Mygalomorphae and Filistatidae) and proposed as a synapomorphy of the ‘non-filistatid araneomorphs’ (Eskov & Marusik 2024*a*: 7). However, this assertion turned out to be incorrect for Mygalomorphae: our new data confirm Lehtinen’s (1996: 402) documentation of ‘ridged’ cuticle into this infraorder.

Only a few genera from phylogenetically distant mygalomorph families possess this rare cuticular type, likely representing parallel autapomorphies at the generic level. Notably, the bothria of mygalomorphs with ‘fingerprint-like’ cuticle differ fundamentally from the longitudinally ridged bothria of araneomorphs bearing this cuticle type (cf. Figs 4E, 9B and Eskov & Marusik 2024*a*: fig. 2C–F).

(5) *Pustulose cuticle*. This advanced variation of the scaly type, characterized by rows of protruding pustules outlining scale edges (Figs 4F, 21A, 22C), is unique to Mygalomorphae. Being initially described in Microstigmatidae (Raven & Platnick 1981: figs 7, 23) and considered a synapomorphy of this family by Opatova *et al*. (2020: 702, 703), it has since been found in other lineages (Figs 13F, 23A).

In addition to these primary types, some mygalomorphs exhibit unique cuticular modifications such as those in the microstigmatid *Envia* Ott & Höfer, 2004 (Fig. 22E) and the diplurid *Masteria* L. Koch, 1873 (Fig. 23F).

Typology of the trichobothrial bases in the Mygalomorphae

Platnick and Gertsch (1976: 9–12) distinguished two bothrial types in Mygalomorphae: (1) “a rounded dome covered on one side by a flattened plate” and (2) “a dome only, bear numerous parallel [radial] wrinkles”. They noted that the first type occured in most mygalomorph genera, listing 14 genera of Antrodiaetidae, Atypidae, Hexathelidae, Microhexuridae and Halonoproctidae (according to its modern family belonging). The second bothrial type was recorded in the 12 genera representing Migidae, Actinopodidae, Paratropididae, Barychelidae, Nemesiidae, Pycnothelidae and Euctenizidae.

These divisions broadly correspond to Raven’s (1985*a*: 21) ‘collarlike bothria’ and ‘corrugiform bothria’. Goloboff (1993: char. 30) proposed an alternative classification, dividing mygalomorph bothria into ‘corrugiform’ (e.g., *Fufius* Simon, 1888) and ‘smooth’ (e.g., *Idiops* Perty, 1833), noting that “Corrugiform bothria appear to be much more widely distributed than previously thought”. However, many bothria remain unclassified under this scheme, prompting Goloboff (1993: char. 64) to introduce and additional distinction—‘bothria normal’ vs ‘bothria with a sinuous impression around tricheme aperture’—for the unique case of Actinopodidae.

Critically, Platnick and Gertsch (1976) made two key observations often overlooked in later studies:

(1) Their first bothrial type (‘dome covered by a flattened plate’) occurs not only in basal atypoids (Antrodiaetidae, Atypidae) and hexatheloids (Hexathelidae, Microhexuridae) but also in distal ctenizoids (Halonoproctidae).

(2) Both types may coexist within a single family, as seen in Theraphosidae (*Psalistops* Simon, 1889 vs *Avicularia* Lamarck, 1818) and Idiopidae (*Galeosoma* Purcell, 1903 vs *Idiosoma* Ausserer, 1871 and *Arbanitis* L. Koch, 1874).

Further complicating Raven’s (1985*a*: 21) claim that ‘collarlike bothria’ are restricted to basal lineages while ‘corrugiform bothria’ characterize distal lineages, the both types, as well intermediate forms, occur in, e.g., Migidae (Griswold & Ledford 2001: 12; Eskov *et al*. 2024: fig. 3D–F). Thus, while Raven’s framework has merit, it oversimplifies the diversity of bothrial morphology.

Notably, Platnick and Gertsch (1976) illustrated only three of the listed 26 genera (all atypoids: figs 13, 15, 17). In our view, the bothria of the atracid *Atrax* O. Pickard-Cambridge, 1877 (Fig. 14B), euagrid *Euagrus* Ausserer, 1875 (Fig. 7C) and pycnothelid *Acanthogonatus* Karsch, 1880 (Fig. 2D) cannot be classified as ‘dome covered by a flattened plate’/’collarlike’. Similarly, the bothria of actinopodids *Actinopus* Perty, 1833 and *Missulena* Walckenaer, 1805 (Fig. 14D, E) exhibit a unique “sinuous impression around the tricheme aperture” (Goloboff & Platnick 1987: 11–12), and cannot be classified as ‘a dome only’/’corrugiform’. Also, we concur with Goloboff (1993) that ‘corrugiform’ bothria dominate in Mygalomorphae.

Proposed typology

Building on the demonstrated homology of bothria in Mygalomorphae and Araneomorphae (Platnick & Gertsch 1976; Eskov *et al*. 2024), we adopt a typology analogous to Eskov and Marusik (2024*a*) framework for Araneoidea:

(1) Ancestral (*Erigone* type): 'hooded' bothrium with a transversal ridge separating proximal and distal plates (Eskov & Marusik 2024*a*: fig. 3A–D).

(2) Advanced (*Theridion* type): solid dome-shaped bothrium with fully fused, without ridge vestiges, proximal and distal plates (Eskov & Marusik 2024*a*: fig. 3E–F).

(3) Intermediate (*Argiope* type): variably fused plates with partial ridge reduction (Eskov & Marusik 2024*a*: fig. 4A–F).

Given the greater diversity of mygalomorph bothria, we further divide each type into morphological subtypes.

1. Ancestral 'hooded' bothria (= *Erigone* type)

1.1. *Idiops* subtype (Id). This bothrium has a smooth proximal plate with a slightly concave or direct distal margin (Fig. 5A, B). We consider it the most plesiomorphic due to its clear similarity with the dorsal bothria of Liphistiomorphae (Fig. 2F; Eskov *et al.* 2024: fig. 5A–F). This bothrial type occurs in several ctenizoid and theraphosoid families, including idiopids, halonoproctids, migids and theraphosids (Fig. 27A–B), as well as in ischnothelid, the basalmost clade of hexatheloids and the 'non-atypoid mygalomorphs' in general (Fig. 26 B).

1.2. *Macrothele* subtype (Ma). These bothria are commonly referred to as 'collar-like' (e.g., Raven 1985*a*: 21). They possess longitudinally ridged proximal plate with a strongly concave, not folded anterior margin (Fig. 5C). As noted by Coyle (1995: 12): "This collar, unlike that of the ischnothelines, has parallel ridges and lobed ends". The *Macrothele* subtype appears to be derived from the more plesiomorphic *Idiops* subtype, particularly resembling the ischnothelid bothrium. It is strictly limited to the basalmost lineage of 'non-atypoids', i.e. hexatheloids: macrothelids, hexathelids and microhexurids (Fig. 26B). Notably, in the atypoid genus *Hexura* Simon, 1885 (Figs 5D, 10B), anterior margin of proximal plate is also strongly concave, but its fine structure differs distinctly from the *Macrothele* subtype (see below).

1.3. *Atypus* subtype (At). In this hooded bothrium, the anterior margin of the proximal plate forms several irregular folds (Fig. 5D–F), unlike the single transverse ridge seen in the two aforementioned mygalomorph types (Fig. 5A–C) and all liphistiomorphs (Fig. 2F; Eskov *et al*., 2024: fig. 5A–F).

In some atypoid genera, as e.g. *Megahexura* Kaston, 1972 (Fig. 9C), the anterior margin of the proximal plate is concave, while in *Hexura* Simon, 1885 it is so deeply notched that the bothrium superficially resembles the 'collar-like' *Macrothele* subtype (Figs 5D, 10B; Gertsch & Platnick 1976: fig. 13). However, the folded anterior margin of the proximal plate clearly distinguishes atypoid bothria from the 'collar-like' bothria of hexatheloids, such as *Macrothele* Ausserer, 1871 (cf. Figs 5C,

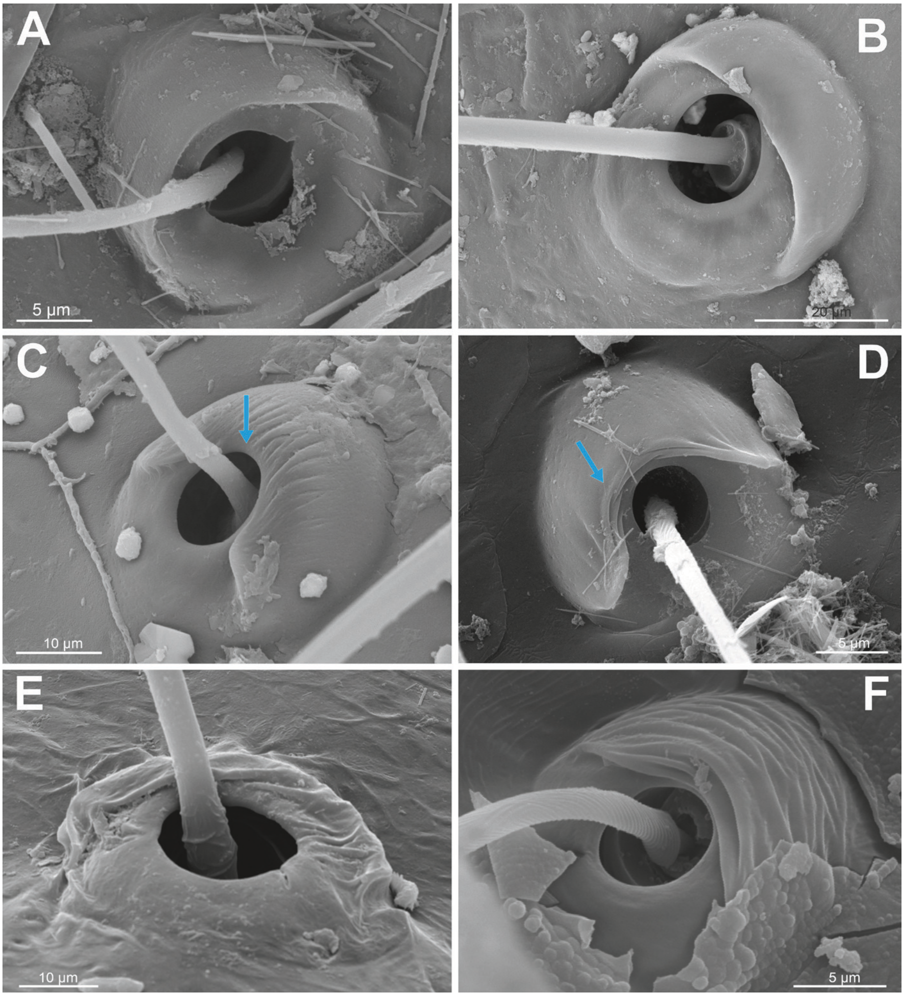

Fig. 5. Typology of mygalomorph bothria: ancestral hooded types: (A) *Thelechoris rutenbergi* (Ischnothelidae), ti3 (Id); (B) *Idiops* sp. (Idiopidae), ti3 (Id); (C) *Macrothele* aff. *camerunensis* (Macrothelidae), ti3 (Ma: arrow – unfolded anterior edge of the posterior plate); (D) *Hexura picea* (Antrodiaetidae), mt3 (At: arrow – folded anterior edge of the posterior plate); (E) *Atypus muralis* (Atypidae), ti1 (At); (F) *Hexurella* sp. (Hexurellidae), ti4 (At). Abbreviations: At – *Atypus* subtype, Id – *Idiops* subtype, Ma – *Macrothele* subtype.

arrow, and 5D, arrow) and *Microhexura* Crosby & Bishop, 1925 (Fig. 12A; Coyle 1995: fig. 47). Thus, the key diagnostic character, separating the *Atypus* subtype from the *Macrothele* subtype is the fine structure of the anterior margin (folded vs non-folded), rather than the overall outline of the proximal plate (collar-like vs non-collar-like).

The *Atypus* subtype is strictly limited to Atypoidea, occurring in all its constituent families without exception (Fig. 26A). It appears another 'trichobothrial' synapomorphy of this clade, alongside the reduction of tarsal trichobothria (Coddington & Levi 1991: 575; Eskov & Marusik 2024*a*: 6).

2. Advanced bothria: 'solid corrugated' and 'solid non-corrugated'
(= *Theridion* type)

2.1. *Fufius* subtype (Fu). This domed bothrium features by completely fused initial proximal and distal plates and is commonly referred to as 'corrugiform' (e.g., Raven 1985*a*: 21). It appears to represent the final stage in the evolutionary sequence from *Ummidia* to *Neocteniza* subtypes, characterized by radial wrinkles forming a circular or nearly circular corrugated surface around the aperture at the dome's apex (Fig. 7A, B). Notably, the two lateral plicae of this 'corrugation' – located at the 4 o'clock and 8 o'clock positions – are occasionally enlarged (Fig. 7B), potentially leading to confusion with the eroded lateral edges of the proximal plate in *Neocteniza* subtype of bothria (Fig. 6D).

The *Fufius* subtype is most prevalent bothrial form among mygalomorphs, occurring in all families of all distal lineages (i.e., ctenizoids, theraphosoids and nemesioids) without exceptions. It is the sole type observed in ctenizids and euctenizids, as well as in all nemesioid families except pycnothelids (Figs 27A, B, 28).

2.2. *Euagrus* subtype (Eu). This bothrium forms a flattened, teardrop-shaped tubercle with irregular longitudinal wrinkles behind the aperture (Fig. 7C, arrowed). In some cases, the lateral wrinkles encircle the aperture, converging at the ends anterior to it (Fig. 7D, arrowed; Passanha & Brescovit 2018: fig. 1E).

The *Euagrus* subtype is readily distinguishable from the *Fufius* subtype, which exhibits a strongly convex dome with regular radial wrinkles (Fig. 7A, arrowed). Despite their differences, these two types are often conflated under the term 'corrugiform' (e.g., Coyle 1988; Passanha & Brescovit 2018).

This type is relatively rare: it is recorded once in the basal hexatheloid lineage (Euagridae) and, on the other hand, in the distal nemesioid lineage (Dipluridae: Masteriinae – but not in Diplurinae – and Microstigmatidae) (Figs 26B, 28).

2.3. *Paratropis* subtype (Pa). Although classified here as 'solid corrugated', this bothrium exhibits strongly reduced corrugation, appeared as an almost smooth ridge with vestigial wrinkles posteriorly (Fig. 8C, left arrow). This ridge forms a broad, crater-like circle around the aperture. The inner surface of the trichobothrial socket displays concentric folds (Dupérré & Tapia 2020: fig. 71), a feature seemingly unique and more akin to scorpion bothria (Eskov *et al*. 2024: fig. 7A).

This subtype likely derives from the *Neocteniza* subtype: the lateral lobes of its horseshoe-shaped proximal plate may have extended forward, encircling the aperture and fusing anteriorly. If such interpretation is correct, the flat ring along the inner 'crater' surface, wider anteriorly (Fig. 8C, right arrow; Dupérré & Tapia 2020: fig. 71) should be regarded as remnants of the distal plate.

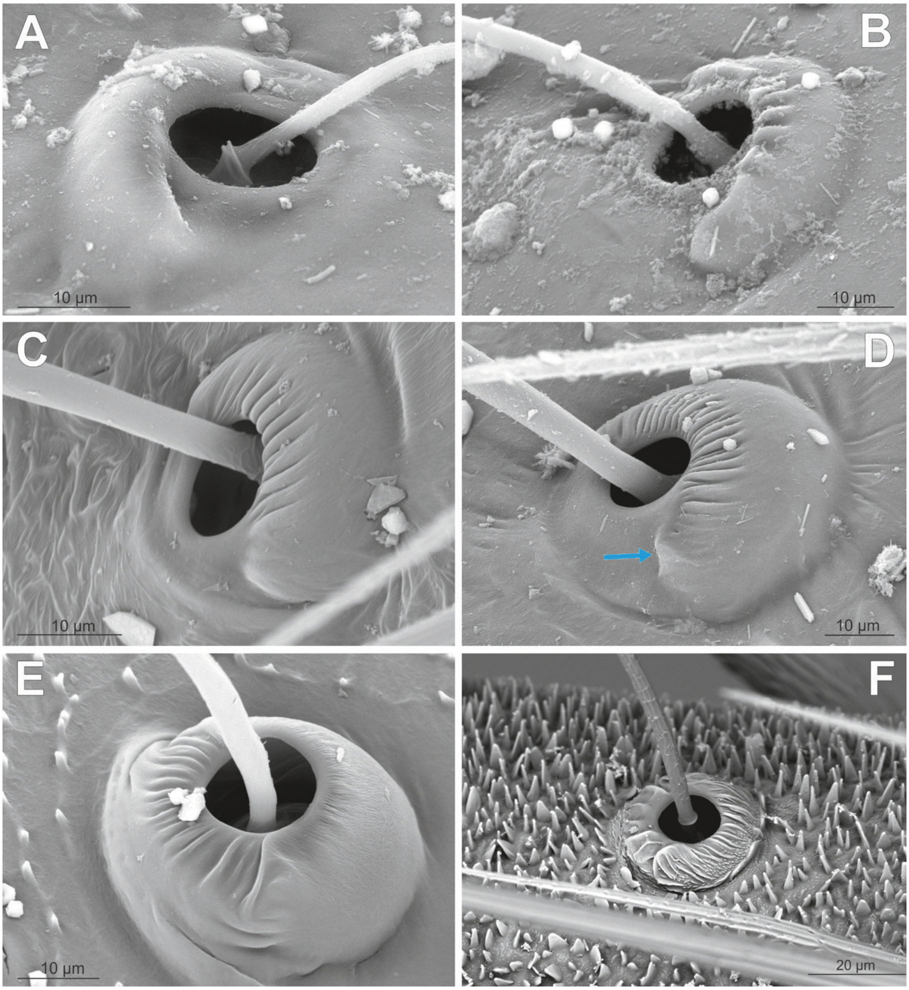

Fig. 6. Typology of mygalomorph bothria: intermediate types: (A) *Titanidiops syriacus* (Idiopide), ti1 (Ti); (B) *Ummidia dudkoi* (Halonoproctidae), ti2 (Um); (C) *Acanthogonatus huaquen* (Pycnothelidae), ti3 (Ne); (D) *Neocteniza toba* (Idiopidae), ti1 (Ne: arrow – eroded lateral ends of the posterior plate); (E) *Diplura* aff. *sanguinea* (Dipluridae), ti3 (Di); (F) *Ixamatus musgravei* (Microstigmatidae), leg1 (Di). Abbreviations: Di – *Diplura* subtype, Ne – *Neocteniza* subtype, Ti – *Titanidiops* subtype, Um – *Ummidia* subtype.

In our view, this crater-like structure is as unique and noteworthy as remarkable bothria of actinopodids (see below). The *Paratropis* subtype is exclusively restricted to the controversial family Paratropididae, which is placed by Opatova *et al*. (2020) in the actinopodoid lineage (Fig. 26C).

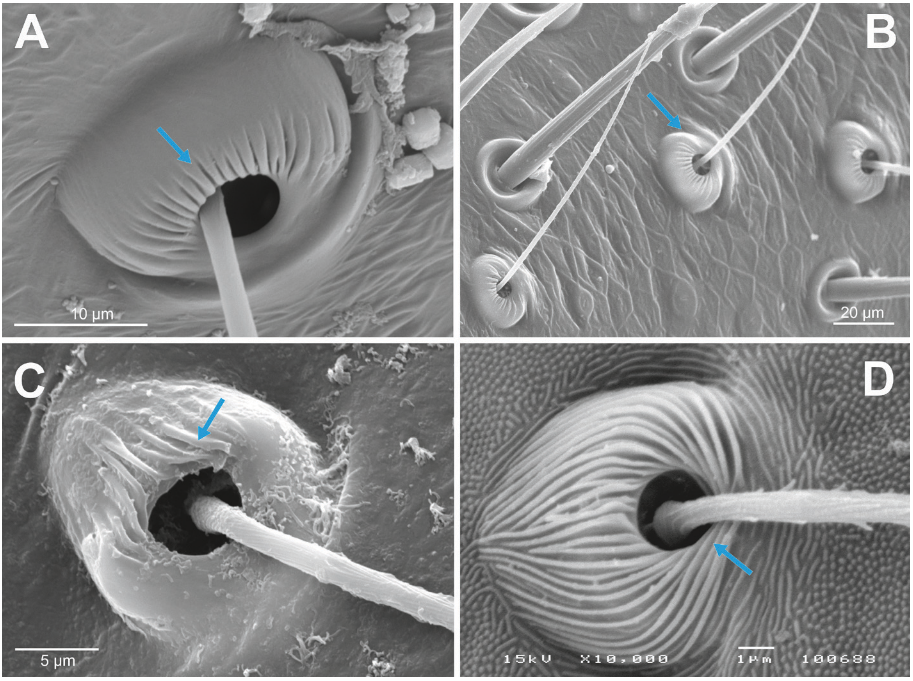

Fig. 7. Typology of mygalomorph bothria: advanced 'solid corrugated' types: (A) *Acanthogonatus* sp. (Pycnothelidae), ta3 (Fu: arrow – regular radial wrinkles); (B) *Fufius agualaniensis* (Rhytidicolidae), mt3 (Fu: arrow – enlarged lateral plicae of the corrugation); (C) *Euagrus chisoseus* (Euagridae), ti3 (Eu: arrow – irregular longitudinal wrinkles behind the aperture); (D) *Tonton* sp. (Microstigmatidae), mt2 (Eu: arrow – the lateral wrinkles encircle the aperture) (courtesy P. Lehtinen). Abbreviations: Eu – *Euagrus* subtype, Fu – *Fufius* subtype.

2.4. *Actinopus* subtype (Ac). This bothrium should be classified as 'solid non-corrugated'. It comprises a rounded, smooth area lacking radial wrinkles, with marginal outgrowths of varying shapes and degrees of development (Fig. 8A, B). Described as "a curiously sinuous impression around tricheme aperture", it has been considered a unique synapomorphy of Actinopodidae (Goloboff & Platnick 1987: 11–12; Goloboff 1993: char. 64).

However, the flattened bothria with reduced outgrowths in the actinopodid *Missulena* Walckenaer, 1805 (Fig. 14D; Goloboff & Platnick 1987: fig. 18, fig. 19) more closely resemble those of Atracidae (Figs 8B, 14B, C) than those of another actinopodid, *Actinopus* Perty, 1833 (Fig. 14E; Goloboff & Platnick 1987: fig. 17).

Intriguingly, recent molecular data support a sister-group relationship between Actinopodidae and Atracidae (Hedin *et al*. 2018; Opatova *et al*. 2020), contradicting all previous morphology-based phylogenies (e.g., Goloboff 1993). Thus, the *Actinopus* subtype bothria represent the first morphological synapomorphy of this molecularly defined clade.

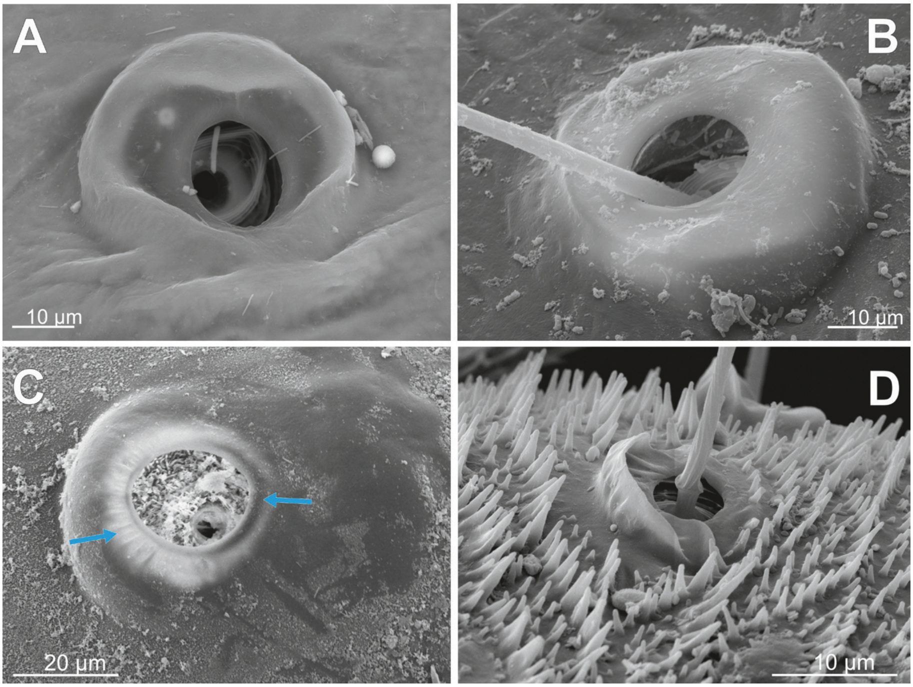

Fig. 8. Typology of mygalomorph bothria: advanced 'solid corrugated' (C) and 'solid non-corrugated' (A, B, D) types: (A) *Actinopus* sp. (Actinopodidae), ti3 (Ac); (B) *Hadronyche cerberea* (Atracidae), mt3 (Ac); (C) *Paratropis papilligera* (Paratropididae), ta4 (Pa: left arrow – vestigial wrinkles, right arrow – supposed remnants of the distal plate) (courtesy B. Mauricio); (D) *Ministigmata minuta* (Microstigmatidae), leg1 (Mi). Abbreviations: Ac – *Actinopus* subtype, Mi – *Ministigmata* subtype, Pa –*Paratropis* subtype.

This type likely originated from the intermediate *Titanidiops* subtype and is strictly confined to the Actinopodoid lineage (Fig. 26C).

2.5. *Ministigmata* subtype (Mi). The second example of 'solid non-corrugated' bothria, this type features a flattened smooth area with three transversal crests surrounding the aperture – one proximal and two lateral (Figs 8D, 22C, D).

The proximal sharp crest may have evolved from the low, rounded ridge of the *Titanidiops* subtype (Fig. 6A) and superficially resembles the 'hood' of the *Idiops* subtype (Fig. 5B). This bothrial form is unique to the microstigmatid genus *Ministigmata* Raven & Platnick, 1981 within the distal nemesioid lineage (Fig. 28).

3. Intermediate bothria (= *Argiope* type**)**

3.1. *Titanidiops* subtype (Ti). In this bothrium, the initial proximal plate is transformed into a smooth, horseshoe-shaped rounded ridge (Fig. 6A). It may represent a basal form for the intermediate subtypes, directly derived from the ancestral *Idiops* subtype (Fig. 5B). Both these subtypes are present in the idiopid subfamily Idiopine, but the rare *Titanidiops* subtype has not recorded outside this group (Fig. 27A).

3.2. *Ummidia* subtype (Um). This bothrium appears to be derived from the *Titanidiops* subtype: the horseshoe-shaped rounded ridge of its proximal plate is not smooth but divided into several sections by deep transverse cuts (Fig. 6B). This subtype is restricted to the ctenizoid lineage and occurs in halonoproctids and migids (Fig. 27A).

3.3. *Neocteniza* subtype (Ne). This bothrium likely represents a further development of the *Ummidia* subtype: the few deep transverse cuts dividing the horseshoe-shaped rounded ridge are replaced by numerous shallow wrinkles, forming a ‘corrugated’ surface. The lateral ends of the ridge are more eroded; and the overall appearance of the bothrium is somewhat ‘domed’ (Fig. 6C, D). This type is widely distributed across all distal lineages: ctenizoids (in idiopids and migids), theraphosoids (in theraphosids, barychelids and bemmerids) (Fig. 27A, B) and nemesioids (in pycnothelids) (Fig. 28), but it is very rare in basal lineages: hexatheloids (in porrhothelids) and actinopodoids (in stasimopids) (Fig. 26B, C).

3.4. *Diplura* subtype (Di). In this domed bothrium, the boundary between the fused initial proximal and distal plates remains clearly discernible, but it is the distal plate that is more ‘corrugated’ than the proximal one (Fig. 6E, F). This subtype is rare and strictly limited to the distal nemesioid lineage, occurring in only in two its subfamilies: Dipluridae: Diplurinae and Microstigmatidae: Ixamatinae (Fig. 28).

Distribution of bothrial types in lineages of Mygalomorphae

The lineages and the families in a lineage are listed in the order they arranged in the Opatova *et al.*’s (2020) cladogram (Fig. 1), from left to right; the genera in a family/subfamily are listed in the alphabetic order.

Distribution, at the family/subfamily level, of the above-identified bothrial types in the six main lineages of Mygalomorphae is summarized in Figs 26–28. It should be emphasized that these are not cladograms in the strict sense: the families/subfamilies within of the main lineages (Fig. 1) are not subordinated. They are arranged in one row so that taxa with the ancestral type of bothria are on the left side of the row, and those with an advanced type are on the right.

