

***Chimerarachne* is the ‘arachnid platypus’: cuticular microstructures confirm the transitional position of a controversial amber fossil (Arachnida: Tetrapulmonata: Chimerarachnidae)**

***Chimerarachne* — это «паукообразное-утконос»: микроструктуры кутикулы подтверждают переходное положение спорного ископаемого из янтаря (Arachnida: Tetrapulmonata: Chimerarachnidae)**

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**КЛЮЧЕВЫЕ СЛОВА:** филогения химерарахнид, микроструктуры, ураранейды, происхождение пауков, «аранеизация тетрапальмонат».

**ABSTRACT.** The mid-Cretaceous genus *Chimerarachne* Wang *et al.*, 2018 occupies a phylogenetic position relative to ‘true spiders’ (Aranei) analogous to that of the monotreme platypus relative to ‘true mammals’ (Theria): it is a sister lineage that retains a mosaic of ancestral and derived characters. Both ancestral features (such as a completely segmented opisthosoma and retention of the flagellum) and derived features (such as spinnerets and the male palpal organ) are well documented in *Chimerarachne*. We analyzed 55 morphological characters of chimerarachnids, including a number of previously overlooked microstructural features, revealing additional plesiomorphic and apomorphic characters. For example, the trichobothrial pattern and bothrial morphology represent plesiomorphies shared with Devonian trigonotarbid, whereas epiandrous spigots associated with sperm-web construction indicate a spider-like mechanism of indirect sperm transfer. No

synapomorphies were identified linking *Chimerarachne* with the classical uraraneids, nor were any found supporting a monophyletic Uraraneida comprising *Attercopus* Selden et Shear in Selden *et al.*, 1991 and *Permarachne* Eskov et Selden, 2005. Although the inclusion of *Chimerarachne* within Aranei can be justified by synapomorphies, its numerous plesiomorphic characters would obscure the diagnosis of such an expanded order. These results suggest that uraraneids and chimerarachnids represent successive grades along the spider stem lineage rather than a monophyletic clade.

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**РЕЗЮМЕ.** Среднемеловой род *Chimerarachne* занимает относительно «настоящих пауков» (Aranei) филогенетическое положение, аналогичное положению однопроходного утконоса относительно «настоящих млекопитающих» (Theria): сестринская линия, сохраняющая мозаику предковых и производных признаков. У *Chimerarachne* хорошо известны как анцестральные признаки (такие как сохранение полной сегментации опистосомы и флагеллюма), так и производные (такие как паутинные бородавки и пальпальный орган самцов). Мы проанализировали 55 морфологических признаков химерарахнид, включая ряд ранее не замеченных микроструктур, выявив дополнительные плезиоморфии и апоморфии. Так, расположение трихоботрий и морфология ботрий представляют собой симплезиоморфии с девонскими тригонотарбидами, тогда как эпиандрусные спиготы, необходимые для построения сперматической паутины, указывают на схожий с пауками механизм непрямого переноса спермы. Не выявлено синапоморфий, связывающих *Chimerarachne* с классическими Uraraneida *Attercopus* и *Permarachne*, а также не обнаружено никаких подтверждений монофилии ураранеид. Хотя включение *Chimerarachne* в состав отряда Aranei и может быть поддержано синапоморфиями, их многочисленные плезиоморфные признаки ведут к размыванию диагноза такого «отряда в расширенном понимании». Эти результаты позволяют предположить, что ураранеиды и химерарахниды представляют собой последовательные грады в стволовой линии пауков, а не монофилетическую кладу.

## Introduction

Chimerarachnids, or ‘tailed spiders’ [Wunderlich, 2019], are tetrapulmonate arachnids discovered only recently in Cretaceous Burmese amber [Wang *et al.*, 2018; Huang *et al.*, 2018], which are well known for their amazing mosaic of ancestral and advanced traits. They retain a completely segmented opisthosoma and the flagellum, but acquired such characteristically spider features as spinnerets and the male palpal organ for sperm transfer (Fig. 1A–C). The discovery of chimerarachnids is of paramount importance for understanding the origin of ‘true spiders’: Aranei.

There is a single genus, *Chimerarachne* Wang *et al.*, 2018 forming a monotypic family Chimerarachnidae Wunderlich, 2019 which is restricted to mid-Cretaceous Burmese (Kachin) amber. Currently, seven specimens of *Chimerarachne* have been studied and described [Wang *et al.*, 2018; Huang *et al.*, 2018; Wunderlich, Müller, 2022; Wunderlich, 2023], belonging — surprisingly — to five species.

Four species — *C. longiflagellum* (Wunderlich et Müller, 2022), *C. patrickmuelleri* Wunderlich, 2023, *C. alexbeigeli* Wunderlich, 2023, and *C. spiniflagellum* Wunderlich, 2023 — are represented only by their holotypes. Of the three specimens assigned to the type species *C. yingi* Wang *et al.*, 2018, two — the paratype NIGP166871 and the specimen NIGP167161, which was discussed

and figured by Huang *et al.* [2018] — appear not to be conspecific with the holotype NIGP166870 (see below).