1. Atypoid lineage (AT)

1.1. Hexurellidae Hedin & Bond, 2019 (Hur)
1.2. Mecicobothriidae Holmberg, 1882 (Mec)
1.3. Atypidae Thorell, 1870 (Aty)
1.4. Megahexuridae Hedin & Bond, 2019 (Meg)
1.5. Antrodiaetidae Gertsch, 1940 (Ant)

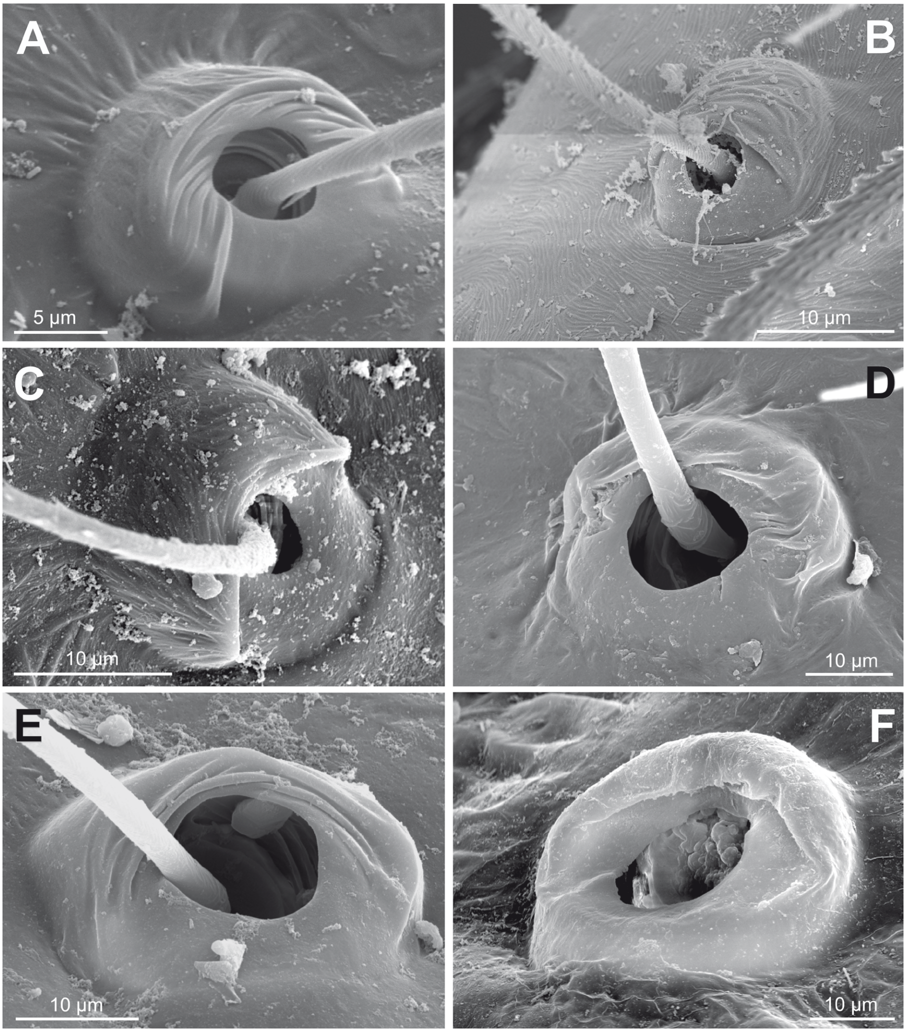

Fig. 9. Bothria of Atypoid lineage, Mecicobothriidae (A), Hexurellidae (B), Megahexuridae (C), Atypidae (D–F): (A) *Mecicobothrium thorelli*, ti2 (At); (B) *Hexurella pinea*, mt4 (At) (courtesy J. Blasco); (C) *Megahexura fulva*, mt3 (At); (D) *Atypus muralis*, ti1 (At); (E) *Sphodros niger*, ti3 (At); (F) *Calommata sundaica*, palal ti (At). Abbreviation: At – *Atypus* subtype.

The atypoids are the only mygalomorph lineage whose composition has remained largely unchanged since Simon (1892), with the sole exception being the separation of the mecicobothriid genera *Hexurella* Gertsch & Platnick, 1979 and *Megahexura* Kaston, 1972 into stand-alone families by Hedin *et al*. (2019).

During the late 20th century, the prevailing view regarded 'atypoids' as a paraphyletic group at the base of the mygalomorph stem (Platnick & Gertsch 1976; Platnick 1977; Gertsch & Platnick 1979). Although morphological evidence supporting the monophyly of Atypoidea was later proposed (Eskov & Zonstein 1990), it was not widely accepted (Goloboff 1993) and remained overlooked for decades. However, recent molecular studies (Hedin & Bond 2006; Bond *et al*. 2012) have provided strong support for the monophyly of Atypoidea, leading to its well-substantiated reinstatement (Hedin *et al*. 2019; Opatova *et al*. 2020).

1.1. Hexurellidae (Hur)

The bothria of the sole member of the famiily, *Hexurella* Gertsch & Platnick, 1979, are studied here. They belong to the *Atypus* subtype of hooded bothria but differ from all other atypoid bothria by their heavily transversely ridged proximal plate (Figs 5F, 9B).

The leg cuticular pattern in *Hexurella* is 'fingerprint-like' (Fig. 9B), which is rare among mygalomorphs in general and unique within atypoids.

1.2. Mecicobothriidae

The bothria of its sole member, *Mecicobothrium* Holmberg, 1882, are studied here. They belong to the *Atypus* subtype of hooded bothria but differ from all other atypoid bothria by numerous heavy transverse folds forming a wide strip at the anterior edge of their longitudinally ridged proximal plate (Fig. 9A).

The leg cuticular pattern in *Mecicobothrium* is 'ornamented imbricate' with additional microsculpture on each scale (Fig. 3C).

1.3. Atypidae

The bothria of all three atypid genera: *Atypus* Latreille, 1804, *Calommata* Lucas, 1837 and *Sphodros* Walckenaer, 1835, are studied here. Bothria of two genera were illustrated previously: *Atypus* (Platnick & Gertsch 1976: fig. 17) and *Calommata* (Fourie *et al*. 2011: figs 41, 44, 47, 50).

All belong to the *Atypus* subtype of hooded bothria, but exhibit significant intergeneric variation. The shape of anterior edges of their smooth proximal plates differs among genera:

- in *Sphodros*, they possess parallel folds typical of this bothrial type (Fig. 9E);
- in *Atypus*, the folds are tangled (Figs 5E, 9D);
- in some *Calommata* species, the folds are irregular and distinct, resembling those of *Atypus* (Fourie *et al*. 2011: fig. 47), while in others, they are vestigial (Fig. 9F; Fourie *et al*. 2011: fig. 44).

The leg cuticular pattern in atypids varies: 'typically scaly' in *Calommata*, and 'transversely imbricate' in *Sphodros* and *Atypus* (own observations).

1.4. Megahexuridae

The bothria of its sole member, *Megahexura* Kaston, 1972, are studied here. They belong to the *Atypus* subtype of hooded bothria, with a slightly concave anterior

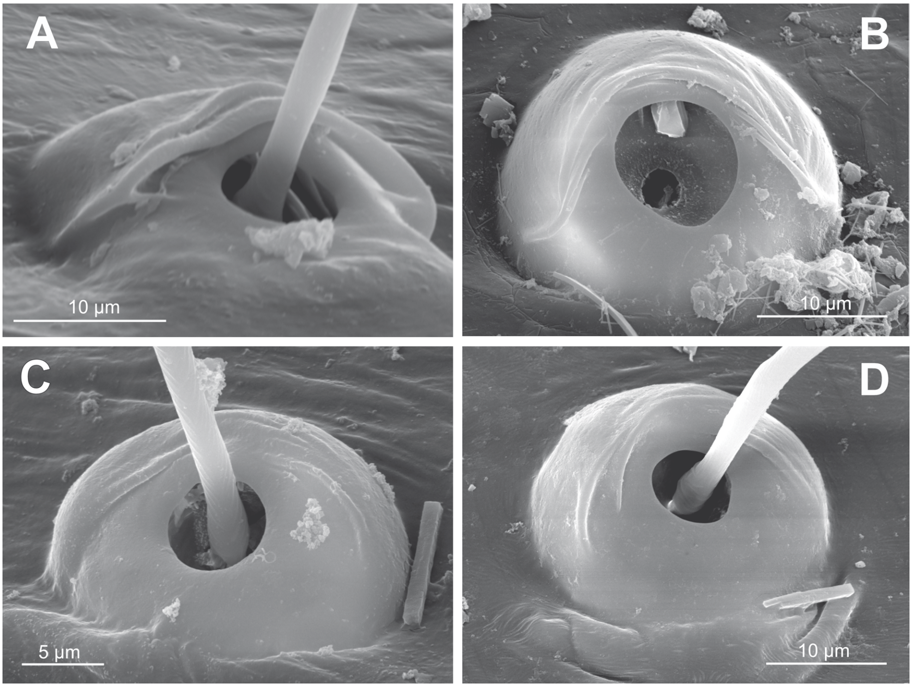

Fig. 10. Bothria of Atypoid lineage, Antrodiaetidae: (A) *Atypoides* sp., ti3 (At); (B) *Hexura picea*, ti3 (At); (C) *Antrodiaetus montanus*, ti3 (At); (D) *Aliatypus janus*, ti3 (At). Abbreviations: At – *Atypus* subtype.

edge of its multidirectionally ridged proximal plate (Fig. 9C). The leg cuticular pattern in *Megahexura* is 'typically scaly' (Fig. 3A).

1.5. Antrodiaetidae

The bothria of all four antrodiaetid genera: *Aliatypus* Smith, 1908, *Antrodiaetus* Ausserer, 1871, *Atypoides* O. Pickard-Cambridge, 1883 and *Hexura* Simon, 1885, are studied here. Bothria of two genera were illustrated previously: *Hexura* and *Atypoides* (Platnick & Gertsch 1976: figs 13 and 15, respectively).

All belong to the *Atypus* subtype of hooded bothria, but exhibit significant intergeneric variation.

Bothria of *Atypoides*, *Antrodiaetus* and *Aliatypus* are highly uniform, nearly indistinguishable, with slightly concave, folded anterior edges of their smooth proximal plates (Fig. 10A, C, D).

In contrary, in *Hexura*, the proximal plate is horseshoe-shaped, with its anterior edge being strongly concave and superficially resembling the *Macrothele* subtype of hooded bothria, yet possessing the diagnostic folds of the *Atypus* subtype (Figs 5D, 10B).

The leg cuticular pattern in antrodiaetids is ancestral scaly. However, in *Hexura* it is 'typically scaly' (Fig. 5D), whereas in the other three genera it is 'transversely imbricate', with widened and shortened scales (Fig. 3B).

Summary of bothrial and cuticular diversity in atypoids

The diversity of bothrial types within this lineage is summarized in Fig. 26A. Atypoids exhibit uniformity in bothrial structure, represented exclusively by the *Atypus* subtype of ancestral hooded bothria.

In contrast, leg cuticular patterns in atypoids are highly diverse:

- 'typically scaly' (Megahexuridae, some Atypidae and some Antrodiaetidae);
- 'transversely imbricate' (some Atypidae and some Antrodiaetidae);
- 'ornamented imbricate' (Mecicobothriidae);
- 'fingerprint-like' (Hexurellidae).

2. Hexatheloid lineage ('HE')

2.1. Ischnothelidae F. O. Pickard-Cambridge, 1897 (Ish)

2.2. Microhexuridae Bond, Opatova & Hedin, 2020 (Mhx)

2.3. Hexathelidae Simon, 1892 (Hex)

2.4. Euagridae Raven, 1979 (Eua)

2.5. Porrhothelidae Hedin & Bond, 2018 (Por)

2.6. Macrothelidae Simon, 1892 (Mac)

This lineage represents a paraphyletic group at the base of the 'non-atypoid mygalomorph' stem (Fig. 1). All its members were formerly classified as Dipluridae *sensu lato*. It now unites Hexathelidae (*sensu* Raven 1980*a*), alongside the hexathelid genera *Macrothele* Ausserer, 1871 and *Porrhothele* Simon, 1892, separated into stand-alone families by Hedin *et al*. (2018), as well as the 'nondiplurine diplurids' (*sensu* Opatova *et al*. 2020: 698). The last comprised Euagrinae, Ischnothelinae and the diplurid genus *Microhexura* Crosby & Bishop, 1925, all elevated to the family status (Opatova *et al*. 2020).

The remaining diplurids (Diplurinae and Masteriinae) and the hexathelid subfamily Atracinae (*sensu* Gray 2010) were placed by Opatova *et al*. (2020) at the outermost parts of their cladogram (see below).

Recently Raven and Douglas (2025) attempted to resurrect Hexathelidae *sensu lato*, rejecting both Macrothelidae and Porrhothelidae as distinct families and reclassifying Atracidae as a hexathelid subfamily; however, they provided no detailed argumentation.

2.1. Ischnothelidae (Ish)

The bothria of three ischnothelid genera: *Ischnothele* Ausserer, 1875, *Lathrothele* Benoit, 1965 and *Thelechoris* Karsch, 1881, are studied here.

Bothria of four genera were illustrated previously: *Ischnothele* (Coyle 1995: figs 43, 44), *Lathrothele* (Raven 1983*b*: pl. II, fig. 2; Coyle 1995: fig. 45), *Thelechoris* (Raven 1983*a*: pl. I, fig. 1; Coyle 1995: fig. 46) and *Tepuithele* Dupérré & Tapia 2025 (Dupérré & Tapia 2025: fig. 7A). All belong to the *Idiops* subtype of hooded

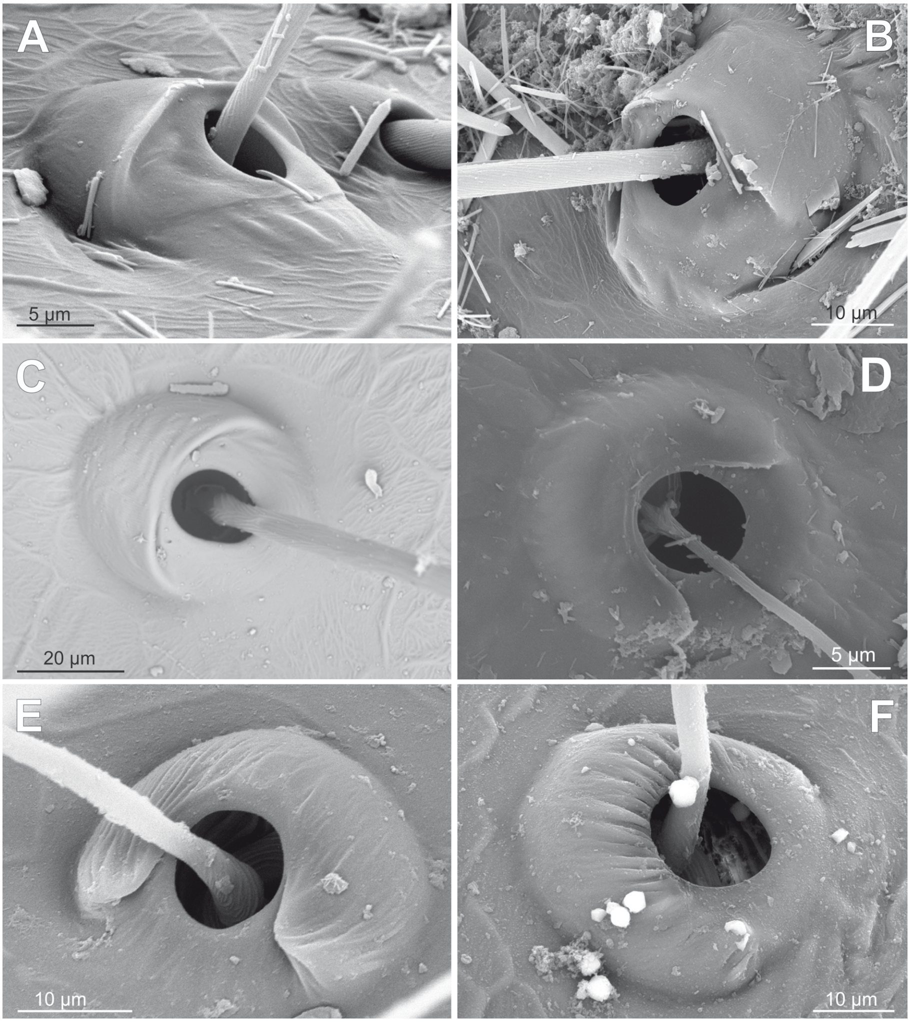

Fig. 11. Bothria of Hexatheloid lineage, Ischnothelidae (A–C), Macrothelidae (D, E), Porrhothelidae (F): (A) *Lathrothele grabensis*, ti3 (Id); (B) *Thelechoris rutenbergi*, ti3 (Id); (C) *Ischnothele annulata*, ti1 (Id); (D) *Macrothele calpeiana*, mt1 (Ma); (E) *Vacrothele* sp., ti3 (Ma); (F) *Porrhothele antipodiana*, mt3 (Ne). Abbreviations: Id – *Idiops* subtype, Ma – *Macrothele* subtype, Ne – *Neocteniza* subtype.

bothria, showing high uniformity: smooth proximal plates with a straight or slightly concave anterior margin (Figs 5A, 11A–C).

Coyle (1995: 12) emphasized that ischnothelid bothria differ from the typical collar-like hexatheloid *Macrothele* subtype due to their smooth (vs ridged) and only slightly concave (vs horseshoe-shaped) posterior plate.

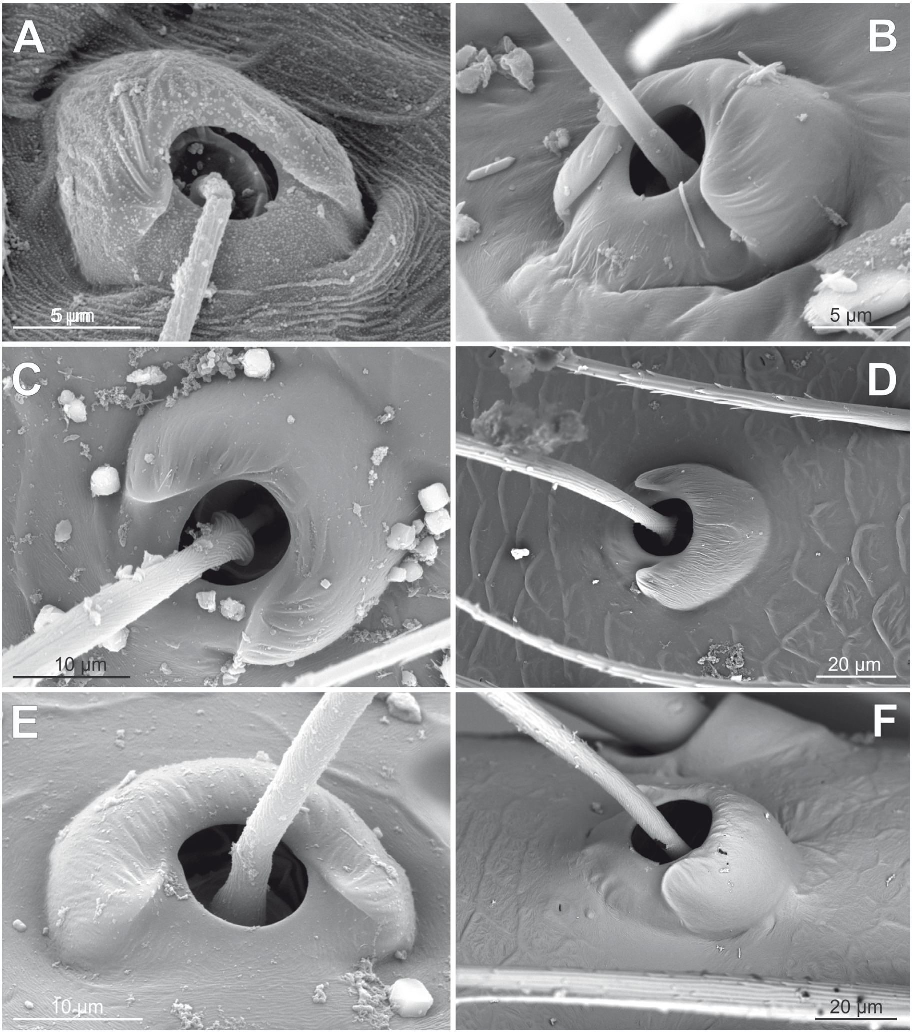

Fig. 12. Bothria of Hexatheloid lineage, Microhexuridae (A), Hexathelidae (B–F): (A) *Microhexura montivaga*, ti3 (Ma); (B) *Mediothele nahuelbuta*, ti3 (Ma); (C) *Scotinoecus major*, mt3 (Ma); (D) *Paraembolides boycei*, leg1 (Ma); (E) *Hexathele petriei*, ti3 (Ma); (F) *Teranodes* sp., lg4 (Ma). Abbreviation: Ma – *Macrothele* subtype.

Notably, Raven (1984: 4) erroneously classified ischnothelid bothria as 'corrugiform' in his family diagnosis; this was based solely on bothria of Euagridae then considered a subtaxon of Ischnothelidae (see below).

The leg cuticular pattern in ischnothelids is uniform, 'typically scaly' (our own observations).

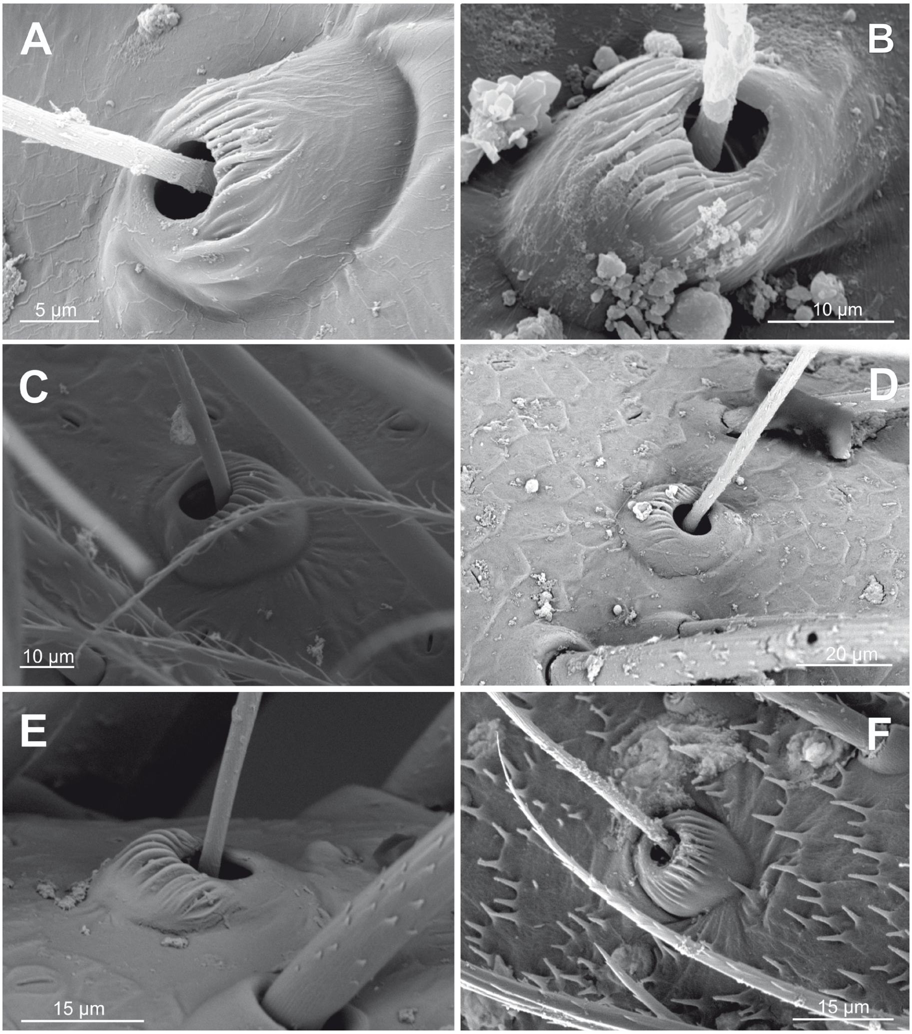

Fig. 13. Bothria of Hexatheloid lineage, Euagridae, Euagrinae (A, B), Australothelinae (C–F): (A) *Chilehexops australis*, mt3 (Eu); (B) *Phyxioschema raddei*, ti3 (Eu); (C) *Cethegus* sp., ta1 (Eu); (D) *Namirea* sp., ta1 (Eu); (E) *Australothele jamiesoni*, ta1 (Eu); (F) *Stenygrocercus* sp., ta1 (Eu). Abbreviation: Eu – *Euagrus* subtype.

2.2. Microhexuridae (Mhx)

The bothria of its sole member, *Microhexura* Crosby & Bishop, 1925, are studied here. Bothria of *Microhexura* were illustrated by Coyle (1995: fig. 47).

They belong to the *Macrothele* subtype of hooded bothria, with a collar-like proximal plate bearing heavy longitudinal ridges (Fig. 12A).

The leg cuticular pattern in *Microhexura* is rare 'imbricate-fingerprint', with additional ridged microsculpture on each scale (Fig. 3D).

2.3. Hexathelidae (Hex)

The bothria of five hexathelid genera: *Hexathele* Ausserer, 1871, *Mediothele* Raven & Platnick, 1978, *Paraembolides* Raven, 1980, *Scotinoecus* Simon, 1892 and *Teranodes* Raven, 1985, are studied here.

All belong to the *Macrothele* subtype of hooded bothria, showing high uniformity in collar-like posterior plate shape (Fig. 12B–F), though its striation varies from distinct to weakly pronounced (cf. Figs 12B and 12F).

Raven (1980*a*: 253) considered 'collariform' bothria diagnostic for the relimited Hexathelidae: "All diplurid genera so far examined have corrugiform trichobothrial bases. All hexathelid genera have collariform bases. Although the *corrugiform condition* may not be a synapomorphy for the diplurids, it is another difference from the Hexathelidae".

The leg cuticular pattern in hexathelids is uniform, 'typically scaly' (Fig. 12D; Lehtinen 1996: fig. 4).

2.4. Euagridae (Eua)

The bothria of seven genera from both euagrid subfamilies are studied here:

Euagrinae Raven, 1979: *Chilehexops* Coyle, 1986, *Euagrus* Ausserer, 1875 and *Phyxioschema* Simon, 1889;

Australothelinae Bond, Opatova & Hedin, 2020: *Australothele* Raven, 1984, *Cethegus* Thorell, 1881, *Namirea* Raven, 1984 and *Stenygrocercus* Simon, 1892.

The bothria of seven genera from both subfamilies were illustrated previously:

Euagrinae Raven, 1979: *Chilehexops* (Coyle, 1986: figs 7, 8; Goloboff 1989*b*: fig. 3), *Euagrus* (Coyle 1988: figs 36, 37) and *Phyxioschema* (Schwendinger 2009: fig. 21C);

Australothelinae Bond, Opatova & Hedin, 2020: *Allothele* Tucker, 1920 (Coyle, 1984: figs 11, 12), *Australothele*, *Cethegus* and *Namirea* (Raven, 1984: figs 18, 20, 29, respectively).

All belong to the *Euagrus* subtype of unusual for hexatheloids advanced 'solid corrugated' bothria. These are highly uniform across subfamilies and likely represent a family-related synapomorphy: a flattened, elongated, teardrop-shaped tubercle with irregular longitudinal wrinkles behind the aperture (Figs 7C, 13A–F), contrasts the domed, radially wrinkled *Fufius* subtype of corrugated bothria. Corrugated bothria were included in Euagridae diagnosis from their inception (Raven 1984: 5, 1985*b*: 15).

Notably, leg cuticle in at least two australotheline genera, *Stenygrocercus* and *Allothele*, is pustulose (Fig. 13F and Coyle 1984: figs 11, 13, respectively). The pustulose cuticle was listed by Opatova *et al*. (2020: 702, 703) as diagnostic for Microstigmatidae, and is still unrecorded outside Nemesioid lineage (see below). Leg cuticular pattern in other euagrids is 'typically scaly' (Fig. 13D).

2.5. Porrhothelidae (Por)

The bothria of its sole member, *Porrhothele* Simon, 1892 (comprising two species), are studied here. They belong to the *Neocteniza* subtype of the unusual, for the hexatheloids, intermediate bothria with a traceable border between fused proximal and distal plates. Its horseshoe-shaped proximal plate has shallow radial wrinkles and obliterated lateral edges (Fig. 11F). The leg cuticular pattern in *Porrhothele* is 'typically scaly' (own observations).

2.6. Macrothelidae (Mac)

The bothria of two macrothelid genera: *Macrothele* Ausserer, 1871 (three species) and *Vacrothele* Tang & Yang, 2022, are studied here. All belong to the *Macrothele* subtype of hooded bothria, showing high uniformity in collar-like posterior plate shape (Figs 2C, 5C, 11D–E), though its striation varies from distinct, via weakly pronounced, to almost smooth (Figs 2C, 5C and 11D, respectively). The leg cuticular pattern in macrothelids is uniform, 'typically scaly' (Fig. 2C).

Summary of bothrial and cuticular diversity in hexatheloids

The bothria types within this lineage (Fig. 26B) are are highly diverse:

- ancestral hooded *Idiops* subtype (in Ischnothelidae);
- ancestral hooded *Macrothele* subtype, most common (in Microhexuridae, Hexathelidae and Macrothelidae);
- intermediate *Neocteniza* subtype (in Porrhothelidae);
- advanced corrugated *Euagrus* subtype (in Euagridae).

Conversely, leg cuticular pattern is nearly uniform, 'typically scaly', in all hexatheloids except Microhexuridae (with rare 'imbricate-fingerprint' cuticle) and some Euagridae: Australothelinae (with rare pustulose cuticle).

Notably, this hexatheloid 'big picture' (diverse bothria vs uniform cuticle) is reversal to the atypoid one (uniform bothria vs diverse cuticle patterns).

3. Actinopodoid lineage ('AC')

3.1. Paratropididae Simon, 1889 (Par)
3.2. Stasimopidae Bond, Opatova & Hedin, 2020 (Sta)
3.3. Actinopodidae Simon, 1892 (Act)
3.4. Atracidae Hogg, 1901 (Atr)

This lineage is paraphyletic and the most controversial, as its composition is based solely on molecular data. "We recovered Paratropididae and Actinopodidae (removed from Bipectina by Bond *et al*. (2012)) alongside the Atracidae as part of that clade. The Bipectina including these three families represent the most inclusive monophyletic arrangement that is consistently recovered in all the molecularmolecular analyses. For this reason, we choose to relimit the Bipectina clade (*sensu* Bond *et al*. (2012)) to include Actinopodidae, Atracidae, Stasimopidae, and Paratropididae alongside the Crassitarsae and Domiothelina" (Opatova *et al*. 2020: 690).

Atracines were found to be phylogenetically distinct from other hexathelids based on both morphological (Raven 1985*a*: 55) and rRNA data (Hedin & Bond

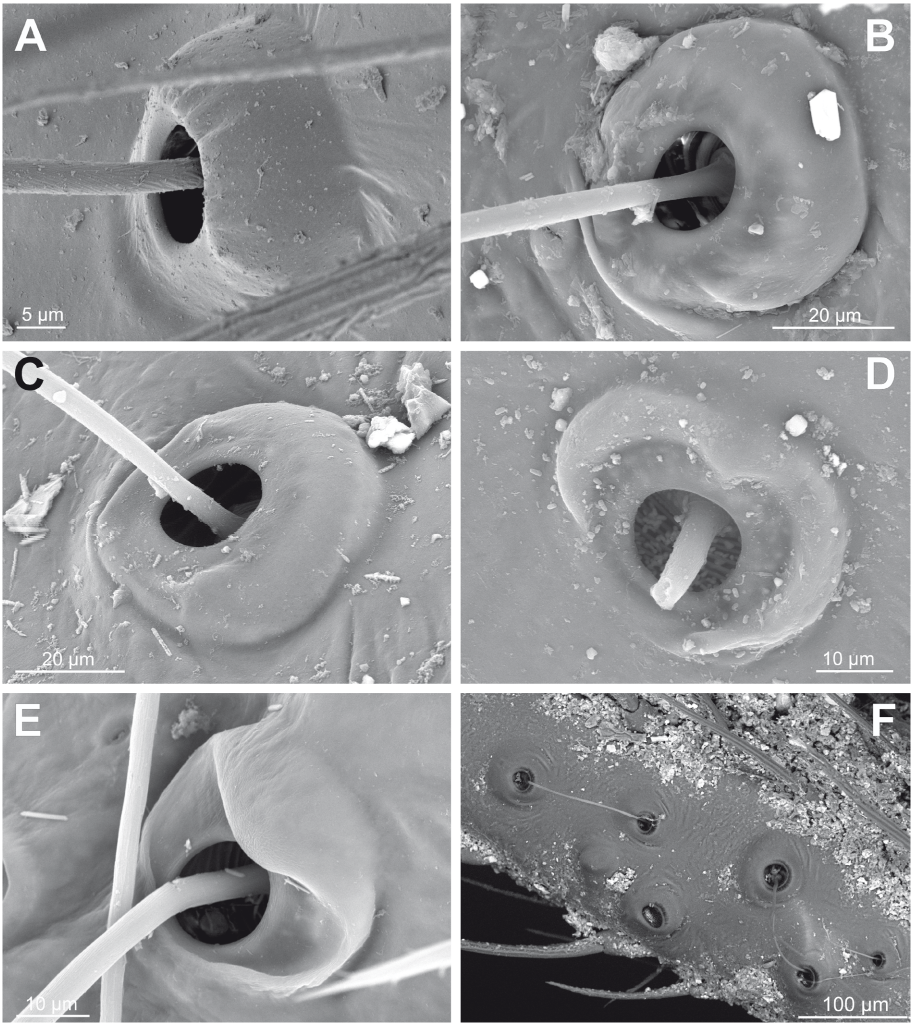

Fig. 14. Bothria of Actinopodoid lineage, Stasimopidae (A), Atracidae (B, C), Actinopodidae (D–E), Paratropididae (F): (A) *Stasimopus minor*, mt1 (Ne) (courtesy C. Haddad); (B) *Atrax* sp., ta3 (Ac); (C) *Hadronyche cerberea*, mt3 (Ac); (D) *Missulena occatoria*, mt3 (Ac); (E) *Actinopus* sp., ta3 (Ac); (F) *Paratropis pristirana*, ta4 (Pa) (courtesy N. Dupérré). Abbreviations: Ac – *Actinopus* subtype, Ne – *Neocteniza* subtype, Pa – *Paratropis* subtype

2006: 467). On the other hand, "Contrary to the hypothesis based on morphological characters (Raven 1985*a*; Goloboff 1993), Atracidae has consistently been recovered [by molecular studies] as sister to Actinopodidae" (Opatova *et al*. 2020: 694). Hedin *et al*. (2018) first demonstrated the sister relationship between Actinopodidae and

Atracidae by using phylogenomic analyses of ultraconserved element (UCE) sequences. These two families form the 'Venom Clade', supported by unique venom protein characteristics (Hedin *et al*. 2018).

Paratropididae, previously considered a sister group of Theraphosidae in morphological classifications (Raven 1985*a*; Goloboff 1993) has been problematic in molecular studies: "The family was recovered as a 'stand-alone' lineage with unresolved and unstable placement (Hedin & Bond 2006; Bond *et al*. 2012), potentially causing conflict in topology and lowering the support of deeper nodes" (Opatova *et al*. 2020: 675).

Further, "despite our best efforts, which included a combination of transcriptomic and AHE data, we are still unable to confidently resolve several of the deepest nodes; Paratropididae remains a difficult taxon to place as do the newly formed Stasimopidae" (Opatova *et al*. 2020: 693).

3.1. Paratropididae (Par)

The bothria of one paratropidid genus, *Paratropis* Simon, 1889 (comprising three species), are studied here. They were illustrated previously (Raven & Platnick 1981: fig. 21; Valdez-Mondragón *et al*. 2014: figs 18, 28, 38, 46–48; Dupérré & Tapia 2020: figs 70, 71).

They belong to the *Paratropis* subtype of advanced 'solid corrugated' bothria (Figs 8C, 14F). This crater-like structure is unique among mygalomorphs. However, due to the lack of data on other paratropidid genera, it remains unclear whether this is a family-level synapomorphy or an autapomorphy of *Paratropis*. The leg cuticular pattern in *Paratropis* is 'strongly rugose' (Fig. 14F).

3.2. Stasimopidae (Sta)

The bothria of its sole member, *Stasimopus* Simon, 1892, are studied here. They belong to the *Neocteniza* subtype of intermediate bothria, common in non-basal mygalomorph lineages. Its horseshoe-shaped proximal plate has shallow radial wrinkles and obliterated lateral edges (Fig. 14A). The leg cuticular pattern in *Stasimopus* is 'smooth' (own observations).

3.3. Actinopodidae (Act)

The bothria of two actinopodid genera, *Actinopus* Perty, 1833 and *Missulena* Walckenaer, 1805, are studied here. Bothria of these genera were illustrated previously: *Actinopus* (Goloboff & Platnick 1987: fig. 17; Miglio *et al*. 2020: fig. 6C, D) and *Missulena* (Goloboff & Platnick, 1987: figs 18, 19); a specimen initially assigned to *Plesiolena* Goloboff & Platnick, 1987 (Goloboff & Platnick 1987: fig. 19) was later reidentified as a *Missulena* species (Goloboff 1994).

All belong to the *Actinopus* type of advanced 'solid non-corrugated' bothria, consist of a rounded, flattened area with variably developed marginal outgrowths. These outgrowths are prominent in *Actinopus* (Figs 8A, 14E) and reduced in *Missulena* (Fig. 14D). The leg cuticular pattern in actinopodids is 'strongly rugose' (Fig. 4D).

3.4. Atracidae (Atr)

The bothria of two atracid genera: *Atrax* O. Pickard-Cambridge, 1877 and *Hadronyche* L. Koch, 1873, are studied here. In addition, bothria of *Hadronyche* were illustrated previously (Gray 2010: fig. 3I).

All belong to the *Actinopus* subtype of 'solid non-corrugated' bothria (Figs 8B, 14B, C). Marginal outgrowths of their smooth flattened area are weakly developed in *Hadronyche* and nearly absent in *Atrax* (cf. Figs 14C and 14B).

Gray (2010: 290) described bothria of Atracinae as 'weakly collariform', when classified this subfamily within Hexathelidae. However, they differ fundamentally from the collariform bothria of all hexatelides (cf. Fig. 12B–F) and instead resemble those of actinopodids (Fig. 14D, E), particularly some *Missulena* (Goloboff & Platnick 1987: fig. 19). The sister relationship between Actinopodidae and Atracidae was proposed by the new molecular data (Hedin *et al*. 2018; Opatova *et al*. 2020; Loria *et al*. 2025). The leg cuticular pattern in atracids is 'typically scaly' (own observations).

Summary of bothrial and cuticular diversity in actinopodoids

The diversity of bothrial types in this lineage is summarized in Fig. 26C.

Notably, the ancestral hooded bothria are entirely absent, while two derived types—*Actinopus* subtype and *Paratropis* subtype—are unique to this lineage. The *Actinopus* subtype provides the first morphological synapomorphy supporting the molecular-based sister relationship between Actinopodidae and Atracidae.

Leg cuticular patterns demonstrate similar evolutionary trends. Ancestral scaly cuticle, common in mygalomorphs, is retained only in Atracidae – 'typically scaly' pattern, whereas rare advanced cuticular patterns dominates in other actinopodoids: 'smooth' in Stasimopidae and 'strongly rugose' in Paratropididae and Actinopodidae.

4. Ctenizoid lineage (CT)

4.1. Halonoproctidae Pocock, 1901 (Hal)
4.2. Migidae Simon, 1889 (Mig)
4.3. Idiopidae Simon, 1889 (Idi)
4.4. Ctenizidae Thorell, 1887 (Cte)
4.5. Euctenizidae Raven, 1985 (Euc)

All members of this lineage have historically been classified either as subtaxa of Ctenizidae *sensu lato* or as their closest relatives, such as idiopids and migids (Godwin *et al*. 2018).

Platnick and Shadab (1976) originally identified Actinopodidae as the sister group of Migidae, a relationship later formalized by Raven (1985*a*: 36) under the proposed 'superfamily Migoidea'. Subsequent morphological analyses appeared to support the monophyly of this group (Griswold & Ledford 2001).

However, molecular evidence has challenged this classification: "The superfamily Migoidea, which comprises Migidae plus Actinopodidae ... is never recovered in

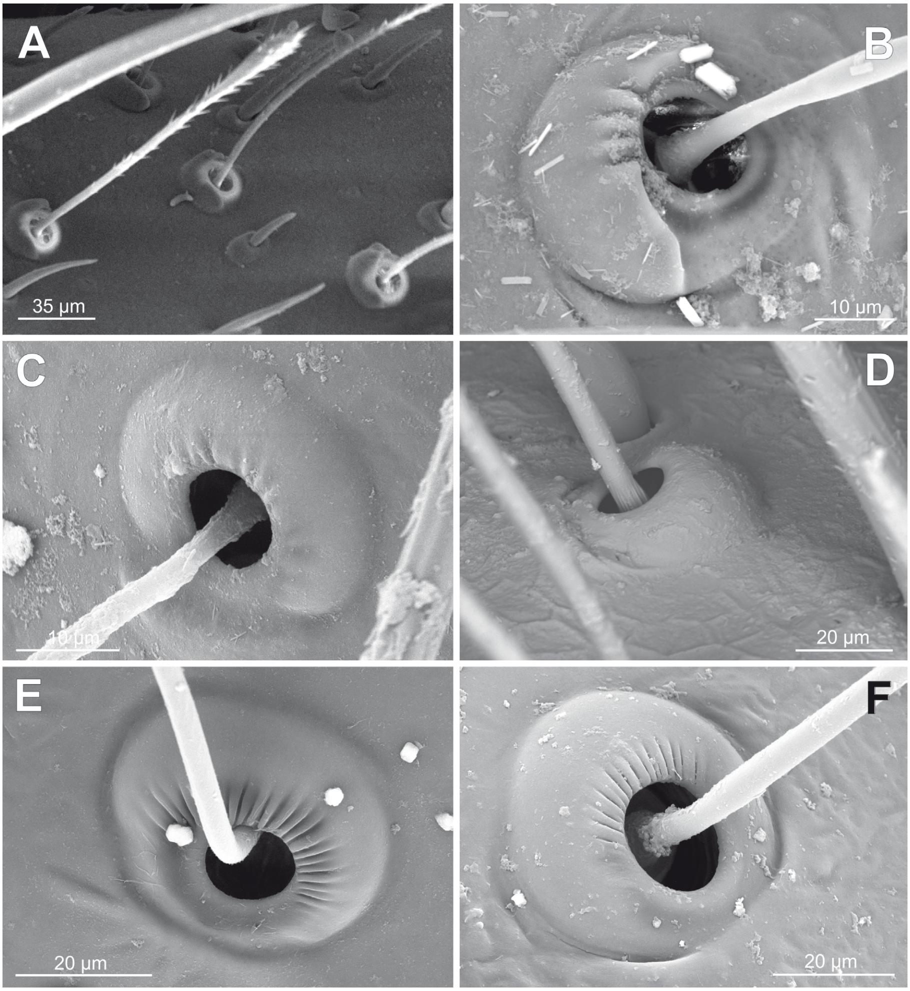

Fig. 15. Bothria of Ctenizoid lineage, Halonoproctidae Ummidiinae (A–C), Halonoproctidae Halonoproctinae (D), Ctenizidae (E), Euctenizidae (F): (A) *Conothele* sp., leg1 (Id); (B) *Ummidia dudkoi*, ti2 (Um); (C) *Sterrhochrotus ferghanensis*, mt1 (Fu): (D) *Bothriocyrtum californicum*, leg1 (Fu); (E) *Cyrtocarenum cunicularium*, ti2 (Fu); (F) *Myrmekiaphila torreya*, mt3 (Fu). Abbreviations: Id – *Idiops* subtype, Fu – *Fufius* subtype, Ne – *Neocteniza* subtype, Um – *Ummidia* subtype.

rRNA analyses" (Hedin & Bond 2006: 465), and later genomic data (Opatova *et al*. 2020: 694) further contradicted the grouping. As a result, Actinopodidae is no longer considered the closest relative of Migidae and was removed from 'Ctenizoid lineage', instead being placed with Atracidae in the 'Venom Clade'.

4.1. Halonoproctidae (Hal)

The bothria of four genera from both halonoproctid subfamilies are studied here:

Halonoproctinae Pocock, 1901: *Bothriocyrtum* Simon, 1891;

Ummidiinae Ortiz, 2007: *Conothele* Thorell, 1878, *Sterrhochrotus* Simon, 1892 and *Ummidia* Thorell, 1875. [N.B.: We consider *Conothele* and *Sterrhochrotus* as valid genera distinct of *Ummidia*, contrary to Decae (2010) and Decae *et al*. (2019).

Bothria of *Ummidia* were illustrated previously (Goloboff 1993: fig. 6). A high diversity of bothrial types is represented in halonoproctids.

In Ummidiinae, there is a remarkable evolutionary sequence: from the ancestral hooded bothria of *Idiops* subtype in *Conothele* (Fig. 15A), via the intermediate bothria of the *Ummidia* subtype in *Ummidia* (Fig. 15B), to the advanced domed bothria of *Fufius* subtype in *Sterrhochrotus* (Fig. 15C).

In the halonoproctin *Bothriocyrtum* the advanced domed bothria of the *Fufius* subtype have unusually reduced corrugaions (Fig. 15D).

The leg cuticular pattern is 'typically scaly' in *Conothele*, *Sterrhochrotus* and *Bothriocyrtum*, but 'weakly rugose' in *Ummidia* (own observations).

4.2. Migidae (Mig)

The bothria of eight genera from all three migid subfamilies are studied here:

Miginae: *Migas* L. Koch, 1873, *Poecilomigas* Simon, 1903;

Paramiginae: *Heteromigas* Hogg, 1902, *Micromesomma* Pocock, 1895, *Moggridgea* O. Pickard-Cambridge, 1875, *Paramigas* Pocock, 1895;

Calathotarsinae: *Calathotarsus* Simon, 1903 and *Goloboffia* Griswold & Ledford, 2001 (N.B.: Griswold & Ledford (2001: 44) stated the monophyly of the clade comprising *Calathotarsus*, *Goloboffia* and *Mallecomigas* Goloboff & Platnick, 1987).

Bothria of eight migid genera from all three subfamilies were illustrated previously:

Miginae: *Poecilomigas* (Griswold 1987*b*: figs 9, 11);

Paramiginae: *Micromesomma*, *Paramigas* and *Thyropoeus* Pocock, 1895 (Griswold & Ledford 2001: figs 24C, 42D and 55C, respectively), and *Moggridgea* (Griswold 1987*a*: figs 41, 42);

Calathotarsinae: *Goloboffia*, *Mallecomigas* Goloboff & Platnick, 1987 and *Calathotarsus* (Goloboff & Platnick 1987: figs 20, 21 and 22, respectively).

A high diversity of bothrial types is represented in migids: "Trichobothrial base distally embedded, with proximal hood, smooth or weakly corrigiform" (Griswold & Ledford 2001: 12).

Calathotarsinae: there is a sequence from the ancestral hooded bothria of the *Idiops* subtype in *Goloboffia* (Fig. 17A; Goloboff & Platnick 1987: fig. 20) and *Calathotarsus* (Fig. 17B; Goloboff & Platnick 1987: fig. 22), to the advanced domed bothria of the *Fufius* subtype in *Mallecomigas* (Goloboff & Platnick 1987: fig. 21).

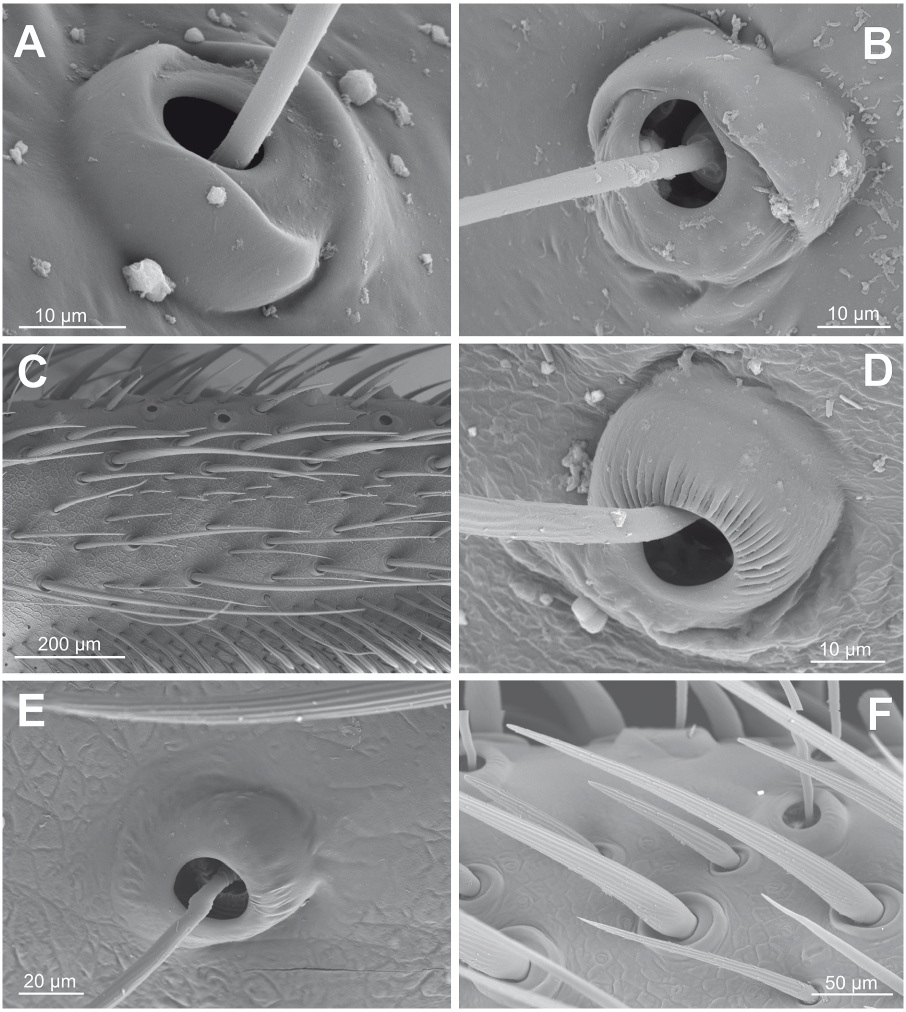

Fig. 16. Bothria of Ctenizoid lineage, Idiopidae, Idiopinae (A, B), Arbanitinae (C–F): (A) *Idiops clarus*, ta3 (Id); (B) *Heligmomerus* sp., ti3 (Id); (C) *Idiosoma* sp., ta1 (Ne); (D) *Cantuaria minor*, mt3 (Fu); (E) *Euoplos variabilis*, ta1 (Fu); (F) *Arbanitis* sp., ta1 (Fu). Abbreviations: Id – *Idiops* subtype, Fu – *Fufius* subtype, Ne – *Neocteniza* subtype.

Miginae: there is a sequence from the intermediate bothria of the *Neocteniza* subtype in *Migas* (Fig. 17C) to the advanced domed bothria of the *Fufius* subtype in *Poecilomigas* (Fig. 17D; Griswold 1987*b*: fig. 11).

Paramiginae: there is a sequence from the intermediate bothria of the *Ummidia* type in some *Moggridgea* (Fig. 18A) and *Thyropoeus* (Griswold & Ledford 2001: fig. 55C) to the advanced domed bothria of the *Fufius* subtype in a part of *Moggridgea*

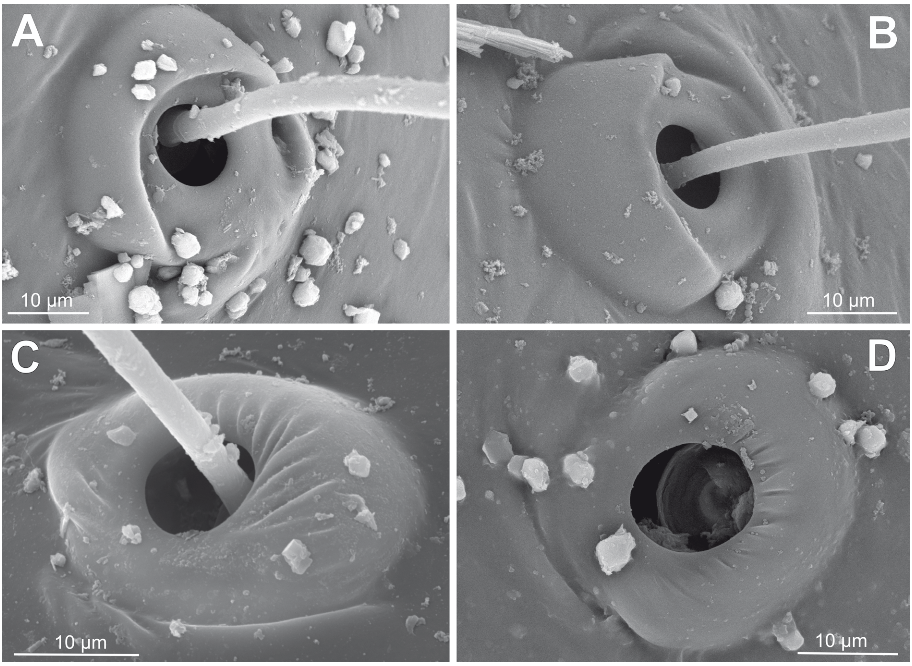

Fig. 17. Bothria of Ctenizoid lineage, Mididae, Calathotarsinae (A, B), Miginae (C, D): (A) *Goloboffia megadeth*, ta3 (Id); (B) *Calathotarsus simoni*, mt3 (Id); (C) *Migas nitens*, ti3 (Ne); (D) *Poecilomigas abrahami*, mt3 (Fu). Abbreviations: Id – *Idiops* subtype, Fu – *Fufius* subtype, Ne – *Neocteniza* subtype.

(Griswold 1987*a*: figs 41, 42), *Micromesomma*, *Heteromigas* and *Paramigas* (Figs 18B, 18C and 18D).

The domes of the *Fufius* subtype bothria in paramigines may be flattened in *Paramigas* (Fig. 18D; Griswold & Ledford 2001: fig. 42D), and their radial wrinkles may be replaced by a few radial folds in *Micromesomma* (Fig. 18B; Griswold & Ledford 2001: fig. 24C).

The coexistence of two bothrial types in the single genus *Moggridgea* should especially be noted: *Ummidia* subtype in *M. anactenidia* Griswold, 1987 (Fig. 18A) and *Fufius* subtype in *M. crudeni* Hewitt, 1913 and *M. breyeri* Hewitt, 1915 (Griswold 1987*a*: figs 41 and 42, respectively). Such cases in mygalomorphs are rare but not unique – at least two theraphosid and three pycnothelid genera demonstrate the same diversity (see below).

Leg cuticular patterns are highly diverse in migids, as are bothrial types:

Calathotarsinae: uniformly 'typically scaly' (own observations);

Miginae: varying from the 'typically scaly' in *Poecilomigas* (own observations) to the 'smooth with vestigial borders between initial scales' in *Migas* (Fig. 4B);

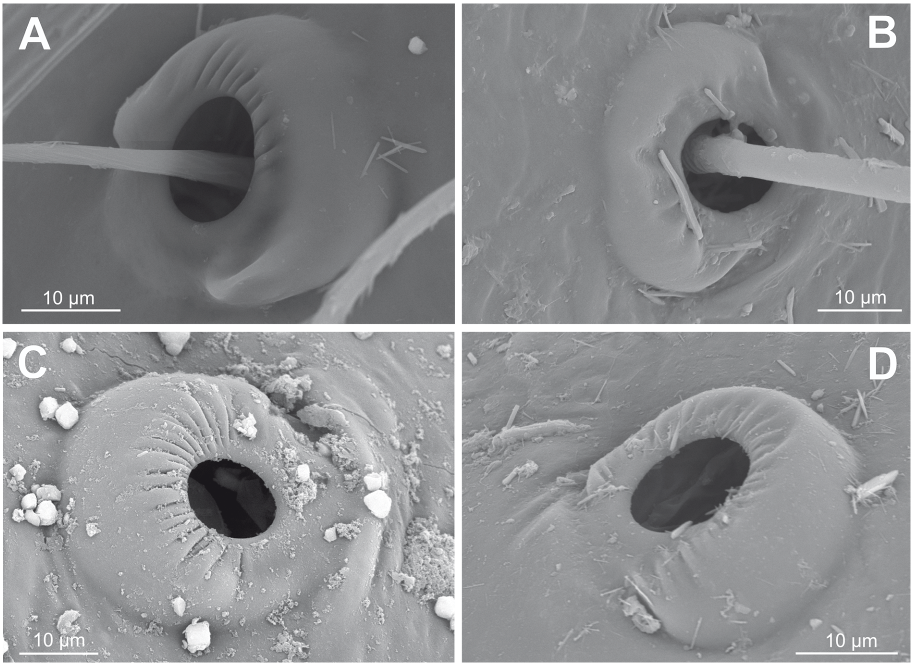

Fig. 18: Bothria of Ctenizoid lineage, Mididae Paramiginae: (A) *Moggridgea* aff. *anactenidia*, ta3 (Um); (B) *Micromesomma cowani*, mt3 (Fu); (C) *Heteromigas dovei*, mt3 (Fu); (D) *Paramigas perroti*, ta2 (Fu). Abbreviations: Fu – *Fufius* subtype, Um – *Ummidia* subtype.