A well-known mosaic of ancestral and advanced characters of chimerarachnids has led to conflicting interpretations of their ordinal affinities. Huang *et al.* [2018] classified *Chimerarachne* as a member of the tailed arachnid order Uraraneida. Wunderlich [2019] included *Chimerarachne* in the order Aranei as the sister group of all ‘true spiders’, and Selden [2021: 323] supported this decision: “Like uraraneids and uropygids, *Chimerarachne* bears a flagelliform post-anal telson. Apart from this feature *Chimerarachne* could be considered as a spider”.

Finally, Wang *et al.* [2018: 621] chose not to provide a definitive answer to this question: “Irrespective of its exact relationships, we conclude that *Chimerarachne* reveals a grade of organization when spiders, or one of their closest relatives, developed a male palpal organ and at least part of the modern spinning apparatus, but retained the ancestral character of a whip-like telson. We reiterate that there must have been a continuum of character reduction and character acquisition on the lineage towards the modern spiders and we leave open the question of whether Araneae *sensu stricto* should be defined by loss of the telson or by the appearance of the spinnerets and/or male palpal organ”.

The aim of the present study is to clarify the phylogenetic position and taxonomic status of these controversial arachnids. To achieve this, we re-examined the available material of *Chimerarachne* using imaging techniques that revealed a number of previously undocumented characters, including several microstructural features.

## Material and Methods

The Burmese (Kachin) amber inclusion of the single male of *Chimerarachne* cf. *patrickmuelleri* Wunderlich, 2023 (PIN 5608/475) explored herein is deposited in the Borissiak Paleontological Institute, Moscow (Fig. 1A). The amber piece contains a syninclusion: a mite Prostigmata: Raphignathoidea?, det. Alexander Khaustov, Tyumen State University (Fig. 1E). The specimen was acquired prior to the conflict period in Myanmar.

The amber was mined near Tanaing Town, State of Kachin in the north of Myanmar [Xing, Qiu, 2020]. A recent study, using U–Pb zircon dating, determined the age of the rock to be  $98.79 \pm 0.62$  Ma [Shi *et al.*, 2012], which corresponds to the early Cenomanian. The amber from Kachin was, therefore, dated to the Albion–Cenomanian boundary [Rasnitsyn *et al.*, 2016].

The amber sample with *Chimerarachne* was cut and polished following the protocols of Sidorchuk & Vorontsov [2018]. Imaging in transmitted and reflected light was done using a Nikon E-800 compound microscope equipped with Olympus OM-D E-M10-II digital camera in the Borissiak Paleontological Institute, Moscow. Stacks of images, comprising multiple focal planes, were treated for color, digital noise, and sharpness with Adobe Lightroom. Focus stacking was performed with Helicon Focus software. Unless otherwise indicated, all micrographs in the figures are results of focus-stacking. Confocal laser scanning microscopy (CLSM) imaging was done using a Zeiss LSM-880 microscope in the Koltzov Institute of Developmental Biology; excitation wavelength 543 nm. Selected image stacks are available at Figshare (<https://doi.org/10.6084/m9.figshare.32826884>).

SEM images were taken on a Tescan Vega2 and a Tescan Vega3 scanning electron microscopes in Borissiak Paleontology