Paramiginae: maximally diverse: 'typically scaly' in *Moggridgea*, 'ornamented imbricate' in *Paramigas*, 'weakly rugose' in *Micromesomma* (own observations), and 'smooth' in *Heteromigas* (Fig. 4A).

4.3. Idiopidae (Idi)

Bothria of eight genera from all three idiopid subfamilies are studied here:

Idiopinae Simon, 1889: *Idiops* Perty, 1833 (two species), *Heligmomerus* Simon, 1892 and *Titanidiops* Simon, 1903;

Arbanitinae Simon, 1903: *Arbanitis* L. Koch, 1874, *Euoplos* Rainbow, 1914, *Cantuaria* Hogg, 1902 and *Idiosoma* Ausserer, 1871;

Genysinae Simon, 1903: *Neocteniza* Pocock, 1895.

Additionally, the bothria of four idiopid genera from two subfamilies were illustrated previously:

Arbanitinae: *Cataxia* Rainbow, 1914 and *Euoplos* (Rossi *et al*. 2021: figs 23B and 23C, respectively);

Genysinae: *Neocteniza* (Rossi *et al*. 2021: fig. 12D);

Idiopidae *incertae sedis* (Rix *et al*. 2017): *Prothemenops* Schwendinger, 1991 (Schwendinger & Hongpadharakiree 2014: fig. 1C).

A high diversity of the bothrial types is represented in idiopids:

Idiopinae: there is a sequence from the ancestral hooded bothria of the *Idiops* subtype in *Idiops* (Fig. 16A) and *Heligmomerus* (Fig. 16B) to the intermediate bothria of the *Titanidiops* subtype in *Titanidiops* (Fig. 6A).

Arbanitinae: there is a sequence from the intermediate bothria of the *Neocteniza* subtype in *Idiosoma* (Fig. 16C) to the advanced domed bothria of the *Fufius* subtype in *Cantuaria* (Fig. 16D), *Euoplos* (Fig. 16E), *Arbanitis* (Fig. 16F) and *Cataxia* (Rossi *et al*. 2021: fig. 23B).

The bothria of the single studied Genysinae, *Neocteniza*, belong to the intermediate *Neocteniza* subtype (Fig. 6D; Rossi *et al*. 2021: fig. 12D).

The bothria of *Prothemenops* (Idiopidae *incertae sedis*), also appear to belong to the *Neocteniza* subtype (Schwendinger & Hongpadharakiree 2014: fig. 1C).

Leg cuticular patterns are highly diverse in idiopids, as are bothrial types. Ancestral 'typically scaly' cuticle seems absent in the family, while there are several derived its modifications.

The 'ornamented imbricate' pattern is most common: in Arbanitinae: *Cantuaria* (Fig. 16D), *Arbanitis* (Fig. 16F; Rossi *et al*. 2021: fig. 23A), *Idiosoma* (Fig. 16C; Rossi *et al*. 2021: fig. 23D); in Genysinae: *Neocteniza* (own observations; Rossi *et al*. 2021: figs 12D, 23F); and in Idiopidae *incertae sedis*: *Prothemenops* (Schwendinger & Hongpadharakiree 2014: fig. 1C).

The 'transversely imbricate' pattern presents in Idiopinae: *Idiops* (own observations; Rossi *et al*. 2021: fig. 23E) and *Titanidiops* (own observations), its strip-like scales are frontally edged by small tubercles.

The 'smoothed imbricate' pattern presents in *Cataxia* (Arbanitinae) (Rossi *et al*. 2021: fig. 23B).

Finally, the 'weakly rugose' pattern is present in *Euoplos* (Arbanitinae) (Fig. 16E; Rossi *et al*. 2021: fig. 23C) and in the idiopine *Heligmomerus* (our own observations).

4.4. Ctenizidae (Cte)

The bothria of one ctenizid genus, *Cyrtocarenum* Ausserer, 1871, are studied here (Fig. 15E). They belong to the *Fufius* subtype of domed corrugated bothria. The leg cuticular pattern is 'weakly rugose' (own observations).

4.5. Euctenizidae (Euc)

The bothria of one euctenizid genus, *Myrmekiaphila* Atkinson, 1886, are studied here (Fig. 15F). They belong to the *Fufius* subtype of domed corrugated bothria. The leg cuticular pattern is 'weakly rugose' (own observations).

Summary of bothrial and cuticular diversity in ctenizoids

The diversity of bothrial types within this lineage is summarized in Fig. 27A. A parallel evolutionary sequence of bothrial types—from the ancestral hooded *Idiops* subtype to the advanced domed *Fufius* subtype via several intermediate forms—occur in all three basal families in the superfamily cladogram (Fig. 1): Halonoproctidae,

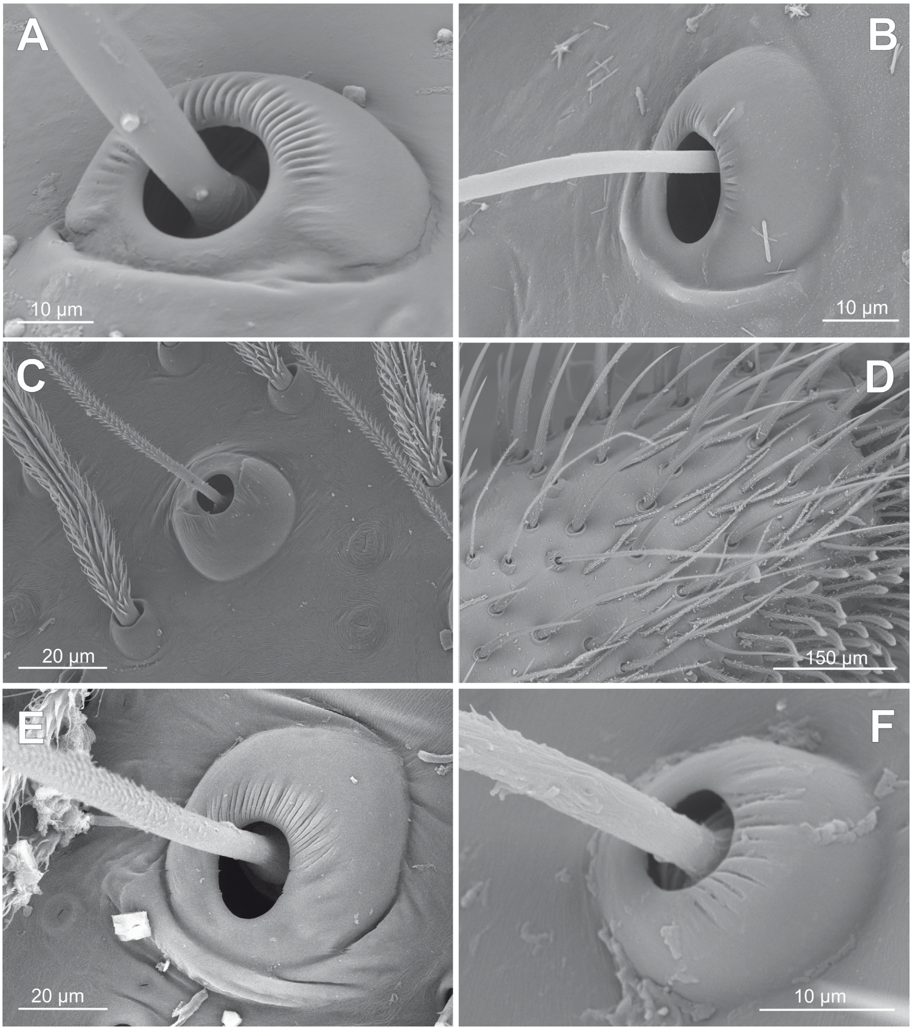

Fig. 19. Bothria of Theraphosoid lineage, Bemmeridae (A, B), Barychelidae Barychelinae (C, E), Barychelidae Sasoninae (D, F): (A) *Atmetochilus* (?) *songsangchotei*, ti3 (Ne); (B) *Damarchus* sp., ta3 (Fu); (C) *Cyphonisia* sp., ti4 (Ne); (D) *Neodiplothele martinsi*, ta1 (Fu); (E) Barychelidae gen.sp., mt3 (Ne); (F) *Sason* aff. *sundaicum*, ta3 (Fu). Abbreviations: Fu – *Fufius* subtype, Ne – *Neocteniza* subtype.

Migidae and Idiopidae. In contrast, only the advanced domed *Fufius* subtype is present in both distalmost families, Euctenizidae and Ctenizidae.

Leg cuticle patterns in ctenizoids demonstrate similar evolutionary trends. Parallel sequences from the ancestral scaly cuticle, typical and 'ornamened imbricate', to the advanced smooth and rugose types exist in the same three basal families (Halonoproctidae, Migidae and Idiopidae), while only the advanced rugose cuticle occur in the same distalmost lineage families (Euctenizidae and Ctenizidae).

5. Theraphosoid lineage (TH)

5.1. Bemmeridae Simon, 1903 (Bem)

5.2. Barychelidae Simon, 1889 (Bar)

5.3. Theraphosidae Thorell, 1870 (The)

"The clade comprising Bemmeridae + Barychelidae + Theraphosidae is recovered with high support as sister to all the remaining Bipectina families" (Opatova *et al*. 2020: 679). Barychelids and theraphosids form a sister pair in all classifications. Bemmeridae, however, was originally described by Simon (1903) as a ctenizid tribe, later transferred to Nemesiidae and supplemented with some cyrtaucheniids by Raven (1985*a*). Its placement within 'theraphosoids' is based solely on molecular data (Hedin & Bond 2006; Bond *et al*. 2012).

5.1. Bemmeridae (Bem)

The bothria of two bemmerid genera, *Atmetochilus* Simon, 1887 and *Damarchus* Thorell, 1891, are studied here.

There is a shortened sequence of bothrial types from the intermediate *Neocteniza* subtype in *Atmetochilus* (Fig. 19A) to the advanced domed *Fufius* subtype in *Damarchus* (Fig. 19B).

Leg cuticular patterns are 'smoothed imbricate' in *Damarchus* (Fig. 4D) and typically 'smooth' in *Atmetochilus* (own observations).

5.2. Barychelidae (Bar)

The bothria of four genera from both barychelid subfamilies are studied here:

Barychelinae Simon, 1889: *Cyphonisia* Simon, 1889 and undescribed Barychelinae gen. sp.;

Sasoninae Simon, 1892: *Neodiplothele* Mello-Leitão, 1917, *Sason* Simon, 1887.

Bothria of *Cyphonisia*, *Sason* and *Neodiplothele* were illustrated previously (Guadanucci 2012: figs 7, 12 and 20, respectively).

There are similar sequences of bothrial types in both subfamilies:

In barychelines, there is a sequence from the intermediate bothria of *Neocteniza* subtype in *Cyphonisia* (Fig. 19C) to the advanced domed bothria of *Fufius* subtype in the undescribed Barychelinae gen. sp. (Fig. 19E).

In sasonines, there is a sequence from the *Neocteniza* subtype in *Neodiplothele* (Fig. 19D) to the *Fufius* subtype in *Sason* (Fig. 19F).

Barychelidae is the only mygalomorph family containing multiple genera with the rare 'fingerprint-like' cuticular pattern, present in both its subfamilies: barychelines *Cyphonisia* (Fig. 19C) and *Encyocrypta* Simon, 1889 (Lehtinen 1996: fig. 6), and sasonine *Sason* (Fig. 3D). The 'smooth' pattern occurs in an undescribed Barychelinae gen. sp., while the 'smoothed imbricare' pattern is found in the sasonin *Neodiplothele* (own observations).

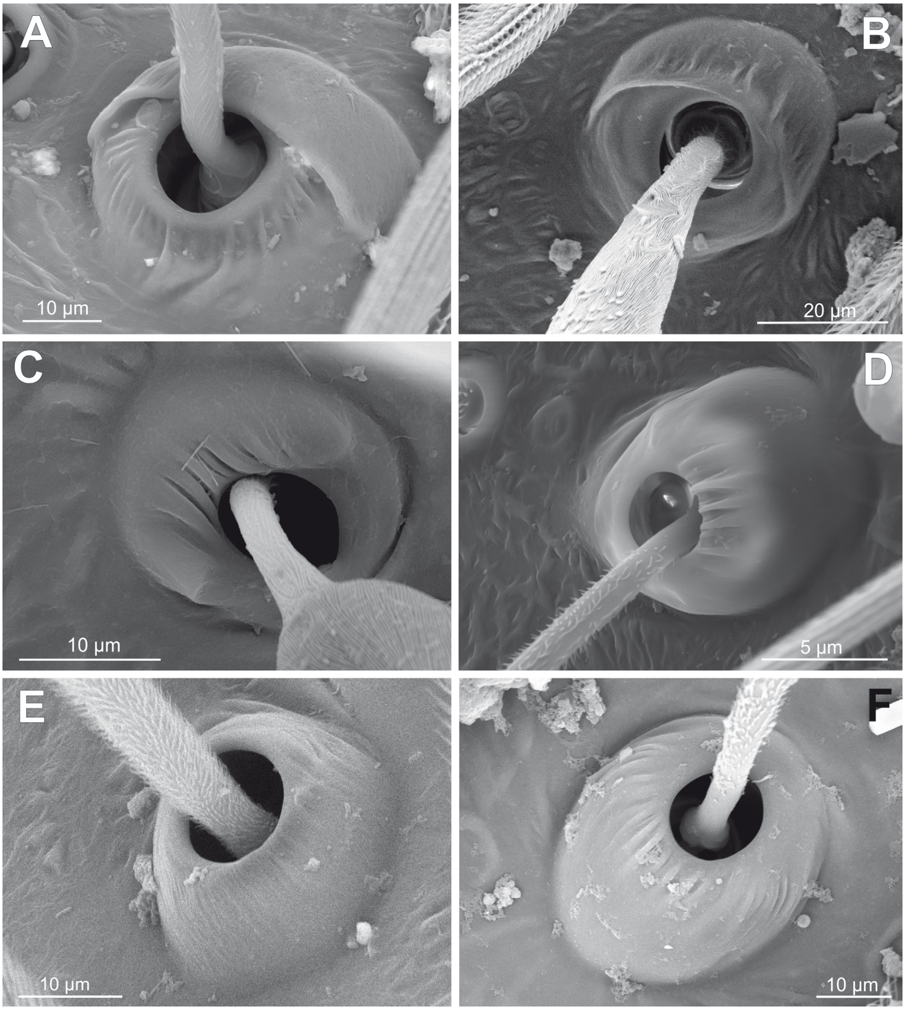

Fig. 20. Bothria of Theraphosoid lineage, Theraphosidae, Ischnocoline (A, C, E), Selenocosminae (B), Theraphosinae (D, F): (A) *Chaetopelma concolor*, ti3 (Id); (B) *Selenocosmia crassipes*, ta1 (Id); (C) *Ischnocolus meron*, ta1 (Ne); (D) *Pamphobeteus* sp., ta3 (Ne); (E) *Heterothele affinis*, ta3 (Fu); (F) *Grammostola rosea*, ta4 (Fu). Abbreviations: Id – *Idiops* subtype, Fu – *Fufius* subtype, Ne – *Neocteniza* subtype.

5.3. Theraphosidae (The)

The bothria of eight genera from four theraphosid subfamilies are studied here:

Ischnocolinae Simon, 1892: *Chaetopelma* Ausserer, 1871, *Heterothele* Karsch, 1879 and *Ischnocolus* Ausserer, 1871;

Selenocosminae Simon, 1889: *Selenocosmia* Ausserer, 1871;

Theraphosinae Thorell, 1870: *Grammostola* Simon, 1892, *Hapalopus* Ausserer, 1875 and *Pamphobeteus* Pocock, 1901;

Trichopelmatinae Raven, 1985): *Trichopelma* Simon, 1888.

Bothria of 33 genera representing all 11 theraphosid subfamilies were illustrated by Guadanucci (2012). High diversity of the bothrial types is represented in Theraphosidae. There are remarkable complete sequences in ischnocolines and selenocosmines. Ischnocolinae – from the ancestral hooded bothria of *Idiops* subtype in *Chaetopelma* (Fig. 20A), *Nesiergus* Simon, 1903, *Ischnocolus* (part.), *Plesiophrictus* Pocock, 1899 and *Heterophrictus* Pocock, 1900 (Guadanucci 2012: figs 130, 144, 148 and 152, respectively); via the intermediate bothria of *Neocteniza* subtype in *Ischnocolus* (part.) (Fig. 20C), *Schismatothele* Karsch, 1879 and *Guyruita* Guadanucci, Lucas, Indicatti & Yamamoto, 2007 (Guadanucci 2012: figs 83 and 90, respectively); to the advanced domed bothria of *Fufius* subtype in Heterothele (Fig. 20E) and *Sickius* Soares & Camargo, 1948 (Guadanucci 2012: fig. 95).

Selenocosminae: from the *Idiops* subtype in *Selenocosmia* (part.) (Fig. 20B), via the *Neocteniza* subtype in *Phlogiellus* Pocock, 1897 and *Selenocosmia* (part.) (Guadanucci 2012: figs 157 and 162, respectively), to the *Fufius* subtype in *Psalmopoeus* Pocock, 1895 (Guadanucci 2012: fig. 166).

In contrast to these complete sequences, all other theraphosid subfamilies (except Ischnocolinae and Selenocosminae) exhibit only shortened sequences lacking the ancestral hooded *Idiops* subtype. There are, for example:

Theraphosinae: from the *Neocteniza* subtype in *Pamphobeteus* (Fig. 20D) and *Eupalaestrus* Pocock, 1901 (Guadanucci 2012: fig. 184) to the *Fufius* subtype in *Grammostola* (Fig. 20F);

Trichopelmatinae: from the *Neocteniza* subtype in *Trichopelma* (Guadanucci 2012: fig. 26) to the *Fufius* subtype in *Reichlingia* Rudloff, 2001 (Guadanucci 2012: fig. 22).

Two cases of two bothrial type coexistence within a single genus are recorded in Theraphosidae (similar to the migid genus *Moggridgea*: see above).

Within the ischnocoline genus *Ischnocolus*, the *Idiops* subtype occurs in *I. tomentosus* Thorell, 1899 (Guadanucci 2012: fig. 144) and the *Neocteniza* subtype occurs in *I. meron* Zonstein, 2023 (Fig. 20C).

Within the selenocosmine genus *Selenocosmia*, the *Idiops* subtype occurs in *S. crassipes* (L. Koch, 1874) (Fig. 20B) and the *Neocteniza* subtype in occurs in *Selenocosmia* sp. (Guadanucci 2012: fig. 162).

In contrast to the diverse bothrial types, leg cuticular patterns in theraphosids are highly uniform. Nearly all studied genera from four subfamilies possess the 'ornamened imbricate' cuticle, except for the theraphosin genus *Hapalopus* which exhibits 'weakly rugose' cuticle (own observations).

Summary of bothrial and cuticular diversity in theraphosoids

The diversity of bothrial types within this lineage is summarized in Fig. 27B.

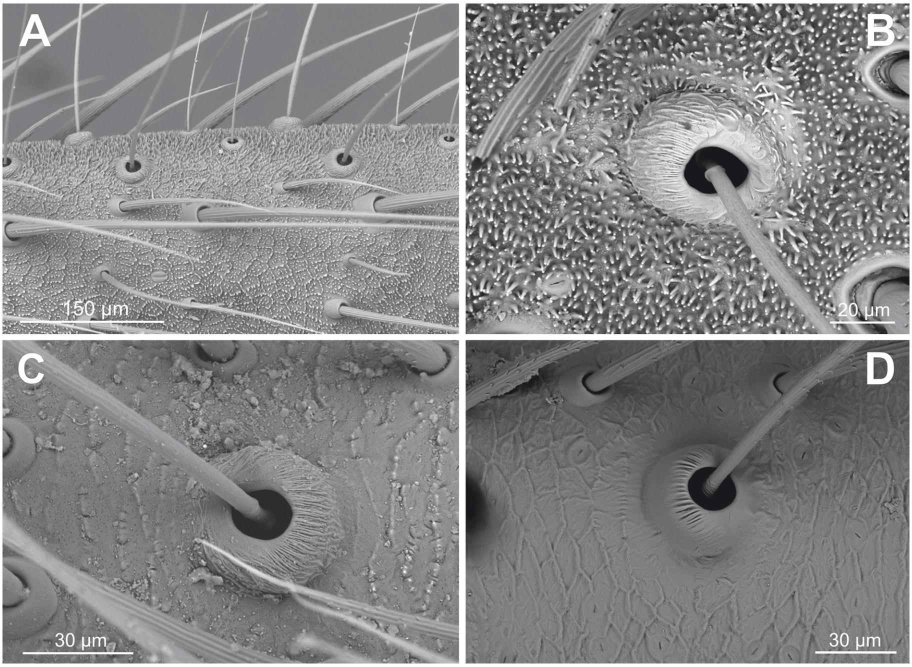

Fig. 21. Bothria of Nemesioid lineage, Microstigmatidae Ixamatinae: (A) *Ixamatus musgravei*, leg1 (Di); B – *Xamiatus rubrifrons*, leg1 (Di); (C) *Kiama lachrymoides*, leg1 (Eu); (D) *Angka hexops*, leg1 (Fu). Abbreviations: Di – *Diplura* subtype; Eu – *Euagrus* subtype; Fu – *Fufius* subtype.

Ancestral hooded bothria of *Idiops* subtype are restricted to the basal theraphosid subfamilies, Ischnocoline and Selenocosminae.

Parallel continuous evolutionary sequences from the ancestral hooded type to the advanced solid dome type via intermediate forms occur within these two subfamilies similar to several ctenizoid lineages (see above). In contrast, the distal theraphosid subfamilies, as well as Barychelidae and Bemmeridae, exhibit shortened sequences lacking the ancestral bothria types.

Leg cuticle patterns in theraphosoids demonstrate a similar trend. The ‘ornamented imbricate’ type of ancestral scaly cuticle dominates in Theraphosidae, whereas in both Barychelidae and Bemmeridae scaly cuticle is presented only by intermediate ‘smoothed imbricate’ type, and advanced ‘smooth’ and ‘fingerprint-like’ patterns dominates.

6. Nemesioid lineage (NE)

6.1. Microstigmatidae Roewer, 1942 (Mst)
6.2. Dipluridae Simon, 1889 (Dip)
6.3. Pycnothelidae Chamberlin, 1917 (Pyc)

6.4. Anamidae Simon, 1889 (Ana)
6.5. Entypesidae Bond, Opatova & Hedin, 2020 (Ent)
6.6. Cyrtaucheniidae Simon, 1889 (Cyr)
6.7. Nemesiidae Simon, 1889 (Nem)
6.8. Rhytidicolidae Simon, 1903 (Rhy)

Molecular data nest Cyrtaucheniidae (*sensu* Raven 1985*a*) and Nemesiidae (*sensu* Raven 1985*a*) within a single lineage, despite their previous placement in distant clades in morphological cladograms of the infraorder (see Opatova *et al*. 2020: figs 1, 2). Some subtaxa of these subfamilies were elevated to family rank (Anamidae, Entypesidae, Rhytidicolidae) or revalidated (Pycnothelidae) (Opatova *et al*. 2020; Montes de Oca *et al*. 2022), while Bemmeridae were removed from this lineage and transferred to the 'theraphosoids' (see above).

The position of 'relimited Dipluridae' (Diplurinae + Masteriinae) and 'enlarged Microstigmatidae' within the nemesioid lineage remains ambiguous, as their monophyly lacks molecular confirmations. Opatova *et al*. (2020: 691) did not place Masteriines in their cladogram due to missing molecular data. Furthermore, Opatova *et al*. (2020: 697) suggested: "The relimited family [Dipluridae] herein conservatively also includes Masteriinae which we predict is likely to be recognized as a stand-alone family, perhaps closely related to [hexatheloid] Microhexuridae".

Similarly, while Microstigmatidae is well-defined morphologically, its monophyly lacks strong molecular support: only the genus *Microstigmata* Strand, 1932 has been studied in this respect (Opatova *et al*. 2020: 702).

Thus, molecular data are available for: (1) the tribe Microstigmatini Roewer, 1942 (South African *Microstigmata*), and (2) the nemesiid subfamily Ixamatinae Raven, 1985 recently transferred to Microstigmatidae (Australian *Ixamatus* Simon, 1887 and *Kiama* Main & Mascord, 1971) (Harvey *et al*. 2018: 409; Opatova *et al*. 2020: 702).

In contrast, molecular data still lacking for: (3) the tribe Pseudonemesiini Caporiacco, 1955, and (4) subfamily Micromygalinae Platnick & Forster, 1982. As a result, Montes de Oca *et al*. (2022: 16) concluded: "Microstigmatidae probably remains as non-monophyletic, mainly in the Neotropical genera". Notably, Wunderlich (2004) have separated Micromygalinae into a stand-alone family, but this reranking is still unaccepted.

The bothria of Dipluridae and Microstigmatidae are remarkably diverse, whereas those of all other nemesioids are remarkably uniform. For this reason, nemesioid families are discussed below in order of their bothrial diversity, rather than following their arrangement in the cladogram in Opatova *et al*. (2020).

6.1. Microstigmatidae (Mst)

The bothria of nine genera from all three extant microstigmatid subfamilies and both microstigmatin tribes are studied here:

Ixamatinae Raven, 1985: *Angka* Raven & Schwendinger, 1995, *Ixamatus* Simon, 1887, *Kiama* Main & Mascord, 1969 and *Xamiatus* Raven, 1981;

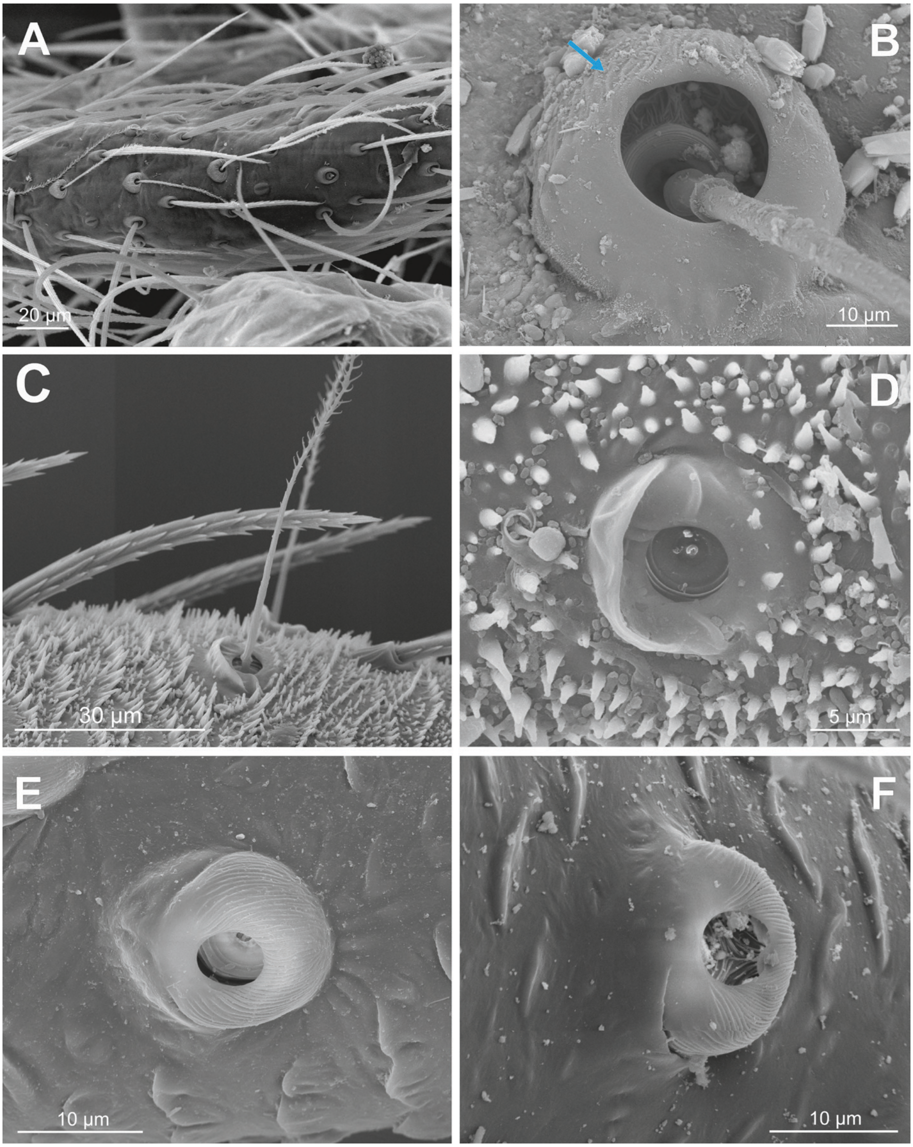

Fig. 22. Bothria of Nemesioid lineage, Microstigmatidae-Micromygalinae (A); Microstigmatidae Microstigmatinae Microstigmatini (B–D); Microstigmatidae Pseudonemesiinae Pseudonemesiini (E–F): (A) *Tonton* sp., mt2 (Eu) (courtesy P. Lehtinen); B – *Microstigmata longipes*, ti3 (Fu) (arrow – subtle corrugation); (C) *Ministigmata minuta*, leg1 (Mi); (D) *Ministigmata minuta*, leg1 (Mi); E – *Envia garciai*, leg1 (Eu); (F) *Pseudonemesia tabiskey*, leg1 (Eu). Abbreviations: Eu – *Euagrus* subtype; Fu – *Fufius* subtype; Mi – *Ministigmata* subtype.

Micromygalinae Platnick & Forster, 1982: *Tonton* Passanha, Cizauskas & Brescovit, 2019;

Microstigmatinae Roewer, 1942:

Microstigmatini Roewer, 1942: *Microstigmata* Strand, 1932 and *Ministigmata* Raven & Platnick, 1981;

Pseudonemesiini Caporiacco, 1955: *Envia* Ott & Höfer, 2004 and *Pseudonemesia* Caporiacco, 1955.

Additionally, the bothria of ten microstigmatid genera from all listed subfamilies/tribes were illustrated earlier:

Ixamatinae: *Ixamatus* (Raven 1980*b*: fig. 13; 1981: fig. 63), *Kiama* and *Angka* (Raven & Schwendinger 1995: figs 5A, 5C and 5B, respectively) and *Xamiatus* (Raven 1981*c*: fig. 68);

Micromygalinae: *Micromygale* Platnick & Forster, 1982 (Platnick & Forster 1982: figs 8, 9) and Tonton (Passanha *et al*. 2019: fig. 1C);

Microstigmatini: *Microstigmata* (Raven & Platnick 1981: figs 37; Griswold 1985: fig. 11; Montes de Oca *et al*. 2022: fig. 11D) and *Ministigmata* (Raven & Platnick 1981: fig. 38);

Pseudonemesiini: *Envia* (Ott & Höfer 2003: fig, 13; Miglio & Bonaldo 2011: fig. 18) and *Pseudonemesia* (Raven & Platnick 1981: figs 39, 40).

Ixamatinae

In this subfamily bothria are highly diverse. There is a sequence from the intermediate *Diplura* subtype in *Ixamatus* (Figs 6F, 21A) and *Xamiatus* (Fig. 21B) to the advanced *Euagrus* subtype in *Kiama* (Fig. 21C) and the advanced *Fufius* subtype in *Angka* (Fig. 21D).

In *Ixamatus* and *Xamiatus* (Ixamatinae *sensu* Raven 1985*a*), which possess intermediate bothria, the leg cuticle is pustulose (Figs 6F, 21B) – a subfamilial character noted by Raven (1985*a*: 48). In contrast, *Kiama* and *Angka* (formerly 'Kiamaoidina' *sensu* Bond & Opell, 2002, later transferred to Ixamatinae), which have advanced bothria, exhibit 'typically scaly' leg cuticle (Fig. 21C, D). The claim of pustulose cuticle in *Kiama* by Bond & Opell (2002: 498): "39. Small cuticular projections observed on legs and spinnerets: [...] This character, visible using scanning electron microscopy of the taxa we examined, is present only in *Kiama* and *Microstigmata* (Bond & Opell 2002: 498)" is erroneous. It was based solely on the superficially similar spinneret microsculpture (cf. Fig. 21C and Bond & Opell 2002: fig. 3A).

Micromygalinae

Bothria of both genera of the subfamily: *Micromygale* (Platnick & Forster 1982: fig. 9) and *Tonton* (Figs 7D, 22A; Passanha *et al*. 2019: fig. 1C), are uniform. They belong to the advanced *Euagrus* subtype, with lateral wrinkles encircle the aperture, meeting at the ends in front of it. Trichobothria of micromygalines resemble those of masteriines, characterized by flattened, longitudinally ridged bothria and extremely elongated, plumose setal shafts (compare Fig. 22A and Platnick & Forster 1982: fig. 8 to Passanha & Brescovit 2018: fig. 1E).

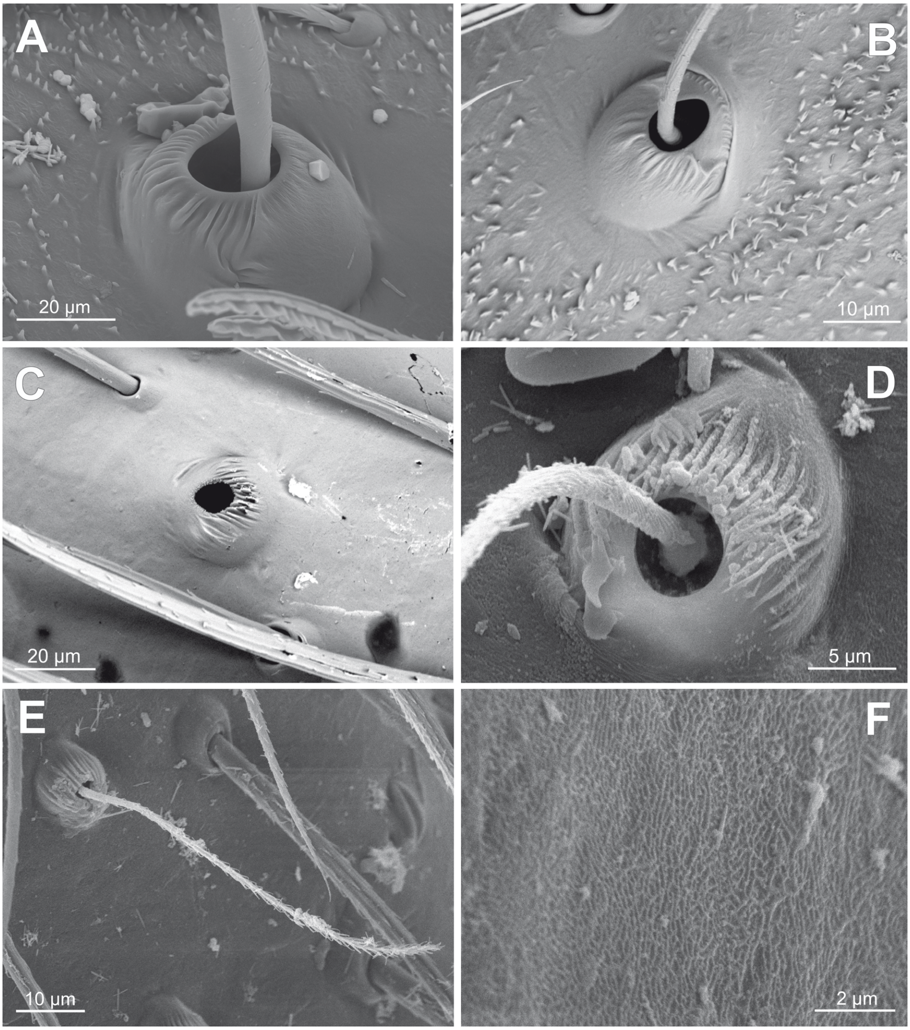

Fig. 23. Bothria and cuticle of Nemesioid lineage, Dipluridae, Diplurinae (A–C), Masteriinae (D–F): (A) *Diplura* aff. *sanguinea*, ti3 (Di); B – *Trechona venosa*, ta4 (Di); (C) *Linothele* sp., ta1 (Fu); (D) *Masteria* sp., ti3 (Eu); E – *Masteria* sp., mt3 (Eu); (F) *Masteria* sp., mt3. Abbreviations: Di – *Diplura* subtype; Eu – *Euagrus* subtype; Fu – *Fufius* subtype.

In contrast, leg cuticular patterns in micromygalines are diverse. It is 'typically scaly' in *Micromygale* (Platnick & Forster 1982: fig. 8) but the 'smooth' with unique additional microsculpture in *Tonton* (Fig. 7D). Notably, a pustulose cuticle is absent in the subfamily.

Pseudonemesinae Pseudonemesiini

Bothria of both genera of the tribe: *Pseudonemesia* (Fig. 22F; Raven & Platnick 1981: fig. 40) and *Envia* (Fig. 22E; Miglio & Bonaldo 2011: fig. 18), are uniform and belong to the advanced *Euagrus* subtype.

Leg cuticle in pseudonemesiins is distinctive: *Envia* (Fig. 22E; Miglio & Bonaldo 2011: fig. 18) and particularly *Pseudonemesia* (Fig. 3E; Raven & Platnick 1981: fig. 6) show protruding scales, a condition unique among mygalomorphs. This 'pseudoscale' cuticle resembles that of liphistiomorphs and whip-spiders (Eskov & Marusik 2024*b*: fig. 2B, E). It represents a tribal autapomorphy of the Pseudonemesiini and likely derived from typical scaly cuticle (cf. Miglio & Bonaldo 2011: figs 17, 18).

Microstigmatinae Microstigmatini

Bothria of both genera of the tribe are 'advanced solid', but differ sharply.

Microstigmata exhibits 'solid corrugated' bothria of the *Fufius* subtype with subtle corrugation (Fig. 22B, arrow), that have been overlooked in previous genus diagnoses (e.g., Raven & Platnick 1981: 15; Griswold 1985: 15).

Trichobothria of *Ministigmata* are unique, with 'solid non-corrugated' bothria belong to the *Ministigmata* subtype of its own (Figs 8D, 22D), and extremely elongated, plumose setal shafts (Fig. 22D). In contrast, *Microstigmata* has unmodified setal shafts (Montes de Oca *et al*. 2022: fig. 11D).

Leg cuticle in both genera is pustulose (Figs 4F, 22C; Griswold 1985: fig. 4), a probable tribal character.

Summary of bothrial and cuticular diversity in microstigmatids

The diversity of bothrial types in this family appears to be greatest among all Mygalomorphae (Fig. 28), cuticular patterns are also highly diverse. Notably, the ancestral hooded bothria are entirely absent in microstigmatids.

Opatova *et al*. (2020: 702) proposed pustulose leg cuticle as a diagnostic family-level character but stipulated: "Although a scaly or pustulose cuticle may be a diagnostic character uniting all microstigmatids [...], future SEM study of all genera will be necessary to confirm".

New SEM data presented here refute this supposition. Even if we accept such a diagnosis—which problematically groups the truly unique pustulose cuticle with the most common in mygalomorphs scaly cuticle—*Tonton* possesses a smooth cuticle with unique microsculpture (Fig. 7D), and the pseudonemesiines have a 'pseudoscale' cuticle (Figs 3E, 22E). However, while the pustulose cuticle is not 'a diagnostic character uniting all microstigmatids', it appears phylogenetically significant (see below).

6.2. Dipluridae (Dip)

The bothria of four genera from both diplurid subfamilies are studied here:

Diplurinae Simon, 1889: *Diplura* C. L. Koch, 1850, *Linothele* Karsch, 1879 and *Trechona* C. L. Koch, 1850;

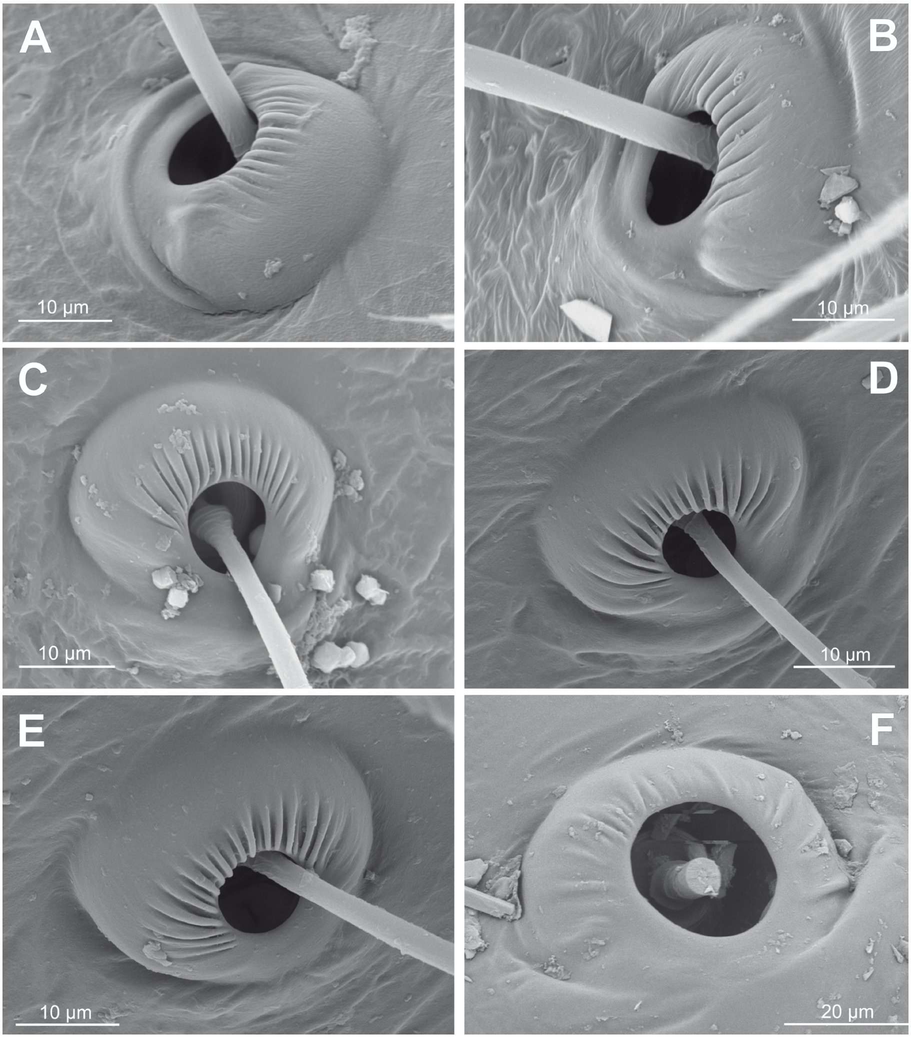

Fig. 24. Bothria and cuticle of Nemesioid lineage, Pycnothelidae: (A) *Acanthogonatus confusus*, mt3 (Ne); B – *Acanthogonatus huaquen*, ta3 (Ne); (C) *Acanthogonatus nahuelbuta*, ti3 (Fu); (D) *Acanthogonatus* sp., ti3 (Fu); (E) *Acanthogonatus* sp., ti3, (Fu); (F) *Stanwellia* sp., ti2 (Fu). Abbreviations: Fu – *Fufius* subtype, Ne – *Neocteniza* subtype.

Masteriinae Simon, 1889: *Masteria* L. Koch, 1873.

The bothria of all three masteriine genera were illustrated previously: *Masteria* (Raven 1991: fig. 65; Passanha & Brescovit 2018: fig. 1E), *Striamea* Raven, 1981 (Passanha & Brescovit 2018: fig. 36D) and *Siremata* Passanha & Brescovit, 2018 (Passanha & Brescovit 2018: fig. 41B).

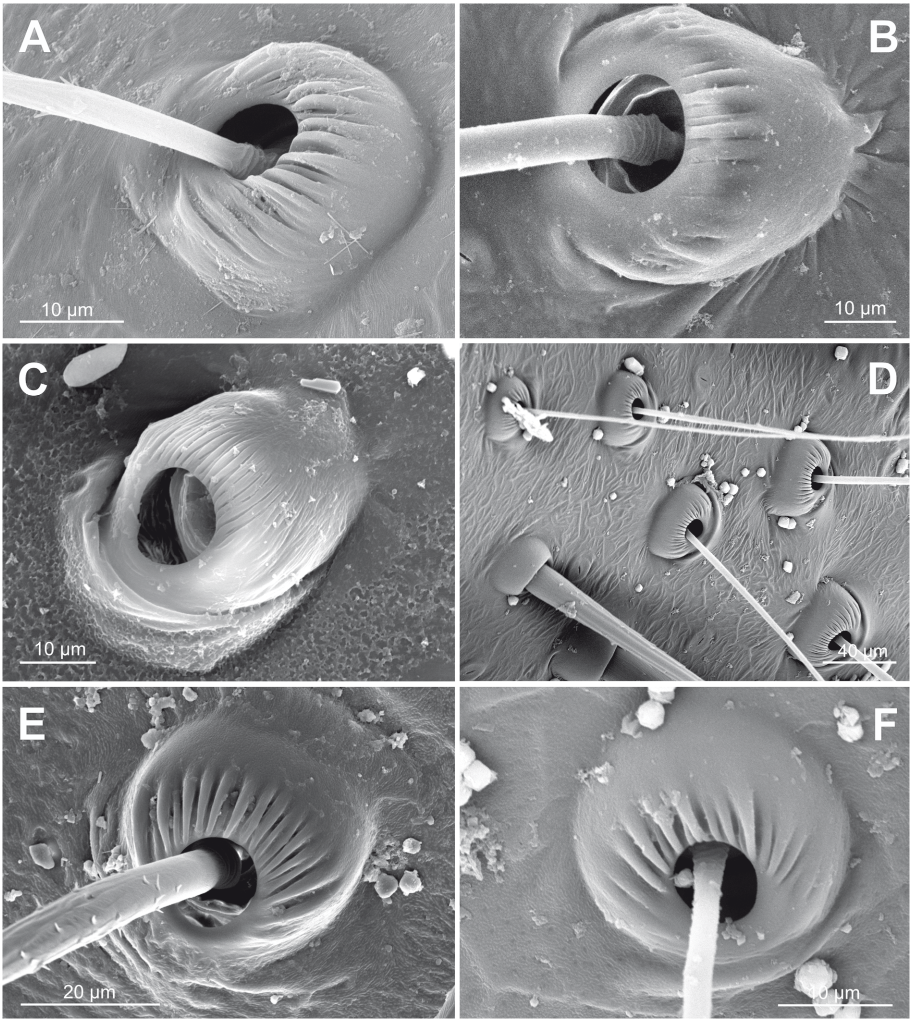

Fig. 25. Bothria and cuticle of Nemesioid lineage, Nemesiidae (A), Cyrtaucheniidae (B), Entypesidae (C), Rhytidicolidae (D), Anamidae (E, F): (A) *Raveniola songi*, ta2 (Fu); B – *Anemesia karatauvi*, mt1 (Fu); (C) *Hermacha septemtrionalis*, mt4 (Fu); (D) *Fufius* sp., mt3 (Fu); E – *Aname* sp., ti3 (Fu); (F) *Proshermacha tepperi*, mt4 (Fu). Abbreviation: Fu – *Fufius* subtype.

A high diversity of the bothrial types is represented in diplurids, with a sequence from the intermediate bothria of *Diplura* subtype in *Diplura* and *Trechona* (Fig. 23A, B) to the advanced domed bothria of the *Fufius* subtype in *Linothele* (Fig. 23C).

The trichobothria of all three masteriine genera: *Masteria* (Fig. 23D, E; Raven 1991: fig. 65; Passanha & Brescovit 2018: fig. 1E), *Striamea* and *Siremata* (Passanha

& Brescovit 2018: figs 36D and 41B, respectively), are uniform and characterized by flattened, longitudinally ridged bothria of the advanced *Euagrus* subtype, along with extremely elongated, plumose setal shafts.

The leg cuticle is pustulose in *Diplura* and *Trechona* (Fig. 23A–B), representing only the third known occurrence of this rare cuticular type in Mygalomorphae, alongside Microstigmatidae and hexatheloid Euagridae (see above). In contrast, the diplurin *Linothele* exhibits a smooth cuticle (Fig. 23C).

The cuticle of masteriines appear to be a smooth at first glance, but it possess a unique reticulate microsculpture in all three genera: *Masteria* (Fig. 23F; Passanha & Brescovit 2018: fig. 1C, D), *Striamea*, and *Siremata* (Passanha & Brescovit 2018: figs 36B, 41D, respectively). This microsculpture likely represents a synapomorphy of the subfamily, and shows some resemblance to that of the microstigmatid *Tonton* (see above).

Interestingly, the rare pustulose cuticle found in diplurines *Diplura* and *Trechona*, and in ixamatines *Ixamatus* and *Xamiatus* appears to be associated with the similarly rare intermediate *Diplura* subtype of bothria with wrinkles on both proximal and distal plates.

6.3. Pycnothelidae (Pyc)

The bothria of two genera from a single pycnothelid subfamily (of the five recognized by Montes de Oca *et al*. 2022) are studied here:

Diplothelopsinae Schiapelli & Gerschman, 1967: *Acanthogonatus* Karsch, 1880 (four species) and *Stanwellia* Rainbow & Pulleine, 1918.

The bothria of six pycnothelid genera from three subfamilies were illustrated previously:

Diplothelopsinae: *Acanthogonatus* (Goloboff 1995: fig. 15), *Chilelopsis* Goloboff, 1995 (Goloboff 1995: figs 10–12.), *Lycinus* Thorell, 1894 (Goloboff 1995: figs 13–16);

Pselligminae Mello-Leitão, 1923: *Stenoterommata* Holmberg, 1881 (Goloboff 1995: fig. 14);

Pycnothelinae Chamberlin, 1917: *Pycnothele* Chamberlin, 1917 (Goloboff 1995: fig. 18; Montes de Oca *et al*. 2022: fig. 11B, C) and *Xenonemesia* Goloboff, 1989 (Goloboff 1989a: fig. 13; Montes de Oca *et al*. 2022: fig. 11A).

Pycnothelidae is the only one nemesioid family (apart from separately classified Microstigmatidae and Dipluridae) that possesses more than a single *Fufius* subtype of the advanced domed bothria. Furthermore, among pycnothelids, there are as many as three documented cases where two different bothrial types coexist within a single genus. This phenomenon is also observed in *Moggridgea* (Migidae) and the theraphosid genera *Ischnocolus* and *Selenocosmia*, as previously mentioned.

In *Acanthogonatus* (Diplothelopsinae), there are the *Neocteniza* subtype in *A. confuses* Goloboff, 1995 (Figs 2D, 24A) and *A. huaquen* Goloboff, 1995 (Fig. 24B), and the *Fufius* subtype in *A. nahuelbuta* Goloboff, 1995 (Fig. 24C; Goloboff 1995: fig. 15) and *Acanthogonatus* sp. (Figs 7A, 24D, E).

In *Chilelopsis* (Diplothelopsinae), there are the *Neocteniza* subtype in *C. uerto-viejo* Goloboff, 1995 (Goloboff 1995: figs 11, 12), and the *Fufius* subtype in *C. minima* (Goloboff, 1995) (Goloboff 1995: fig. 10, as *Flamencopsis m*.).

In *Xenonemesia* (Pycnothelinae) there are the *Neocteniza* subtype in *X. platensis* Goloboff, 1989 (Goloboff 1989*a*: fig. 13) and the *Fufius* subtype in *Xenonemesia* sp. (Montes de Oca *et al*. 2022: fig. 11A).

All other studied pycnothelids possess only the *Fufius* subtype: diplothelopsines *Stanwellia* sp. (Fig. 24F), *Lycinus* (Goloboff 1995: figs 13, 16) and *Stenoterommata* (Goloboff 1995: fig. 14), and pycnothelines *Pycnothele* (Goloboff 1995: fig. 18; Montes de Oca *et al*. 2022: fig. 11C).

Leg cuticular patterns in pycnothelids are moderately diverse. They are 'typically scaly' in *Stanwellia* sp. (own observations) and 'weakly rugose' in *Chilelopsis* (Goloboff 1995: figs 10–12), *Xenonemesia* and *Pycnothele* (Montes de Oca *et al*. 2022: fig. 11A and 11C, respectively).

Interestingly, within *Acanthogonatus*, the coexistence of two different cuticular patterns, alongside the coexistence of two bothrial types, is observed: 'typically scaly' in *A. nahuelbuta* and 'ornamented imbricate' in all other studied species (own observations).

6.4. Anamidae (Ana)

The bothria of four anamid genera, *Aname* L. Koch, 1873, *Proshermacha* Simon, 1908, *Chenistonia* Hogg, 1901 and *Teyl* Main, 1975, are studied here. Bothria of *Aname* (Raven 1981: figs 64, 65) and *Teyl* (Raven 1981: fig. 59) were illustrated previously. All belong to the *Fufius* subtype of the advanced domed bothria (Fig. 25E, F). The leg cuticlar patterns are 'typically scaly' in *Proshermacha* and 'ornamened imbricate' in *Aname*, *Chenistonia* and *Teyl* (own observations).

6.5. Entypesidae (Ent)

The bothria of two entypesid genera, *Hermacha* Simon, 1889 and *Entypesa* Simon, 1902 (two species), are studied here. Bothria of *Entypesa* (Zonstein 2018: fig. 403) and *Afropesa* Zonstein & Ríos-Tamayo, 2021 (Raven 1983*b*, pl. II: fig. 1) were illustrated previously. All belong to the *Fufius* subtype of advanced domed bothria (Fig. 25C). The leg cuticlar patterns are the 'fingerprint-like' in *Hermacha* and 'weakly rugose' in other genera (own observations).

6.6. Cyrtaucheniidae (Cyr)

The bothria of one cyrtaucheniid genus are studied here: *Anemesia* Pocock, 1895. Bothria of four cyrtaucheniid genera were illustrated earlier: *Anemesia* (6 species) (Zonstein 2018: figs 158, 159, 161, 163, 165, 166, 169, 171), *Acontius* Karsch, 1879 (Raven 1983*b*, pl. II: fig. 4; Raven & Schwendinger 1995: fig. 5D; Zonstein 2018: fig. 396), *Ancylotrypa* Simon, 1889 (Zonstein 2018: fig. 399), and *Cyrtauchenius* Thorell, 1869 (Zonstein 2018: fig. 401). All belong to the *Fufius* subtype of the advanced domed bothria (Fig. 25B). The leg cuticlar pattern is 'weakly rugose' (our own observations).

6.7. Nemesiidae (Nem)

The bothria of two nemesiid genera, *Raveniola* Zonstein, 1987 (two species) and *Nemesia* Audouin, 1826, are studied here. Bothria of both genera were illustrated earlier: *Nemesia* (Zonstein 2018: fig. 405) and *Raveniola* (Raven & Schwendinger 1995: fig. 4 B; Zonstein *et al*. 2018, figs 13–18; Zonstein 2024, figs 321–323, 327, 331, 332, 338, 339, 342, 347). All belong to the *Fufius* subtype of the advanced domed bothria (Fig. 25A). The leg cuticlar pattern is 'weakly rugose' (our own observations).

6.8. Rhytidicolidae (Rhy)

The bothria of the one rhytidicolid genus are studied here: *Fufius* Simon, 1888. They belong to the *Fufius* subtype of the advanced domed bothria (Figs 7B, 25D). The leg cuticlar pattern is 'ornamened imbricate' (Fig. 25D).

Summary of bothrial and cuticular diversity in nemesioids

The diversity of bothrial types within this lineage is summarized in Fig. 28. As mentioned above, the bothria of Dipluridae and Microstigmatidae are remarkably diverse, including rare *Euagrus* subtype and unique *Diplura* subtype and *Ministigmata* subtype. In contrast, the bothria of all other nemesioids are remarkably uniform, exhibiting the advanced *Fufius* subtype (with few exceptions in pycnothelids).

The leg cuticle patterns exhibit a similar evolutionary trend. They are equally diverse and distinct in microstigmatids and diplurids, including rare pustulose cuticle, a unique 'pseudoscale' type, and smooth cuticle with two distinct types of additional microsculpture (both unique). Conversely, all other nemesioids exhibit a uniform sequence of cuticular patterns ranging from the ancestral 'typically scaly' via the intermediate 'ornamented imbricate' to the advanced 'slightly rugose'. The sole exception is the fingerprint-like cuticle found in one entypesid genus.

DISCUSSION

Forster (1988: 15) has supposed: "The reduction of the posterior hood of the bothrium is a derived character which has developed apparently in parallel in many of the [araneoid] families". This old hypothesis is convincingly confirmed by the modern 'big picture' of bothrial evolution in araneoids. Parallel continuous sequences—from the ancestral hooded bothria (*Erigone* type) to the advanced domed ones (*Theridion* type) through some intermediate stages (*Argiope* type)—are evident in each of the seven main phylogenetic lineages of the superfamily Araneoidea (Eskov & Marusik 2024*a*).

The same pattern of bothria transformation occurs in the distant araneomorph clade, Dionycha, as described by Ramírez (2014: char. 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 [...]. In some cases, the margin is well marked, although not overhanging [...]. 1. Not well differentiated. The distal margin of the hood is tenuous, superficial, not

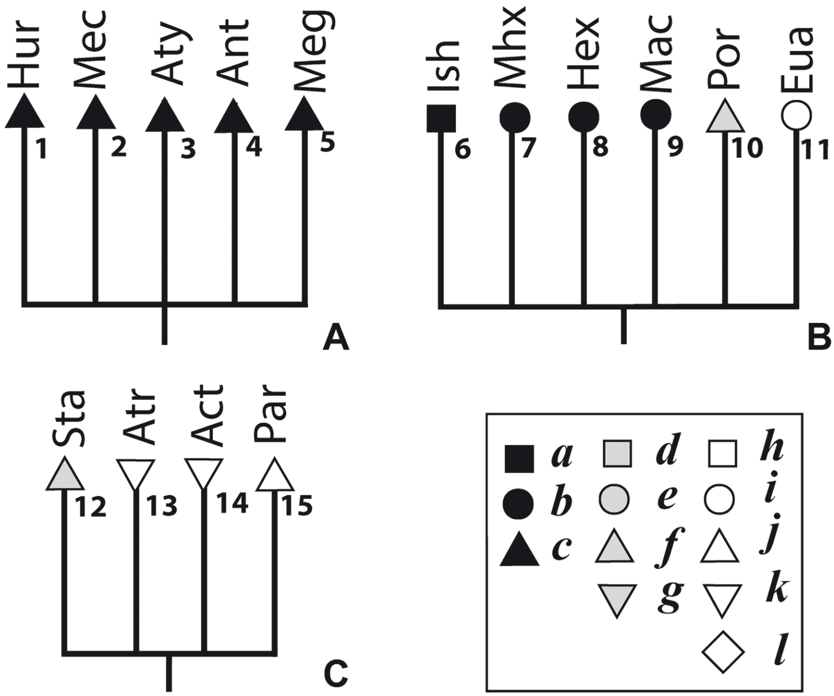

Fig. 26. Distribution of bothrial types in the basal mygalomorph lineages: (A) Atypoid lineage (Hur – Hexurellidae, Mec – Mecicobothriidae, Aty – Atypidae, Ant – Antrodiaetidae, Meg – Megahexuridae); B – Hexatheloid lineage (Ish – Ischnothelidae, Mhx – Microhexuridae, Hex – Hexathelidae, Mac – Macrothelidae, Por – Porrhothelidae, Eua – Euagridae); C – Actinopodoid lineage (Sta – Stasimopidae, Atr – Atracidae, Act – Actinopodidae, Par – Paratropididae). Symbols of ancestral hooded (a–c), intermediate (d–g) and advanced solid (h–l) bothrial types: (a) *Idiops* subtype, Id; (b) – *Macrothele* subtype, Ma; (c) – *Atypus* subtype, At; (d) – *Titanidiops* subtype, Ti; (e) – *Ummidia* subtype, Um; (f) – *Neocteniza* subtype, Ne; (g) – *Diplura* subtype, Di; (h) – *Fufius* subtype, Fu; (i) – *Euagrus* subtype, Eu; (j) – *Paratropis* subtype, Pa; (k) – *Actinopus* subtype, Ac; (l) – *Ministigmata* subtype, Mi. The numbers refer to the studied genera (genera known only from the literature are indicated by square brackets): (1) *Hexurella*; (2) *Mecicobothrium*; (3) *Atypus*, *Calommata*, *Sphodros*; (4) *Aliatypus*, *Antrodiaetus*, *Atypoides, Hexura*; (5) *Megahexura*; (6) *Ischnothele*, *Lathrothele*, *Thelechoris*; (7) *Microhexura*; (8) *Hexathele*, *Mediothele*, *Paraembolides*, *Scotinoecus*, *Teranodes*; (9) *Macrothele*, *Vacrothele*; (10) *Porrhothele*; (11) *Australothele*, *Cethegus*, *Namirea*, *Stenygrocercus*, [*Allothele*] – Australothelinae; *Chilehexops*, *Euagrus*, *Phyxioschema* – Euagrinae; (12) *Stasimopus*; (13) *Atrax*, *Hadronyche*; (14) *Actinopus*, *Missulena*; [*Plesiolena*]; (15) *Paratropis*.

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”. Thus, this evolutionary trend appears universal for the Araneomorpha.

The principal structure of bothria is identical in the araneomorphs and mygalomorphs, having been directly inherited in both infraorders from liphistiomorphs

(Eskov *et al*. 2024). However, earlier 'big pictures' of bothrial types distribution in mygalomorph lineages (Platnick & Gertsch 1976; Raven 1985*a*; Goloboff 1993) looked more confused than those for araneomorphs (Ramírez 2014; Eskov & Marusik 2024*a*). Two factors may explain this discrepancy.

First, bothrial typology was overly simplistic, recognizing only two opposing types: 'a rounded dome covered on one side by a flattened plate' vs 'a dome only, bear numerous parallel [radial] wrinkles' (Platnick & Gertsch 1976: 9–12), 'collarlike bothria' vs 'corrugiform bothria' (Raven 1985*a*: 6, 21), 'corrugiform' vs 'smooth' (Goloboff 1993: char. 30). Intermediate variants were overlooked. Second, parallelisms were minimized in phylogenetic schemes due to the prevailing cladistic paradigm at the time.

Removing these confounding factors reconciles Raven's (1985*a*) and Platnick & Gertsch's (1976) schemes with each other and with Opatova *et al.*'s (2020) phylogeny (Fig. 1). As Raven (1985*a*) concluded, ancestral hooded bothria characterize basal mygalomorph lineages, while advanced solid domed bothria predominate in distal lineages. Similarly, Platnick & Gertsch (1976) noted that multiple bothrial types may coexist within a single taxon, allowing identification of sequences—complete or truncated—from ancestral to advanced states.

Thus, the transformation of bothria from ancestral hooded forms to advanced solid domes via intermediate stages represents a universal evolutionary trend in both mygalomorphs and araneomorphs. This trend is detectable at the levels of infraorders, lineages (e.g., ctenizoids), families (e.g., Theraphosidae) and even subfamilies (e.g., Ummidiinae).

Mapping bothrial types onto Opatova *et al.*'s (2020) cladogram (Fig. 1) reveals three distinct segments: the basal lineages (Atypoid and Hexatheloid), the intermediate lineages (Ctenizoid and Theraphosoid), and the distalmost lineage (Nemesioid). Ancestral hooded bothria characterize the basal lineages (the only type in the atypoids and predominant in the hexatheloids). Their frequency sharply decreases in the intermediate lineages, and they completely disappear in the distalmost lineage. In contrast, advanced corrugated bothria are absent in the basalmost Atypoid lineage, appear in a single hexatheloid family, Euagridae, increase sharply in frequency within the intermediate lineages, and become the only type of bothria in the majority of distalmost nemesioid families (Figs 26–28).

The 'actinopodoids', nested by Opatova *et al*. (2020) between the basal lineages and intermediate lineages (Fig. 1), exhibit an unusual set of bothrial types: no hooded bothria, but instead the distinct advanced *Paratropis* subtype and *Actinopus* subtype (Fig. 26C). This paraphyletic, molecular-based lineage remains controversial in several aspects (see below).

The distribution of bothrial types within the intermediate lineages is particularly noteworthy. Where ancestral hooded bothria occur within a family, they are restricted to a single, apparently basalmost subfamily: Ummidiinae in Halonoproctidae, Calathotarsinae in Migidae, and Idiopinae in Idiopidae (Fig. 27A). Theraphosidae

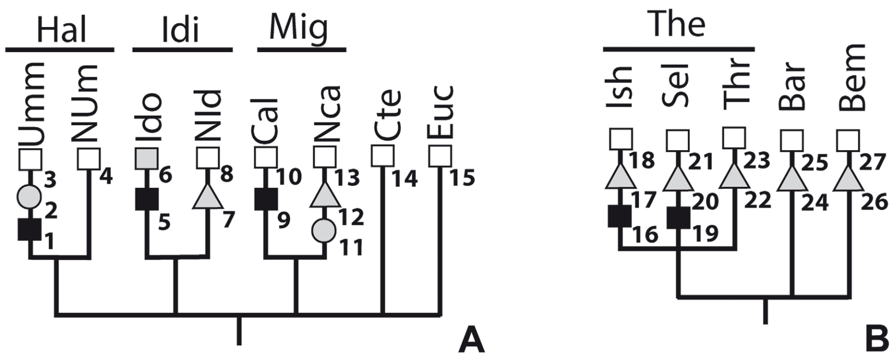

Fig. 27. Distribution of bothrial types in the intermediate mygalomorph lineages: (A) Ctenizoid lineage (Hal – Halonoproctidae, Umm – Ummidiinae, NUm – 'non-ummidiin halonoproctids'; Idi126– Idiopidae, Ido – Idiopinae, NId – 'non-idiopin idiopids'; Mig – Migidae, Cal – Calathitarsinae, NCa – 'non-calathotarsin migids'; Cte – Ctenizidae, Euc – Euctenizidae); B – Theraphosoid lineage (The – Theraphosidae, Ich – Ischnocolinae, Sel – Selenocosmiinae, Thr – other theraphosid subfamilies; Bar – Barychelidae, Bem – Bemmeridae). Symbols of bothrial types as in Fig. 26. The numbers refer to the studied genera (genera known only from the literature are indicated by square brackets): (1) *Conothele*; (2) *Ummidia*; (3) *Sterrhochrotus*; (4) *Bothriocyrtum*; (5) *Heligmomerus*, *Idiops*; (6) *Titanidiops*; (7) *Aganippe* – Arbanitinae, *Neocteniza* – Genysinae, [*Prothemenops*]; (8) *Cantuaria*, *Arbanitis*, *Euoplos*, [*Cataxia*] – Arbanitinae; (9) *Calathotarsus*, *Goloboffia*; (10) [*Mallecomigas*]; (11) *Moggridgea* (part.), [*Thyropoeus*] – Paramiginae; (12) *Migas* – Miginae; (13) *Poecilomigas* – Miginae, *Micromesomma*, *Heteromigas*, *Paramigas,* [*Moggridgea* (part.)] – Paramiginae; (14) *Cyrtocarenum*; (15) *Myrmekiaphila*, (16) *Chaetopelma*, [*Heterophrictus*, *Nesiergus*, *Plesiophrictus*]; (17) *Ischnocolus*, [*Guyruita*, *Schismatothele*]; (18) *Heterothele,* [*Sickius*, *Dolichothele*]; (19) *Selenocosmia*; (20) [*Phlogiellus*]; (21) [*Poecilotheria*, *Psalmopoeus*]; (22) *Pamphobeteus*, *Hapalopus*, [*Eupalaestrus*] – Theraphosinae, *Trichopelma* – Trichopelmatinae; (23) *Grammostola* – Theraphosinae, [*Reichlingia*] – Trichopelmatinae; (24) *Cyphonisia* – Barychelinae, *Neodiplothele* – Sasoninae; (25) Barychelidae gen. sp. – Barychelinae, *Sason* – Sasoninae; (26) *Atmetochilus*; (27) *Damarchus*.

is the sole exception, with hooded bothria recorded in more than one subfamily – in ischnocolines and selenocosmiines (Fig. 27B). However, both Ischnocolinae and Selenocosmiinae are paraphyletic lineages, their limits are controversial, and at least some African ischnocolines (e.g., *Heterothele*) seem closely related to selenocosmiines (J. Guadanucci, pers. observ.).

Significantly, all 15 families comprising the basal portion of Opatova *et al.*'s (2020) cladogram (Fig. 1) (i.e., Atypoid, Hexatheloid and Actinopodoid lineages) possess only a single bothrial type (Fig. 26A–C). Conversely, each of the 8 families within the intermediate portion of the cladogram (i.e., Ctenizoid and Theraphosoid lineages) (Fig. 27A, B) exhibits multiple bothrial types; however, no conclusions can currently be drawn for Ctenizidae and Euctenizidae, each represented in our material by only one genus.

Within the distalmost lineage Nemesioidea, a single bothrial type dominates once more. The advanced *Fufius* subtype occurs in 5 families. Additionally, within

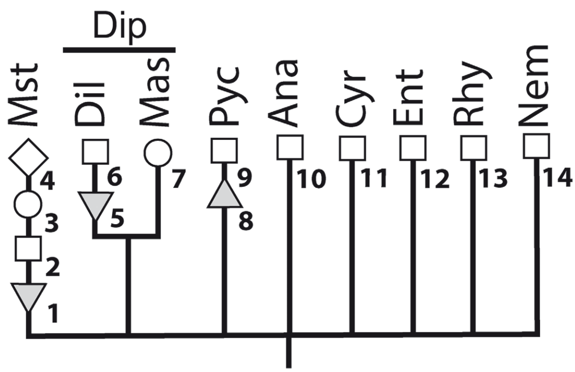

Fig. 28. Distribution of bothrial types in the distalmost mygalomorph Nemesioid lineage: Mst – Microstigmatidae; Dip – Dipluridae, Dil – Diplurinae, Mas – Masteriinae; Pyc – Pycnothelidae, Ana – Anamidae, Cyr – Cyrtaucheniidae, Ent – Entypesidae, Rhy – Rhytidicolidae, Nem – Nemesiidae. Symbols of bothrial types as in Fig. 26. The numbers refer to the studied genera (genera known only from the literature are indicated by square brackets): (1) *Ixamatus*, *Xamiatus* – Ixamatinae; (2) *Angka* – Ixamatinae, *Microstigmata* – Microstigmatini; (3) *Kiama* – Ixamatinae, *Tonton*, *Micromygale* – Micromygalinae, *Envia*, *Pseudonemesia* – Pseudonemesiini; (4) *Ministigmata* – Microstigmatini; (5) *Diplura*, *Trechona*; (6) *Linothele*; (7) *Masteria*, [*Siremata*, *Striamea*]; (8) *Acanthogonatus* (part.), *Chilelopsis* (part.), *Xenonemesia* (part.)]; (9) *Acanthogonatus* (part.), *Stanwellia*, [*Chilelopsis* (part.), *Lycinus*, *Pycnothele*, *Stenoterommata*, *Xenonemesia* (part.)]; (10) *Aname*, *Chenistonia*, *Proshermacha*, *Teyl*; (11) *Anemesia*, [*Acontius*, *Ancylotrypa*, *Aporoptychus*, *Cyrtauchenius*]; (12) *Entypesa*, *Hermacha*, [*Afropesa*]; (13) *Fufius*; (14) *Raveniola*; *Nemesia*.

Pycnothelidae, three genera retain species with intermediate *Neocteniza* subtype (see above). Dipluridae and Microstigmatidae are remarkable exceptions, exhibiting an extremely diverse array of bothrial types distinct from all other nemesioid families (Fig. 28). Consequently, the phylogenetic placement of this pair within the Nemesioid lineage appears to require revision (see below).

The overall patterns of bothrial transformation in the Mygalomorphae (the basalmost opisthothelian lineage), and in the Araneoidea (the most advanced opisthothelian superfamily), are strikingly similar (cf. Figs 26–28 and Eskov & Marusik 2024*a*: figs 28–33). However, one remarkable difference emerges. We observe at least 6 cases where two bothrial types coexist within a single mygalomorph genus: *Moggridgea* (Migidae), *Ischnocolus* and *Selenocosmia* (Theraphosidae), and *Acanthogonatus*, *Chilelopsis* and *Xenonemesia* (Pycnothelidae). In stark contrast, not a single case of such coexistence has been recorded in the 137 studied genera from all 22 families of Araneoidea (Eskov & Marusik 2024*a*).

These mygalomorph genera are unrelated, belonging to diverse lineages (ctenizoids, theraphosoids, and nemesioids, respectively), and to different theraphosid and pycnothelid subfamilies. This suggests that such co-occurrence represents parallel autapomorphies, reflecting at the genus level a broader infraorderal trend in bothrial transformation: from ancestral to intermediate types (theraphosids) or from the intermediate to advanced types (migids and pycnothelids). In contrast, within more evolutionary advanced spider lineages like Araneoidea, traces of this transformation process are no longer detectable at the generic level, where bothria are invariably uniform within a genus.

The system of Mygalomorphae proposed by Opatova *et al*. (2020) introduced several radical innovations compared to the previously standard systems of the infraorder, such as Raven's (1985*a*) and Goloboff's (1993). Therefore, let us consider: which of these innovations are supported by the bothrial data presented herein, and which are not.

1. Phylogenetic innovations of Opatova *et al*. (2020) supported by the new bothrial data

1.1. Monophyly of the atypoids and primary split of infraorder stem into 'atypoid' and 'non-atypoid' branches

The derived *Atypus* subtype of hooded bothria (Fig. 5D–F), evolving from the ancestral *Idiops* subtype (Fig. 5A, B), supports the monophyly of the Atypoid lineage. The *Atypus* subtype is strictly limited to Atypoidea, present in all atypoid genera without exception (Fig. 26A), and constitutes an additional 'trichobothrial' synapomorphy for this clade, alongside the reduction of tarsal trichobothria (Coddington & Levi 1991: 575; Eskov & Marusik 2024*a*: 6).

1.2. Revised circumscription of Mecicobothriidae

The family now comprises only the type genus *Mecicobothrium*. The genus *Hexura* is transferred to Antrodiaetidae, while *Hexurella* and *Megahexura* are placed in their own families, Hexurellidae and Megahexuridae (Hedin *et al*. 2019). The bothrium of *Mecicobothrium*, characterized by transversal folds forming a wide strip at the anterior edge of its longitudinally ridged proximal plate (Fig. 9A) differs sharply from all other atypoid bothria, including those of *Hexura*, *Hexurella* and *Megahexura*. Additionally, *Mecicobothrium* possesses 'ornamented imbricate' leg cuticle (Fig. 3C), contrasting with the typically scaly cuticle of *Megahexura* (Fig. 3A) and *Hexura* (Fig. 5D) and fingerprint-like pattern in *Hexurella* (Fig. 9B).

1.3. Establishment of Hexurellidae as a stand-alone family

The bothria of the family's sole member, *Hexurella*, differ from all other atypoid bothria by their heavily transversely ridged proximal plate (Fig. 5F). Furthermore, the fingerprint-like leg cuticular pattern in *Hexurella* (Fig. 9B) is unique among atypoids.

1.4. Establishment of Megahexuridae as a stand-alone family

The bothria of its sole member, *Megahexura*, differ from all other atypoid bothria by their multidirectionally ridged proximal plate with a distinctly concave anterior edge (Fig. 9C).

1.5. Basalmost position of Hexurellidae and revised Mecicobothriidae within atypoids

Both hexurellid and mecicobothriid bothria appear the most aberrant among atypoids, although they do not represent a single type.

1.6. 'Hexatheloids' as the basalmost lineage of the 'non-atypoids' branch

Ancestral hooded bothria predominate in this lineage, comprising hexathelids and 'non-diplurine diplurids'. 'Collar-like' hooded bothria (*Macrothele* subtype) are most common within hexatheloids and strictly limited to this lineage (Fig. 25B). Additionally, the leg cuticular pattern in almost all hexatheloids (except for few euagrid genera) is most plesiomorphic, typically scaly.

1.7. Ischnothelidae (elevated to family rank) as the basalmost lineage of hexatheloids

Ischnothelidae is the only hexatheloid group that possesses the most plesiomorphic hooded type, the *Idiops* subtype (Fig. 11A, B), rather than the common in hexatheloids *Macrothele* subtype.

1.8. Establishment of Microhexuridae as a stand-alone family

The bothria of its sole member, *Microhexura*, belong to the *Macrothele* subtype, common for hexatheloids. However, its collar-like proximal plate possesses a distinct heavy longitudinal striation unique among hexatheloids (Fig. 12A). Additionally, *Microhexura* exhibits a very rare 'imbricate-fingerprint' leg cuticular pattern (Fig. 3D).

1.9. Establishment of Porrhothelidae as a stand-alone family

The bothria of its sole member, *Porrhothele*, belong to the intermediate *Neocteniza* subtype (Fig. 11F). This represents a unique autapomorphy among hexatheloids, which typically possess ancestral hooded bothria.

1.10. Elevation of Euagridae to family rank

Bothria in all euagrid genera are advanced corrugated and belong to the rare *Euagrus* subtype (Fig. 13A–F). This is the second instance (besides porrhothelids, see 1.9) of non-hooded bothria occurring within hexatheloids. Euagrid bothria are highly uniform in both subfamilies (Euagrinae and Australothelinae), and should be considered a family synapomorphy.

1.11. Revised circumscription of Dipluridae

The suites of bothrial types differ drastically between the 'non-diplurine diplurids' (assigned to hexatheloids), and the Diplurinae (nested within the Nemesioid lineage). 'Non-diplurine diplurids' possess ancestral hooded bothria: *Idiops* subtype in the ischnothelids (Fig. 5A) and *Macrothele* subtype in microhexurids (Fig. 12A), plus advanced corrugated *Euagrus* subtype in the euagrids (Fig. 7C). Diplurinae possess two bothrial types, absent in 'non-diplurine diplurids': the intermediate *Diplura* subtype and advanced *Fufius* subtype (Fig. 23A–C).

1.12. Support for Masteriinae as a stand-alone family close to hexatheloids

The phylogenetic position of masteriines is controversial; they were excluded from Opatova *et al*. (2020: 691) due to lack of molecular data. Opatova *et al*. (2020: 697) predicted: "The relimited family [Dipluridae] herein conservatively also includes Masteriinae which we predict is likely to be recognized as a stand-alone family, perhaps closely related to [hexatheloid] Microhexuridae". All masteriine genera possess bothria of the rare advanced *Euagrus* subtype (Fig. 23D,E), supporting their predicted status as a "stand-alone family, perhaps closely related to" hexatheloids. However, within hexatheloids, they appear closer to Euagridae than to Microhexuridae. The extremely elongated plumose setal shafts (Fig. 23E) and the unique reticulate cuticular pattern (Fig. 23F) present in all masteriin genera constitute additional synapomorphies supporting Masteriinae as a stand-alone family.

1.13. Elevated to family rank, Atracidae is unrelated to Hexathelidae

Previously a subfamily of Hexathelidae, Atracidae possesses the advanced 'solid non-corrugated' bothria of the rare *Actinopus* subtype (Fig. 14B,C). In contrast, all other Hexathelidae exhibit highly uniform ancestral hooded bothria of *Macrothele* subtype (Fig. 12B–F).

1.14. Atracidae is sister to Actinopodidae

Both families form the 'Venom Clade' in Opatova *et al*.'s (2020) cladogram, and share the rare *Actinopus* subtype of the advanced 'solid non-corrugated' bothria. The 'Venom Clade' was previously supported solely by molecular data; the *Actinopus* subtype of bothria—strictly limited to this group—is now recognized as its first morphological synapomorphy.

1.15. Paratropididae does not belong to the Theraphosoid lineage

The 'solid corrugated' bothria of paratropidids represent a distinct *Paratropis* subtype. Their crater-like morphology (Fig. 8C) differs fundamentally from the bothria of all Theraphosidae and Barychelidae without exception (cf. Guadanucci 2012).

1.16. Elevated to family rank, Bemmeridae is transferred into the Theraphosoid lineage

Previously a subfamily of Nemesiidae, Bemmeridae now joins the Theraphosoid lineage based solely on molecular data. It exhibits a bothrial sequence ranging from the intermediate *Neocteniza* subtype to the advanced domed *Fufius* subtype (Fig. 19A, B). Such sequences are typical in theraphosoids (Theraphosidae and Barychelidae: Fig. 27B), whereas Nemesiidae and other nemesioids possess only uniform *Fufius* subtype of bothria.

1.17. Cyrtaucheniidae and Nemesiidae belong to a single lineage (Nemesioidea)

Though earlier morphological cladograms placed these families in distant clades (Raven 1985*a*; Goloboff 1993), molecular data now nests them within Nemesioidea. This clade—the distalmost lineage in Opatova *et al*.'s (2020) cladogram—is supported by the uniform advanced bothria of *Fufius* subtype, which are shared by both families.

2. Phylogenetic innovations of Opatova *et al*. (2020) neutral to the new bothrial data

2.1. Euagridae and Hexathelidae together form a monophyletic clade

However, this clade lacks morphological synapomorphies and is based solely on molecular data. Opatova *et al*. (2020: 695) state: “The family Hexathelidae now comprises seven genera […], of which we only sampled the Australian *Bymainiella*. It was recovered as sister to the family Euagridae with high support, which was previously indicated by EF-1gamma data […], albeit the support for this relationship was low”.

Similarly, bothrial morphology provides no support for this clade. Hexathelids possess the uniform ancestral hooded bothria of the *Macrothele* subtype, whereas euagrids have the uniform advanced corrugated bothria of the *Euagrus* subtype.

Notably, in Bond *et al*.’s (2012: figs 1, 2) and Hedin *et al*.’s (2018: fig. 2) earlier molecular-based cladograms, Hexathelidae and Euagridae form closely arranged parallel lineages at the base of ‘non-atypoid mygalomorphs’, rather than a monophyletic clade. Hedin *et al*.’s (2018: fig. 2) phylogeny of hexatheloids is based on analyses of UCE matrices, comprising five euagrid and all seven hexathelid genera, and we find this configuration more convincing.

2.2. Establishment of Macrothelidae as a stand-alone family

This family contains only *Macrothele* (Hedin *et al*. 2018), now divided into several molecularly defined genera of uncertain status (e.g., Shao *et al*. 2025). Macrothelid bothria belong to the *Macrothele* subtype (Fig. 11D, E), which is widespread in hexatheloids. These data neither support nor oppose the family elevation.

2.3. Establishment of Stasimopidae as a stand-alone family and its transfer to the ‘Actinopodoid lineage’

The bothria of *Stasimopus* (listed previously in Ctenizidae) belong to the intermediate *Neocteniza* subtype (Fig. 14A), common in non-basal mygalomorph lineages. New bothrial data neither support nor contradict its reclassification as a stand-alone family or its transfer within actinopodoids.

2.4. A controversial position of Paratropididae as a stand-alone lineage

Opatova *et al*. (2020, p. 675) recovered Paratropididae as a “lineage with unresolved and unstable placement [...], potentially causing conflict in topology and lowering the support of deeper nodes”. Paratropidid bothria, which belong to the distinct advanced *Paratropis* subtype of its own, support removal of the family from the Theraphosoid lineage (see 1.15) but cannot clarify its placement in the infraorder cladogram.

2.5. Close relationships among members of the ‘Actinopodoid lineage’

This lineage, defined solely by molecular data (Opatova *et al*. 2020: 690), includes Actinopodidae, Atracidae, Stasimopidae, and Paratropididae. Bothrial data provide the first morphological synapomorphy for the sister pair Actinopodidae + Atracidae (see 1.14) but do not support the other proposed relationships.

Two unique derived bothrial types (*Actinopus* subtype and *Paratropis* subtype) are strictly limited to the 'actinopodoids' but appear unrelated. The complete absence of the ancestral hooded bothria in this lineage (Fig. 26C) is intriguing, since they are widely represented even in more distal clades of the infraorder cladogram (Fig. 1), such as ctenizoids and theraphosoids (Fig. 27A, B).

Thus, the composition of this molecularly defined lineage remains controversial, with bothrial data offering neither support nor contradiction.

2.6. Elevation of nemesioid taxa to the family rank

Molecular data prompted the reclassification of several cyrtaucheniid and nemesiid subtaxa as families: Anamidae, Entypesidae, Rhytidicolidae (Opatova *et al*. 2020; Montes de Oca *et al*. 2022). All possess the advanced bothria of *Fufius* subtype, which are uniform across the Nemesioid lineage. These data neither support nor contradict their revised status.

3. Phylogenetic innovations of Opatova *et al*. (2020) that seem to contradict the new bothrial data

3.1. Position of the genus Hexura within the Antrodiaetidae

The phylogenetic position of *Hexura* relative to other antrodiaetids varies significantly across molecule-based cladograms. It has been recovered either as the sister group to all other Antrodiaetidae (Hedin & Bond 2006: fig. 5; Bond *et al*. 2012: fig. 1) or nested within the family as the sister group to *Atypoides* + *Antrodiaetus* (Hedin *et al*. 2019: fig. 3; Opatova *et al*. 2020: fig. 6).

Based on data from bothria and cuticular patterns, *Hexura* occupies an isolated position among antrodiaetids. In *Hexura*, the anterior edge of the proximal plate is uniquely strongly concave, making the bothrium superficially similar to the *Macrothele* subtype of hooded bothria (cf. Fig. 5C and 5D). In contrast, all other antrodiaetid genera (*Atypoides*, *Antrodiaetus* and *Aliatypus*) possess proximal plates characteristic of the *Atypus* subtype (Fig. 10A, C, D, respectively). Additionally, the leg cuticular pattern in *Hexura* is 'typically scaly' (Fig. 5D), whereas in the other three genera it is 'transversely imbricate' (Fig. 3B).

Thus, both bothrial and cuticular data support the division of Antrodiaetidae into two clades: (1) *Hexura*, possessing apomorphic bothria with a horseshoe-like posterior plate and the plesiomorphic 'typically scaly' cuticle; and (2) all other genera, possessing the apomorphic 'transversely imbricate' cuticle and plesiomorphic bothria with unmodified posterior plates.

Intriguingly, these new morphological data support the earlier molecule-based cladograms (Hedin & Bond 2006; Bond *et al*. 2012), but contradict more recent ones (Hedin *et al*. 2019; Opatova *et al*. 2020).

As Hedin *et al*. (2019: 16) noted: "One could argue that *Aliatypus* and *Hexura* each deserve family-level status (the latter an available family rank name, Hexurinae Simon, 1889), sister to other antrodiaetids". In our opinion, the horseshoe-shaped posterior plate of *Hexura* bothria, unique among the atypoids, provides an additional argument in favor of recognizing a distinct family Hexuridae.

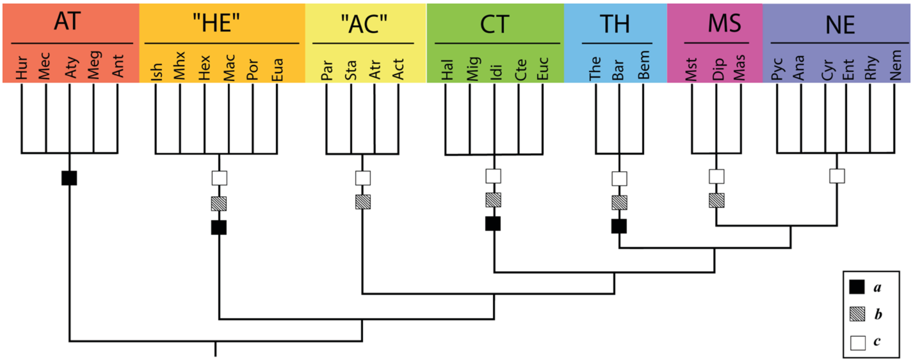

Fig. 29. Opatova *et al.*'s (2020: fig. 8) cladogram, modified after the new bothrial data. Abbreviations of lineages and families as in Fig. 1; added by MS – Microstigmatoid lineage. Symbols bothrial types: a – ancestral hooded, b – intermediate, c – advanced solid.

3.2. Dipluridae and Microstigmatidae are nested within the distant clades of the Nemesioid lineage as sister groups of Cyrtaucheniidae and Entypesidae, respectively

Critically, molecular data are lacking for Dipluridae Masteriinae and most subtaxa of the 'enlarged Microstigmatidae'; indeed, "Microstigmatidae probably remains as non-monophyletic, mainly in the Neotropical genera" (Montes de Oca *et al.* 2022: 16). Thus, the proposed close relationships in both the 'Dipluridae + Cyrtaucheniidae' and 'Microstigmatidae + Entypesidae' sister pairs were initially questionable.

The bothrial data (Fig. 28) suggest the complete loss of ancestral hooded bothria as a morphological synapomorphy of the Nemesioidea, distinguishing two subgroups within this monophyletic distalmost lineage.

A further reduction in bothrial diversity—culminating in the single advanced *Fufius* subtype—is a synapomorphy of the clade which comprises 6 families, termed herein 'Nemesioidea *s.str.*': Anamidae, Cyrtaucheniidae, Entypesidae, Nemesiidae, Rhytidicolidae and Pycnothelidae (though intermediate bothria of *Neocteniza* subtype persist in some pycnothelids). In contrast, Microstigmatidae and Dipluridae retain the greatest diversity of the bothrial types (excluding hooded ones); this lineage, designated herein as 'Microstigmatoidea', is positioned basally within 'Nemesioidea *s.l.*'.

We acknowledge that this proposed 'microstigmatoid lineage' may represent a paraphyletic assemblage at the base of 'Nemesioidea *s.l.*' stem (analogous to 'hexatheloid lineage' at the base of the 'non-atypoid mygalomorph' stem: Fig. 1), especially given the unproven monophyly of Microstigmatidae. However, at least two rare/unique morphological characters appear to be synapomorphies for 'microstigmatoids'.

First is a highly distinctive pustulose cuticle. This was previously listed by Raven (1985*a*: 48) as a subfamily character of Microstigmatidae-Ixamatinae and by Opatova *et al*. (2020: 702–703) as one of two diagnostic characters for Microstigmatidae (Figs 4F, 6F); it is now also documented in Dipluridae (Fig. 23A, B). Second, the unique *Diplura* subtype of bothria represents the sole intermediate bothrial type within the 'microstigmatoids', having completely replaced the *Neocteniza* subtype prevalent in all distal mygalomorph lineages.

Pustulose cuticle and bothria of *Diplura* subtype are not ubiquitous across Dipluridae and Microstigmatidae subtaxa. Two hypotheses arise: these are (1) parallel autapomorphies (noting that pustulose cuticle also arises, undoubtedly independently, in some Euagridae genera); or (2) synapomorphies with their subsequent reduction in some clades. A strong argument for the latter is the consistent co-occurrence of *Diplura* subtype bothria with pustulose cuticle in both families.

For example: In Dipluridae Diplurinae, *Diplura* and *Trechona* possess *Diplura* subtype bothria and pustulose cuticle (Fig. 23A, B), whereas *Linothele* exhibits *Fufius* subtype bothria and smooth cuticle (Fig. 23C).

In Microstigmatidae Ixamatinae, *Ixamatus* and *Xamiatus* have *Diplura* subtype bothria and pustulose cuticle (Fig. 21A, B), while *Kiama* and *Angka* possess scaly cuticle with *Euagrus* subtype and *Fufius* subtype bothria (Figs 21C and 21D, respectively).

In summary, our new bothrial data support the primary molecular Opatova *et al*.'s (2020) phylogenetic innovations in 17 cases and do not contradict them in 6 cases. The only two points contradicting Opatova *et al*.'s (2020) cladogram are the position of *Hexura* within Antrodiaetidae, and the position of Dipluridae and Microstigmatidae within the Nemesioid lineage.

So, we predict that further molecular studies will: (1) reestablish the distinct family Hexuridae Simon, 1889 as the sister group of Antrodiaetidae, or at least the distinct subfamily Antrodiaetidae-Hexurinae; and (2) unite diplurids with microstigmatids into a stand-alone lineage, Microstigmatoidea, the sister group to all other nemesioids (Fig. 29).

CONCLUSIONS

(1) The ancestral bothrial type within the infraorder is the 'hooded' bothria characterized by clearly separated proximal and distal plates. The most advanced type is solid, usually domed, bothria resulting from the complete fusion of the initial proximal and distal plates. Several intermediate forms were also identified, in which the boundary between fused proximal and distal plates remains discernible. The structure of bothria in Mygalomorphae is fundamentally similar to that in Araneomorphae. Character polarity was determined by comparison with the bothria of Liphistiomorpha, the basalmost lineage of the order.

(2) Three distinct sections are recognizable in Opatova *et al*.'s (2020) cladogram: the basal lineages (atypoids and hexatheloids), the intermediate lineages (ctenizoids

and theraphosoids), and the distalmost lineage (nemesioids). Ancestral hooded bothria are characteristic of the basal lineages, dramatically decline in number/proportion within the intermediate lineages, and entirely disappear in the distalmost lineage. Conversely, advanced corrugated bothria are absent in atypoids and nearly absent in hexatheloids (basal lineages), increase markedly in number/proportion in the intermediate lineages, and become the predominant (or sole) type of bothria in the great majority of the distalmost nemesioid families.

(3) Parallel bothrial series from the ancestral hooded type to the advanced solid domed type, via intermediates (widely represented, for example, in ctenizoids and theraphosoids) reflect an evolutionary trend toward the replacing of hooded bothria with advanced solid ones. This trend is common across the infraorder Mygalomorphae and also evident at the level of individual lineages (e.g., ctenizoids), families (e.g., Theraphosidae) and even some subfamilies (e.g., Ummidiinae). Similar parallel patterns of bothrial transformation have been documented in araneomorphs (e.g., within Dionycha and Araneoidea).

(4) Nearly all molecular-based phylogenetic innovations in Opatova *et al*. (2020) are either supported by our new bothrial data (such as the primary split of the infraorder stem into the 'atypoid' and the 'non-atypoid' branches, and the placement of Atracidae distantly from Hexathelidae and as sister to Actinopodidae), or at least not contradicted by it (e.g., a controversial position of Paratropididae as a distinct lineage).

(5) There are only two cases where bothrial data clearly conflict with molecular data: (1) the position of *Hexura* within Antrodiaetidae, and (2) the nesting of Dipluridae and Microstigmatidae into different clades of Nemesioidea in Opatova *et al*.'s (2020) cladogram. We predict that further molecular studies will confirm that *Hexura* is the sister group to all other antrodiaetid genera, while diplurids and microstigmatids together form the sister group to all other nemesioid families.

ACKNOWLEDGEMENTS

We are grateful to Roman A. Rakitov (Borissiak Paleontological Institute, Moscow, Russia) for his help during the preparation of the SEM images and illustrations; to the museum curators for the material under their care: Alexandro B. Bonaldo (MPEG), Antonio Brescovit (IBSP), Sarah Crews (CAS), Nadine Dupérré (MNHZ), Charles Haddad (NMBA), Mark Harvey (WAM), Marshal Hedin (SDSU), Hubert Höfer (SMNK), Rudy Jocqué (RMCA), Seppo Koponen and Pekka Lehtinen (ZMTU), Dmitri V. Logunov (MMUE), Kirill G. Mikhailov (ZMMU), Igor Muratov, John Midgley, Matabaro Ziganira, Kerry Hunter (NMSA), Daniil Osipov (Insectarium of the Moscow Zoo, Russia); Lorenzo Prendini and Louis Sorkin (AMNH), Martin Ramírez and Ivan Magalhaes (MACN), Robert Raven (QMS), Nikolaj Scharff (ZMUC), Petra Sierwald (FMNH); to the colleagues for the donation of some original SEM-images: Javier Blasco (AMNH), Nadine Dupérré (MNHZ), Charles Haddad (NMBA), Pekka Lehtinen (ZMTU), Beatriz Mauricio (IBSP); to Marshal Hedin (SDSU), Vera Opatova (CUPC), Daniella Sherwood (NHM) and Robert Raven (QMS) for important discussions.

Authors' contributions: All authors contributed equally to the design and execution of the research, writing the first draft of the manuscript and responding to reviewers' critique, and approved the final version for publication.

REFERENCES

Bond, J.E. & Opell, B.D. 2002. Phylogeny and taxonomy of the genera of south-western North American Euctenizinae trapdoor spiders and their relatives (Araneae: Mygalomorphae: Cyrtaucheniidae). *Zoological Journal of the Linnean Society* **136** (3): 487–534. https://doi.org/10.1046/j.1096-3642.2002.00035.x

Bond, J.E., Hendrixson, B.E., Hamilton, C.A. & Hedin, M. 2012. A reconsideration of the classification of the spider infraorder Mygalomorphae (Arachnida: Araneae) based on three nuclear genes and morphology. *PLoS One* **7** (6): Art. e38753. https://doi.org/10.1371/journal.pone.0038753

Coddington, J.A. & Levi, H.W. 1991. Systematics and evolution of spiders (Araneae). *Annual Review of Ecology and Systematics* **22**: 565–592. https://doi.org/10.1146/annurev.ecolsys.22.1.565

Coyle, F.A. 1984. A revision of the African mygalomorph spider genus *Allothele* (Araneae, Dipluridae). *American Museum Novitates* **2794**: 1–20. https://www.biodiversitylibrary.org/item/316992#page/1

Coyle, F.A. 1986. *Chilehexops*, a new funnelweb mygalomorph spider genus from Chile (Araneae, Dipluridae). *American Museum Novitates* **2860**: 1–10. https://www.biodiversitylibrary.org/item/317143#page/1

Coyle, F.A. 1988. A revision of the American funnel-web mygalomorph spider genus *Euagrus* (Araneae, Dipluridae). *Bulletin of the American Museum of Natural History* **187**: 203–292. http://hdl.handle.net/2246/924

Coyle, F.A. 1995. A revision of the funnelweb mygalomorph spider subfamily Ischnothelinae (Araneae, Dipluridae). *Bulletin of the American Museum of Natural History* **226**: 1–133. http://hdl.handle.net/2246/1665

Decae, A.E. 2010. The genus *Ummidia* Thorell 1875 in the western Mediterranean, a review (Araneae: Mygalomorphae: Ctenizidae). *Journal of Arachnology* **38** (2): 328–340. https://doi.org/10.1636/A09-85.1

Decae, A., Mammola, S., Rizzo, P. & Isaia, M. 2019. Systematics, ecology and distribution of the mygalomorph spider genus *Cteniza* Latreille, 1829 (Araneae, Mygalomorphae, Ctenizidae). *Zootaxa* **4550** (4): 499–524. https://doi.org/10.11646/zootaxa.4550.4.2

Dupérré, N. & Tapia, E. 2020. On the putatively incorrect identification and "redescription" of *Paratropis elicioi* Dupérré 2015 (Paratropididae, Araneae) with the description of two new sympatric species from Ecuador. *Zootaxa* **4869** (3): 326–346. https://doi.org/10.11646/zootaxa.4869.3.2

Dupérré, N. & Tapia, E. 2025. A new genus in the mygalomorph spider family Ischnothelidae, *Tepuithele* n. gen., from Ecuador. *Arachnology* **20** (2): 238–244. https://doi.org./10.13156/arac.2025.20.2.238

Eskov, K.Y. & Zonstein, S. 1990. First Mesozoic mygalomorph spiders from the Lower Cretaceous of Siberia and Mongolia, with notes on the system and evolution of the infraorder Mygalomorphae (Chelicerata: Araneae). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **178** (3): 325–368. https://doi.org/10.1127/njgpa/178/1990/325

Eskov, K.Y. & Marusik, Y.M. 2024*a*. A comparative morphology of trichobothrial bases in araneoid spiders and its significance for the phylogeny and system of the superfamily Araneoidea (Arachnida, Araneae). *ZooKeys* **1219**: 1–60. https://doi.org/10.3897/zookeys.1219.133002

Eskov, K.Y. & Marusik, Y.M. 2024*b*. The cuticle of liphistiomorph spiders is coated with a cerotegument: the first record for the order (Arachnida: Aranei: Liphistiomorphae). *Arthropoda Selecta* **33** (3): 375–382. https://doi.org/10.15298/arthsel.33.3.06

Eskov, K.Y., Zonstein, S.L. & Marusik, Y.M. 2024. On the liphistiomorph trichobothria and the significance of their structure for tracking the bothria evolution in the order Araneae. *Israel Journal of Entomology* **53**: 93–112. https://doi.org/10.5281/zenodo.12790018

Forster, R.R. 1988. The spiders of New Zealand: Part VI. Family Cyatholipidae. *Otago Museum Bulletin* **6**: 7–34.
Fourie, R., Haddad, C.R. & Jocqué, R. 2011. A revision of the purse-web spider genus *Calommata* Lucas, 1837 (Araneae, Atypidae) in the Afrotropical region. *ZooKeys* **95**: 1–28. https://doi.org/10.3897/zookeys.95.745
Gertsch, W.J. & Platnick, N.I. 1979. A revision of the spider family Mecicobothriidae (Araneae, Mygalomorphae). *American Museum Novitates* **2687**: 1–32. https://www.biodiversitylibrary.org/item/330466#page/1
Godwin, R.L., Opatova, V., Garrison, N.L., Hamilton, C.A. & Bond, J.E. 2018. Phylogeny of a cosmopolitan family of morphologically conserved trapdoor spiders (Mygalomorphae, Ctenizidae) using Anchored Hybrid Enrichment, with a description of the family, Halonoproctidae Pocock 1901. *Molecular Phylogenetics and Evolution* **126**: 303–313. https://doi.org/10.1016/j.ympev.2018.04.008
Goloboff, P.A. 1989*a*. *Xenonemesia*, un nuevo género de Nemesiidae (Araneae, Mygalomorphae). *Journal of Arachnology* **16** (3): 357–363. https://www.biodiversitylibrary.org/page/52977857#page/375
Goloboff, P.A. 1989*b*. Una nueva especie de Dipluridae (Araneae): *Chilehexops misionensis*. *Revista de la Sociedad Entomológica Argentina* **45**: 77–83. https://www.researchgate.net/publication/344678387
Goloboff, P.A. 1993. A reanalysis of mygalomorph spider families (Araneae). *American Museum Novitates* **3056**: 1–32. https://www.biodiversitylibrary.org/item/315804#page/1
Goloboff, P.A. 1994. Migoidea de Chile, nuevas o poco conocidas (Araneae: Mygalomorphae). *Revista de la Sociedad Entomológica Argentina* **53**: 65–74.
Goloboff, P.A. 1995. A revision of the South American spiders of the family Nemesiidae (Araneae, Mygalomorphae). Part I: species from Peru, Chile, Argentina, and Uruguay. *Bulletin of the American Museum of Natural History* **224**: 1–189. http://hdl.handle.net/2246/1624
Goloboff, P.A. & Platnick, N.I. 1987. A review of the Chilean spiders of the superfamily Migoidea (Araneae, Mygalomorphae). *American Museum Novitates* **2888**: 1–15. https://www.biodiversitylibrary.org/item/317100#page/1
Gray, M.R. 2010. A revision of the Australian funnel-web spiders (Hexathelidae: Atracinae). *Records of the Australian Museum* **62**: 285–392. https://doi.org/10.3853/j.0067-1975.62.2010.1556
Griswold, C.E. 1985. A revision of the African spiders of the family Microstigmatidae (Araneae: Mygalomorphae). *Annals of the Natal Museum* **27**: 1–37. https://hdl.handle.net/10520/AJA03040798_441
Griswold, C.E. 1987*a*. The African members of the trap-door spider family Migidae (Araneae: Mygalomorphae) 1: the genus *Moggridgea* O. P.-Cambridge, 1875. *Annals of the Natal Museum* **28**: 1–118. https://hdl.handle.net/10520/AJA03040798_422
Griswold, C.E. 1987*b*. The African members of the trap-door spider family Migidae (Araneae: Mygalomorphae) 2: the genus *Poecilomigas* Simon, 1903. *Annals of the Natal Museum* **28**: 475–497. https://hdl.handle.net/10520/AJA03040798_399
Griswold, C.E. & Ledford, J. 2001. A monograph of the migid trap door spiders of Madagascar and review of the world genera (Araneae, Mygalomorphae, Migidae). *Occasional Papers of the California Academy of Sciences* **151**: 1–120. https://www.researchgate.net/publication/292586943
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
Harvey, M.S., Hillyer, M.J., Main, B.Y., Moulds, T.A., Raven, R.J., Rix, M.G., Vink, C.J. & Huey, J.A. 2018. Phylogenetic relationships of the Australasian open-holed trapdoor spiders (Araneae: Mygalomorphae: Nemesiidae: Anaminae): multi-locus molecular analyses re-

solve the generic classification of a highly diverse fauna. *Zoological Journal of the Linnean Society* **184** (2): 407–452.
https://doi.org/10.1093/zoolinnean/zlx111

Hedin, M. & Bond, J.E. 2006. Molecular phylogenetics of the spider infraorder Mygalomorphae using nuclear rRNA genes (18S and 28S): conflict and agreement with the current system of classification. *Molecular Phylogenetics and Evolution* **41** (2): 454–471.
https://doi.org/10.1016/j.ympev.2006.05.011

Hedin, M., Derkarabetian, S., Ramírez, M.J., Vink, C. & Bond, J.E. 2018. Phylogenomic reclassification of the world's most venomous spiders (Mygalomorphae, Atracinae), with implications for venom evolution. *Scientific Reports* **8**: Art. 1636.
https://doi.org/10.1038/s41598-018-19946-2

Hedin, M., Derkarabetian, S., Alfaro, A., Ramírez, M.J. & Bond, J.E. 2019. Phylogenomic analysis and revised classification of atypoid mygalomorph spiders (Araneae, Mygalomorphae), with notes on arachnid ultraconserved element loci. *PeerJ* **7**: Art. e6864.
https://doi.org/10.7717/peerj.6864

Hinton, H.E. & Wilson, R.S. 1970. Stridulatory organs in spiny orb-weaver spiders. *Journal of Zoology, London* **162** (4): 481–484.
https://doi.org/10.1111/j.1469-7998.1970.tb01282.x

Indicatti, R.P. & Villarreal, E. 2016. *Pseudonemesia tabiskey*, a new species of *Pseudonemesia* Caporiacco 1955 and new ultramorphological data for the Microstigmatinae (Araneae: Microstigmatidae). *Journal of Natural History* **50** (33/34): 2153–2167.
https://doi.org/10.1080/00222933.2016.1196297

Krell, F.-T. & Cranston, P.S. 2004. Which side of the tree is more basal? *Systematic Entomology* **29**: 279–281.
https://doi.org/10.1111/j.0307-6970.2004.00262.x

Lehtinen, P. 1996. The ultrastructure of leg skin in the phylogeny of spiders. *Revue Suisse de Zoologie, Hors Série* **2**: 399–421.

Lopardo, L. & Hormiga, G. 2015. Out of the twilight zone: phylogeny and evolutionary morphology of the orb-weaving spider family Mysmenidae, with a focus on spinneret spigot morphology in symphytognathoids (Araneae, Araneoidea). *Zoological Journal of the Linnean Society* **173** (3): 527–786.
https://doi.org/10.1111/zoj.12199

Loria, S.F., Frank, S.-C., Dupérré, N., Smith, H.M., Jones, B., Buzatto, B.A. & Harms, D. 2025. The world's most venomous spider is a species complex: systematics of the Sydney funnel-web spider (Atracidae: *Atrax robustus*). *BMC Ecology and Evolution* **25**: Art. 7.
https://doi.org/10.1186/s12862-024-02332-0

Miglio, L.T. & Bonaldo, A.B. 2011. On a second species of *Envia* Ott & Höfer, 2003 (Araneae, Microstigmatidae), with notes on the sympatric type species. *Zootaxa* **2971**: 33–39.
https://doi.org/10.11646/zootaxa.2971.1.3

Miglio, L.T., Pérez-Miles, F. & Bonaldo, A.B. 2020. Taxonomic revision of the spider genus *Actinopus* Perty, 1833 (Araneae, Mygalomorphae, Actinopodidae). *Megataxa* **2** (1): 1–256.
https://doi.org/10.11646/megataxa.2.1.1

Montes de Oca, L., Indicatti, R.P., Opatova, V., Almeida, M., Pérez-Miles, F. & Bond, J.E. 2022. Phylogenomic analysis, reclassification, and evolution of South American nemesioid burrowing mygalomorph spiders. *Molecular Phylogenetics and Evolution* **168**: Art. 107377.
https://doi.org/10.1016/j.ympev.2021.107377

Moretto, M., Minelli, A. & Fusco, G. 2015. Cell size versus body size in geophilomorph centipedes. *The Science of Nature* **102**: Art. 16.
https://doi.org/10.1007/s00114-015-1269-4

Opatova, V., Hamilton, C.A., Hedin, M., Montes de Oca, L., Král, J. & Bond, J.E. 2020. Phylogenetic systematics and evolution of the spider infraorder Mygalomorphae using genomic scale data. *Systematic Biology* **69** (4): 671–707.
https://doi.org/10.1093/sysbio/syz064

Ott, R. & Höfer, H. 2004. *Envia garciai*, a new genus and species of mygalomorph spiders (Araneae, Microstigmatidae) from Brazilian Amazonia. *Iheringia, Série Zoologia* **93** (4): 373–379.
https://doi.org/10.1590/S0073-47212003000400004

PASSANHA, V. & BRESCOVIT, A.D. 2018. On the Neotropical spider subfamily Masteriinae (Araneae, Dipluridae). *Zootaxa* **4463** (1): 1–73. https://doi.org/10.11646/zootaxa.4463.1.1

PASSANHA, V., CIZAUSKAS, I. & BRESCOVIT, A.D. 2019. A new genus of Micromygalinae (Araneae, Microstigmatidae) from Brazil, with transfer of *Masteria emboaba* Pedroso, Baptista & Bertani, 2015 and description of six new species. *ZooKeys* **814**: 1–32. https://doi.org/10.3897/zookeys.814.29906

PLATNICK, N.I. 1977. The hypochiloid spiders: a cladistic analysis, with notes on the Atypoidea (Arachnida, Araneae). *American Museum Novitates* **2627**: 1–23. https://www.biodiversitylibrary.org/item/330062#page/3

PLATNICK, N.I. & FORSTER, R.R. 1982. On the Micromygalinae, a new subfamily of mygalomorph spiders (Araneae, Microstigmatidae). *American Museum Novitates* **2734**: 1–13. https://www.biodiversitylibrary.org/item/317058#page/1

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

PLATNICK, N.I. & SHADAB, M.U. 1976. A revision of the mygalomorph spider genus *Neocteniza* (Araneae, Actinopodidae). *American Museum Novitates* **2603**: 1–19. https://www.biodiversitylibrary.org/item/330021#page/3

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. 1979. Systematics of the mygalomorph spider genus *Masteria* (Masteriinae: Dipluridae: Arachnida). *Australian Journal of Zoology* **27** (4): 623–636. https://doi.org/10.1071/ZO9790623

RAVEN, R.J. 1980*a*. The evolution and biogeography of the mygalomorph spider family Hexathelidae (Araneae, Chelicerata). *Journal of Arachnology* **8** (3): 251–266.

RAVEN, R.J. 1980*b*. The Australian mygalomorph spider genus *Ixamatus* Simon (Dipluridae: Diplurinae) and its affinities. *Bulletin of the British Arachnological Society* **5**: 43–49. https://britishspiders.org.uk/node/2460

RAVEN, R.J. 1981. A review of the Australian genera of the mygalomorph spider subfamily Diplurinae (Dipluridae: Chelicerata). *Australian Journal of Zoology* **29** (3): 321–363. https://doi.org/10.1071/ZO9810321

RAVEN, R.J. 1983*a*. Contributions to the knowledge of the mountain fauna of Malawi (Mission R. Jocqué). III. Dipluridae. *Revue Zoologique Africaine* **97**: 345–352.

RAVEN, R.J. 1983*b*. Notes on some mygalomorph spiders in the Musée Royal de l'Afrique Centrale (Dipluridae, Hexathelidae, Ctenizidae: Araneae). *Revue Zoologique Africaine* **97**: 549–562.

RAVEN, R.J. 1984. Systematics of the Australian curtain-web spiders (Ischnotheline: Dipluridae: Chelicerata). *Australian Journal of Zoology Supplementary Series* **93**: 1–102.

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

RAVEN, R.J. 1985*b*. A new and interesting species of *Cethegus* Thorell (Ischnothelinae, Dipluridae) from South Australia. *Records of the South Australian Museum* **19**: 15–17. https://www.biodiversitylibrary.org/page/65207415#page/28

RAVEN, R.J. 1991. A revision of the mygalomorph spider family Dipluridae in New Caledonia (Araneae). *In*: Chazeau, J. & Tillier, S. (Eds), Zoologia Neocaledonica, Vol. 2. *Mémoires du Muséum National d'Histoire Naturelle de Paris* (A) **149**: 87–117.

RAVEN, R.J. & DOUGLAS, J.C. 2025. A review of the relationships of Australian funnel-web spiders with a new species of funnel-web spider from far north-eastern Tasmania (Hexathelidae: Atracinae: Araneae). *Record of the Queen Victoria Museum and Art Gallery* **122**: 1–16.

RAVEN, R.J. & PLATNICK, N.I. 1981. A revision of the American spiders of the family Microstigmatidae (Araneae, Mygalomorphae). *American Museum Novitates* **2707**: 1–20. https://www.biodiversitylibrary.org/page/62323380#page/2

RAVEN, R.J. & SCHWENDINGER, P.J. 1995. Three new mygalomorph spider genera from Thailand and China (Araneae). *Memoirs of the Queensland Museum* **38** (2): 623–641. https://www.biodiversitylibrary.org/page/40060402#page/307

Rix, M.G., Raven, R.J., Main, B.Y., Harrison, S.E., Austin, A.D., Cooper, S.J.B. & Harvey, M.S. 2017. The Australasian spiny trapdoor spiders of the family Idiopidae (Mygalomorphae: Arbanitinae): a relimitation and revision at the generic level. *Invertebrate Systematics* **31** (5): 566–634.
https://doi.org/10.1071/IS16065

Rossi, G.F. de, Ghirotto, V.M., Galleti-Lima, A., Indicatti, R.P. & Guadanucci, J.P.L. 2021. "Flying" or digging? The trapdoor spider genus *Neocteniza* Pocock, 1895: redescription of three species, new records from Brazil, notes on natural history and first record of ballooning for Idiopidae (Araneae, Mygalomorphae). *Zootaxa* **5023** (4): 451–485.
https://doi.org/10.11646/zootaxa.5023.4.1

Schwendinger, P.J. 2009. A taxonomic revision of the genus *Phyxioschema* (Araneae, Dipluridae), I: species from Thailand. *Zootaxa* **2126** (1): 1–40.
https://doi.org/10.11646/zootaxa.2126.1.1

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

Shao, L.L., Zhou, Z.C. & Lin, Y.J. 2025. Taxonomic revision of Macrothelidae Simon, 1892 and description of four new genera (Araneae, Macrothelidae). *The Indochina Entomologist* **1** (36): 337–350.
https://doi.org/10.70590/ice.2025.01.36

Simon, E. 1892. *Histoire naturelle des araignées*. 2nd ed. Vol. 1, fasc. 1. Roret, Paris, pp. 1–256.
https://www.biodiversitylibrary.org/item/119058#page/13

Simon, E. 1903. *Histoire naturelle des araignées*. 2nd ed. Vol. 2, fasc. 4. Roret, Paris, pp. 669–1080.
https://www.biodiversitylibrary.org/item/111074#page/673

Valdez-Mondragón, A., Mendoza, J.I. & Francke, O.F. 2014. First record of the mygalomorph spider family Paratropididae (Arachnida, Araneae) in North America with the description of a new species of *Paratropis* Simon from Mexico, and with new ultramorphological data for the family. *ZooKeys* **416**: 1–21.
https://doi.org/10.3897/zookeys.416.7253

Wunderlich, J. 2004. The fossil mygalomorph spiders (Araneae) in Baltic and Dominican amber and about extant members of the family Micromygalidae. *Beiträge zur Araneologie* **3**: 595–631.

Zonstein, S. 2018. A revision of the spider genus *Anemesia* (Araneae, Cyrtaucheniidae). *European Journal of Taxonomy* **485**: 1–100.
https://doi.org/10.5852/ejt.2018.485

Zonstein, S. 2024. A revision of the spider genus *Raveniola* (Araneae, Nemesiidae). II. Species from Central Asia. *European Journal of Taxonomy* **967**: 1–185.
https://doi.org/10.5852/ejt.2024.967.2699

Zonstein, S., Kunt, K.B. & Yağmur, E.A. 2018. A revision of the spider genus *Raveniola* (Araneae, Nemesiidae). I. Species from Western Asia. *European Journal of Taxonomy* **399**: 1–93.
https://doi.org/10.5852/ejt.2018.399

Appendix

List of the specimens examined (with original labels cited). All families (both mygalomorph and non-mygalomorph) and genera within a family are listed in the alphabetical order. Abbreviations of mygalomorph families (three lowercase letters, in round brackets) are the same as in Figure 1. The non-mygalomorph taxa, not included in the cladograms, are not provided with abbreviations.

Actinopodidae (Act)
Actinopus sp.
♀ (SMNHTAU) – **Panama:** Herrera, 19.i.1980, V. Leyn.

Missulena occatoria Walckenaer, 1805
♂ (SMNHTAU) – **Australia:** *Queensland*: Rockhampton area, 1982, D. Wallace.

Anamidae (Ana)
Aname sp. (det. M.S. Harvey)
♂ (WAM) – **Australia:** *Western Australia:* Boolathana Station, site BO3, 24°24'48.5"S 113°42'23.5"E, wet pitfall traps, 30.ix.1994–15.i.1995, N.L. McKenzie, J. Rolfe.

Chenistonia sp.
♂ (QMS 24399) – **Australia:** *Queensland*: Whypalla, Mt Windsor Tableland, 16°12'39"S 144°58'46"E, S. Burnett.

Proshermacha tepperi (Hogg, 1902)
♂ (ZMTU) – **Australia:** nr. Sera King Pod, 18.vii.1971.

Teyl sp.
♂ (QMS 40534) – **Australia:** *Queensland*: Hann Tableland National Park, north end, 16°49'S 145°11'E, 11–13.xii.1995, D.J. Cook.

Antrodiaetidae (Ant)
Aliatypus janus Coyle, 1975 (det. F. Coyle, 1995)
♂ (CAS) – **USA:** *Nevada*: Esmeralda Co., White Mts, 8500 ft a.s.l., Middle Ck, 16 mi NW Dyer, 5.v.1986–4.ii.1987, D. Givliani.

Antrodiaetus montanus (Chamberlin & Ivie, 1935) (det. S. Crews, 2001)
♂ (CAS) – **USA:** *California*: Sierra Co., SFSU Field Station, 6 mi E of Sierra City, 39°37'N 120°34'W, 5500 ft, 7.viii.2001, S. Crews.

Atypoides sp. (det. M. Hedin, 2024)
♀ (SDSU - MCH 07_155) – **USA:** *California*: El Dorado Co., along S. Fork American R., Sand Flat CG to Alder Creek transect # 4, 38°45'46"N 120°21'52"W, elev. 1190 m, 16.xii.2007, M. Hedin *et al*.

Hexura picea Simon, 1884 (det. S. Crews, 2022)
♂ (CAS 911 8974) – **USA:** *Oregon*: 10 mi N Philomath, in newt stomach, R. Freiburg.

Atracidae (Atr)
Atrax sp.
♀ (SMNHTAU) – **Australia:** *New South Wales*: Sydney, 1984, R. Raven.

Hadronyche cerberea L. Koch, 1873, (det. R. Raven)
♀ (SMNHTAU) – **Australia:** *New South Wales*: Sydney, iv.1984, R. Raven.

Atypidae (Aty)
Atypus muralis Bertkau, 1890
♂ (ZMMU) – **Russia:** Caucasus, Ossetia, Alagir Canyon, 1200 m a.s.l., 3–18.v.1985, S.K. Alexeev.

Calommata sundaica (Doleschall, 1859)
♀ (SMNHTAU) – **Indonesia:** East Java, S. Strőbell.

Sphodros niger (Hentz, 1842) (det. D.T. Jennings, 1989)
♂ (CAS 906 8535) – **USA:** *West Virginia*: Berkeley Co., Sleepy Clc., Hunt & Fish area, Third Hili Mtn., oak-pine forest, p/t, 23–30.v.1986, P.J. Martinat.

Barychelidae (Bar)
Cyphonisia sp.
♂ (ZMUC 10332) – **Tanzania:** Dar es Salaam, University of Dar es Salaam, campus, 21.x.1989, J. Parkin.

Neodiplothele martinsi Gonzalez-Filho, Lucas & Brescovit, 2015
♂ (IBSP 11668) – **Brazil:** *Pernambuco*: Recife, Horto Dois Irmãos, 7°55'S 34°52'W, vii–xi.2000, M. Oerez.

Sason aff. *sundaicum* Schwendinger, 2003
♀ inadult (ZMMU) – **Thailand**, without exact locality, data and collector.
Barychelinae gen. sp.
♀ (RMCA ARA 206.721) – **Madagascar:** Foulpointe, "Foret, terre rogue, litiere", xi.1994, A. Pauly.

Bemmeridae (Bem)
Atmetochilus (?) *songsangchotei* Kunsete & Warrit, 2020
♀ (ZMMU) – **Thailand**, without exact locality, data and collector.

Damarchus sp.
♀ (SMNHTAU) – **Thailand:** Chang Mai, 17.viii.2014, O. Rittner.

Ctenizidae (Cte)
Cyrtocarenum cunicularium (Olivier, 1811)
♀ (SMNHTAU) – **Turkey:** env. of Bursa, 22.9.2010, S. Zonstein.

Cyrtaucheniidae (Cyr)
Anemesia karatauvi (Andreeva, 1968)
♂ (SMNHTAU) – **Tajikistan:** W slope of Vahsh Karatau Mts, 950–1200 m a.s.l., 38°01'N 68°57'E, 3 km NNW of Mt Hojamaston, 21–25.iv.1989, S. Zonstein.

Dipluridae: Diplurinae (Dip)
Diplura aff. *sanguinea* (F. O. Pickard-Cambridge, 1896)
♀ (SMNHTAU) – **Peru:** *Junin Region*: 10 km SE from Satipo, Paratushali, under logs, 22.ix.2017, K. Eskov.

Linothele sp.
♀ (IBSP 8358) – **Brazil:** Rio de Janeiro, Petrópolis, 8–15.ii.2000, J.P.L. Guadanucci, F.S. Cunha.
Masteria sp. (det. J.A. Murphy, 1991)
♀ subadult (MMUE 15170) – **Malaysia:** *West Pahang*: Genting, 1000 m a.s.l., moss forest, 6.ii.1988, J. & F. Murphy.
Trechona venosa (Latreille, 1832)
♂ (IBSP) – **Brazil:** Rio de Janeiro, Teresópolis, N.P. da Serra dos Órgãos, 1100 m a.s.l., 20.xi.2010, R.P. Indicatti, B. Gambaré.

Entypesidae (Ent)
Entypesa sp. 1
♂ (FMNH-INS-3260474) – **Madagascar:** *Antsiranana*: Sava Region, Marojejy Reserve, 14°26.8'S 49°44.1'E, 1975 m a.s.l., 13–20.xi.1996, S.M. Goodman.
Entypesa sp. 2
♂ (FMNH-INS-3260467) – **Madagascar:** *Toleara*: Anosy Region, Andohahela Reserve, Mt Trafonaomby 15–20 km SE Andranondambo Village, 24°33.7'S 46°43.3'E, 1875 m a.s.l., 27.xi–5.xii.1995, S.M. Goodman.
Hermacha septemtrionalis Ríos-Tamayo, Engelbrecht & Goloboff, 2021
♂ (SMNHTAU) – **South Africa:** *Limpopo*: Schoemansdal, Happy Rest N.R., 23°00'36"S 29°43'32"E, 25.i.2020, Y.M. Marusik.

Euagridae (Eua)
Australothele jamiesoni Raven, 1984
♂ (QMS 599) – **Australia:** SE Queensland, Kroombit Tops, 22–26.ii.1982, R. Raven.
Cethegus sp.
♂ (QMS 76127) – **Australia:** *Queensland*: Normanton, 17°48'14"S 141°00'51"E.
Chilehexops australis (Mello-Leitão, 1939)
♂ (SMNHTAU) – **Chile:** La Campana N.P., Sector Ocoa, sandy road, 17.xii.2014, K. Eskov.
Euagrus chisoseus Gertsch, 1939
♂ (SMNHTAU) – **USA:** *Arizona*: Chiricahua Mts, 24.ix.1981, F.A. Coyle.
Namirea sp.
♂ (QMS 9783) – **Australia:** *Queensland*: Mount Nebo, viii.1985, S. Wilson.

Phyxioschema raddei Simon, 1889
♀ (ZMMU) – **Turkmenistan:** Kopet Dag Reserve, Syunt Mt N of Kara-Kala, 400 m, Kala-Legyoz Canyon, 19–26.v.1990, T. Lugarevskaya.

Stenygrocercus sp.
♀ (QMS 17788) – **New Caledonia:** Col d'Amceu, 6.ix.1990, R. Raven.

Euctenizidae (Euc)
Myrmekiaphila torreya Gertsch & Wallace, 1936
♀ (SMNHTAU) – **USA:** *Florida*: Torreya State Park, 31.iii.1964, F.A. Coyle.

Halonoproctidae (Hal)
Bothriocyrtum californicum (O. Pickard-Cambridge, 1874)
♀ (QMS 22523) – **USA:** *California*: San Diego, Poway, 15.vii.1984, R. West.

Conothele sp.
♀ (QMS12276) – **Australia:** *Queensland*: Cape York Penninsula, Torres Strait, Yam Island, 28.xi–2.xii.1986, J. Gallon.

Sterrhochrotus ferghanensis (Kroneberg, 1875)
♂ (SMNHTAU) – **Kyrgyzstan:** Jalal-Abad, 6.iv.1982, S. Zonstein.

Ummidia dudkoi Zamani & Fomichev, 2025
♀ (SMNHTAU) – **USSR:** *Tajikistan*: Khovaling, 38°20'N 70°00'E, 11.x.1987, S. Zonstein.

Hexathelidae (Hex)
Hexathele petriei Goyen, 1887 (det. J.A. Murphy. 1991)
♀ (MMUE 20226) – **New Zealand:** *Otago*: Glendhu Bay, 300 m a.s.l., scrub, 2.i.1991, F. & J. Murphy.

Mediothele nahuelbuta Ríos-Tamayo & Goloboff, 2012 (det. D. Ríos-Tamayo, 2012)
♀ (MACN-Ar-45958) – **Chile:** *Región de La Araucanía*: Dept. Malleco, Monumento Natural Contulmo, 38°02'04"S 73°11'47"W, 11–12.ii.1992, P.A. Goloboff *et al*.

Paraembolides boycei (Raven, 1978)
♂ (QMS 8103) – **Australia:** *Queensland*: Kroombit Tops National Park, ii.1982, R. Raven.

Scotinoecus major Ríos-Tamayo & Goloboff, 2012 (det. D. Ríos-Tamayo, 2012)
♀ (MACN-Ar-45957) – **Chile:** *Región del Maule*: Dept. Talca, 16.5 km E de Linares, 8.ii.1992, P.A Ramírez *et al*.

Teranodes sp.
♀ (QMS 11373) – **Australia:** *Tasmania*: Cradle Mt. N.P., Waldheim forest, 1000 m a.s.l., 41°39'S 145°57'E, 31.01–4.ii.1987, R. Raven, J. Gallon.

Hexurellidae (Hur)
Hexurella pinea Gertsch & Platnick, 1979
♀ (AMNH) – **USA:** *Arizona*: 5 miles west of Prescott, 5.v.1956, V. Roth.

Hexurella sp.
♂ (SDSU - RWM 21_078) – **USA:** *Arizona*: Santa Cruz Co., 1.5 mi W of Harshaw-Duquesne Rd., Duquesne Wsh., Patagonia Mts, 31°23'08"N 110°42'41"W, 5900 ft, Gentle, oak litter, 18.xi.2021, R.W. Mendez, C.A. Hamilton.

Idiopidae (Idi)
Arbanitis sp.
♀ (QMS 20332) – **Australia:** *New South Wales*: Nambucca Shire, 30°39'S 152°58'E, 7.i.1992, N.R. Brown.

Cantuaria minor Forster, 1968 (det. J.A. Murphy, 91)
♀ (MMUE 19983) – **New Zealand:** *Otago*: Saddle Hill, 2300m, primary bush, xii.1990–i.1991, F. & J. Murphy.

Euoplos variabilis (Rainbow & Pulleine, 1918)
♂ (QMS 60958) – **Australia:** SE *Queensland*: Camerons Scrub, 27°31'S 152°44'E, 13.i–16.v.1999, G.B. Monteith.

Heligmomerus sp.
♂ (RMCA ARA 217.658) – **Liberia:** Bong Range Forest, rain forest, p/t, 2.x.2005, D. Flomo.

Idiops clarus (Mello-Leitão, 1946) (det. P.A. Goloboff, 1987)
♀ (MACN-Ar-45955) – **Argentina:** *Salta*: Dept. La Quena, General José de San Martín, 23°14'36.7"S 64°08'02"W, 4–5.ii.1985, P.A. Goloboff.

Idiops sp.
♂ (RMCA ARA 242.378) – **D.R. Congo:** Lubumbashi, Mikembo Sanctuari, Uapaca forest, termite mound, 22.xii.2010, R. Jocqué, M. Hasson.

Idiosoma sp.
♀ (CAD) – **Australia:** *Queensland*: Ocan Lake, Fraser Island, 27.xii.2015, J.P.L. Guadanucci.

Neocteniza toba Goloboff, 1987 (det. P.A. Goloboff, 1987)
♀ (MACN-Ar-45954) – **Argentina:** *Tucumán*: Dept. El Cadillal, Río Loro, 12.iv.1987, P.A. Goloboff, C.L. Szumik.

Titanidiops syriacus (O. Pickard-Cambridge, 1870)
♂ (SMNHTAU) – **Israel:** *Carmel Ridge*: Haifa, 12–23.ix.2005, M. Vonshak.

Ischnothelidae (Ish)
Ischnothele annulata Tullgren, 1905
♂ (CAD 617) – **Brazil:** *Minas Gerais*: Caverna Monte Cristo, 5–10.xi.2012, A.H. Apolinário, J.P.L. Guadanucci.

Lathrothele grabensis Benoit, 1965 (det. F. Coyle, 1991)
♀ (RMCA ARA 162.533) – **Cameroon:** Mt Cameroon**,** nr Buea, 2800 m a.s.l., giant heather zone, pitfalls, 21.iii.1981, R. Bosmans, J. van Stalle.

Thelechoris rutenbergi Karsch, 1881 (det. R.J. Raven, 1982)
♀ (RMCA ARA 203.049) – **Madagascar:** Berevo, i.1948, B. Lasne.

Liphistiidae
Liphistius desultor Schiødte, 1849 (det. N.I. Platnick, 1983)
♀ (MMUE A-136) – **Malaysia:** Penang, vii.1977, E.W. Classey.

Malkaridae
Chilenodes australis Platnick & Forster, 1987
♂ (ZMMU) – **Chile:** Chiloe Island, 15 km E of Ancud, 41°52'56"S 73°40'04"W, lowland forest of *Nothofagus* and *Podocarpus*, in litter, 3–4.i.2014, K. Eskov.

Macrothelidae (Mac)
Macrothele calpeiana (Walckenaer, 1805) (det. R. Jocqué, 1990)
♀ (RMCA ARA 170.753) – **Spain:** Sierra de Ronda, Grazalema, 4.iv.1972, R.C. Swazell.

Macrothele aff. *camerunensis* Simon, 1903
♀ (ZMMU) – **Cameroon:** Ebogo, forest on river bank, viii.2021, V. Govorov.

Macrothele sp.
♀ inadult (ZMMU) – **Vietnam:** Cat Tien NP, 11°27'32"N 107°21'53"E, 25.i.2024, D. Osipov.

Vacrothele sp.
♂ (ZMMU) – **China:** *Yunnan*: Mt Linghao-Shan, 6–15.vi.2023, C. Reuter.

Mecicobothriidae (Mec)
Mecicobothrium thorelli Holmberg, 1882
♀ (MACN-Ar, 42838) – **Argentina:** *Buenos Aires*: Sierra De La Ventana, P.P. Ernesto Tornquist, cerca del Cerro de la Ventana, 22–26.x.1980, L. Zanetic & P. Goloboff.

Megahexuridae (Meg)
Megahexura fulva (Chamberlin, 1919) (det. D. Ubick, 1993)
♂ (CAS 9039672) – **USA:** *California*: Monterey Co., Hastings Natural History Reserve, 36°22'N 121°33'W, 4.ii.1991, J.M. Linsdale.

Microhexuridae (Mhx)
Microhexura montivaga Crosby & Bishop, 1925 (det. F.A. Coyle, 1980)
♀ (CAS 0137) – **USA:** *North Carolina*: Yancy Co., Mt Mitchel, nr start of Commissary R. Tr., 6600 ft, under moss mats on rock ledges, 10.ix.1978, F. Coyle.

Microstigmatidae (Mst)
Angka hexops Raven & Schwendinger, 1995
♂ (QMS 4167) – **Thailand:** *Chiang Mai Province*: Doi Inthanon, 18°33'N 90°28'E, 2530 m a.s.l., 18.iv–23.v.1987, P.J. Schwendinger.

Envia garciai Ott & Höfer, 2004
♂ (SMNK 8624) – **Brazil:** *Amazonas*: Manaus, Reserva Florestal Adolfo Ducke, 2°54'S 59°58'W, 4.ix.1991, H. Höfer.

Ixamatus musgravei Raven, 1982
♂ (QMS 20555) – **Australia:** NE Queensland, Massey Range, 17°14'S 145°48'E, 11–12.x.1991, G. Montheith *et al*.

Kiama lachrymoides Main & Mascord, 1969
♂ (QMS 14855) – **Australia:** New South Wales, without exact locality.

Microstigmata longipes (Lawrence, 1938) (det. C.E. Griswold, 1984)
♂ (NMSA - Ara 01727) – **South Africa:** *KwaZulu-Natal*: Estcourt Nature Reserve, lowlands, 29°06'S 29°53'E, x.1937, R.F. Lawrence.

Ministigmata minuta Raven & Platnick, 1981
♂ (MPEG 8613) – **Brazil:** *Pará*: Vale do Igarapé Mutum, Juruti, Platô do Rio Juruti, 2°36'S 56°11'W, 8–15.viii.2006, D.F. Candiani.

Pseudonemesia tabiskey Indicatti & Villareal, 2016
♂ (IBSP 115438) – **Venezuela:** Trujillo, near Boconó, La Cristalina, 9°21'21"N 70°19'35"W, x.2006–iii.2007, O. Villarreal.

Tonton sp.
♂ (ZMTU) – **Brazil:** *Manaus*: Punta Negra, P. Lehtinen.

Xamiatus rubrifrons Raven, 1981
♀ inadult (QMS) – **Australia:** *Queensland*: Conondale.

Migidae (Mig)

Calathotarsus simoni Schiapelli & Gerschman, 1975 (det. C.J. Grismado, 2023)
♀ (MACN-Ar-44542) – **Argentina:** *Buenos Aires*: Dept. Pdo. Tornquist, Sierra de la Ventana, Balneario El Dique, 38°07'50"S 61°47'36"W, 8–12.viii.2022, División Aracnología MACN leg.

Goloboffia megadeth Ferretti, Ríos-Tamayo & Goloboff, 2019 (det. C.J. Grismado, 2023)
♀ (MACN-Ar-36131) – **Chile:** *Región de Coquimbo*: Monte Redondo, 15 km N de Manto de Hornillos, 1.xi.1988, P.A. Goloboff *et al*.

Heteromigas dovei Hogg, 1902 (det. V.V. Hickman)
♀ inadult (ZMTU) – **Australia:** *Tasmania*: nr. Launceston, 21.ix.1926, V.V. Hickman.

Micromesomma cowani Pocock, 1895 (det. P.L.G. Benoit, 1975)
♀ (RMCA ARA 147.158) – **Madagascar**, without exact locality, 1954, A. Verdier.

Migas nitens Hickman, 1927 (det. V.V. Hickman)
♀ inadult (ZMTU) – **Australia:** *Tasmania*: near Cornelian Bay, 31.i.1973, V.V. Hickman.

Moggridgea aff. *anactenidia* Griswold, 1987
♂ (RMCA ARA 219538) – **Cameroon:** Dja Faunal Reserve, 6.v.2005, I. Deblauwe.

Paramigas perroti (Simon, 1891) (det. P.L.G. Benoit, 1962)
♂ (RMCA ARA 122.888) – **Madagascar**, without exact locality, data and collector.

Poecilomigas abrahami (O. Pickard-Cambridge, 1889) (det. P. Lehtinen)
♀ inadult (ZMTU) – **South Africa**, without exact locality, data and collector.

Nemesiidae (Nem)

Nemesia sp.
♂ (MZSP 69960) – **Italy**, without exact locality, data and collector.

Raveniola songi Zonstein & Marusik, 2012
♂ (SMNHTAU) – **China:** *Yunnan*: Shi Lee Mts, 25.v–6.vi.2006, I. Shokhin, S. Murzin.

Raveniola cucullata Zonstein, 2024
♀ (SMNHTAU) – **Tajikistan:** Vahsh Mts, Mullokoni Canyon, Shikildara Gorge, 38°39'N 70°01'E, 1800 m, 29.iv.1990, S. Zonstein.

Paratropididae (Par)

Paratropis pristirana Dupérré & Tapia, 2020 |
♂ (MNHZ) – **Ecuador:** *Cotopaxi*: San Francisco de Las Pampas, Reserva Biologica Pristirana, pitfall traps, 0°25'29"S 78°57'35"W, 1521 m a.s.l., 15.i.2023, E.E. Tapia.

Paratropis papilligera F.O. Pickard-Cambridge, 1896
♂ (IBSP 217219) – **Brazil:** *Pará*: Belterra, APA de Aramanaí, 28.iv–6.v.2010.

Porrhothelidae (Por)
Porrhothele antipodiana (Walckenaer, 1837) (det. D. Court, 2019)
♀ (SMNHTAU) – **New Zealand:** *South Island*: Hinewai Res., 43°48'36"S 173°01'53"E, 12.ii.2019, Y.M. Marusik.

Porrhothele sp. (det. M. Hedin, 2024)
♀ (SDSU-MY0857) – **New Zealand**, without exact locality, data and collector.

Pycnothelidae (Pyc)
Acanthogonatus confuses Goloboff, 1995
♀ (SMNHTAU) – **Chile:** Temuco, Cerro Nielol National Monument, *Nothofagus* forest, under logs, 21.i.2014, K. Eskov, D. Shcherbakov.

Acanthogonatus huaquen Goloboff, 1995
♀ (SMNHTAU) – **Chile:** N.P. La Campana, Sector Ocoa, 17.xii.2014, D. Shcherbakov.

Acanthogonatus nahuelbuta Goloboff, 1995
♀ (SMNHTAU) – **Chile:** N.P. Nahuelbuta, *Nothofagus–Araucaria* forest, under logs and stones, 22–26.i.2014, K. Eskov.

Acanthogonatus sp.
♀ (SMNHTAU) – **Chile:** Alerce Costero N.P., *Sphagnum* bog, 22.i.2015, K. Eskov.

Stanwellia sp. (det. M.S. Harvey).
♂ (WAM) – **Australia:** *Western Australia,* Porongurup N.P., S end of Millinup Pass, 34°41'43"S 117°53'51"E, wet pitfall traps, 28.iv–2.ix.1996, M.S. Harvey *et al*.

Rhytidicolidae (Rhy)
Fufius agualaniensis Beratz, Ferretti, Chaparro & West, 2026
♀ (SMNHTAU) – **Peru:** *Junin*: Pichiquia 11°23'07"S 74°06'05"W, 500 m a.s.l., valley forest, under bark, 26.ix.2017, K. Eskov.

Stasimopidae (Sta)
Stasimopus minor Hewitt, 1915 (det. C. Haddad, 2024)
♂ (NMBA) – **South Africa:** *Free State*: Bloemfontein, Free State National Botanical Gardens, 29°02.997'S 26°12.692'E, 1380 m), iii.2011, J. Neethling.

Theraphosidae (The)
Chaetopelma concolor (Simon, 1873)
♂ (SMNHTAU) – **Israel:** *Upper Galilee*: Mt Meron, 16.vi.2020, S. Zonstein.

Grammostola rosea (Walckenaer, 1837)
♀ (SMNHTAU) – **Chile:** *Región de Ñuble*: Las Trancas, 1.ii.1976, G. Moreno.

Hapalopus formosus Ausserer, 1875
♀ (ZMMU) – **Colombia**: without exact locality, data and collector.

Heterothele affinis Laurent, 1946
♂ (ZMMU) – **D.R. Congo:** Ekongo Camp, 2°45'S 20°18'E, 3–18.iv.2017, V.D. Kravchenko.

Ischnocolus meron Zonstein, 2023
♀ (SMNHTAU) – **Israel:** *Upper Galilee*: Mt Meron, 16.vi.2020, S. Zonstein.

Pamphobeteus sp.
♀ (SMNHTAU) – **Peru:** *Junin*: Pichiquia, 11°23'07"S 74°06'05"W, 500 m a.s.l., valley forest, under bark, 26.ix.2017, K. Eskov.

Selenocosmia crassipes (L. Koch, 1874) (det. R. Raven)
♀ (SMNHTAU) – **Australia:** *Queensland*: Rockhampton, D. Wallace.

Trichopelma sp.
♀ (DWC-KS160) – **Costa Rica:** Puntarenas, Alto Angeles, 2000.

Theridiidae
Euryopis flavomaculata (C.L. Koch, 1836)
♂ (ZMMU) – **Russia:** *Moscow Region*: Serpukhov District, Prioksko-Terrasny Reserve, Protokskoye Lake, 31.v.2014, R.R. Seifulina.