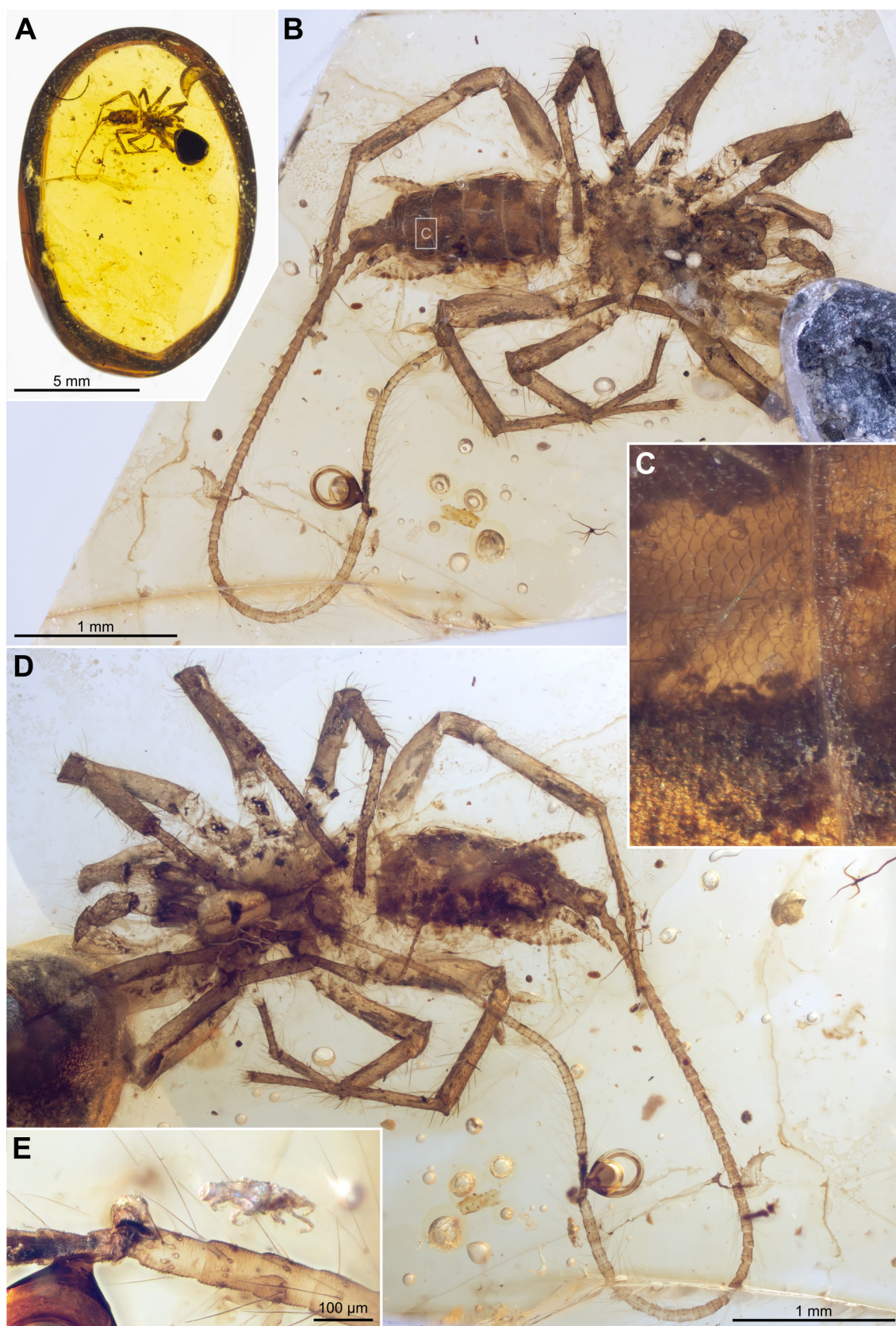


Fig. 1. *Chimerarachne* cf. *patrickmueller* (PIN 5608/475): A — piece of amber before preparation; B — general appearance, dorsally; C — cuticle of opisthosoma, dorsally; D — general appearance, ventrally; E — syninclusion, Raphignathoidea? mite.

Рис. 1. *Chimerarachne* cf. *patrickmueller*: A — кусочек янтаря до обработки; B — общий вид, дорсально; C — кутикула опистосомы, дорсально; D — общий вид, вентрально; E — синиклозия, клещ Raphignathoidea?

cal Institute, Moscow, 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  $\mu\text{m}$ .

Cuticular microstructures of the following extant arachnids were studied as a comparative material using scanning electron microscopy (SEM):

#### Aranei: Mesothelae

Liphistiidae Thorell, 1869

*Heptathela* sp.

1 subad. (ZMMU) — Japan, Kyushu Isl., environs of Beppu, 7.VII.1973, A.G. Ponomarenko.

*Liphistius desultor* Schödte, 1849 (N.I. Platnick det., 1983).

1 ♀ (MMUE) — Malaysia, Penang, VII.1977, “coll. E.W.C.”.

*Liphistius* sp.

1 ♀ (ZMMU) — Vietnam, without strict locality, data and collector.

#### Aranei: Mygalomorphae

Antrodiaetidae Gertsch, 1940

*Antrodiaetus montanus* (Chamberlin et Ivie, 1935) (S. Crews det., 2001)

1 ♂ (CAS) — USA, California, Sierra Co., SFSU Field Station, 6 mi E of Sierra City, 39°37'N 120°34'W, 5500', 7.VIII.2001, S. Crews.

Atypidae Thorell, 1870

*Calommata sundaica* (Doleschall, 1859) (S. Zonstein det., 2020).

1 ♀ (SMNH) — Indonesia, East Java, S. Ströbell.

Mecicobothriidae Holmberg, 1882

*Mecicobothrium thorelli* Holmberg, 1882 (I. Magalhaes det., 2020)

1 ♀ (MACN) — Argentina, Buenos Aires, Sierra De La Ventana, Parque Provincial Ernesto Tornquist, cerca del Cerro de la Ventana, 22–26.X.1980, A. Zanetic, P. Goloboff.

Microhexuridae Bond, Opatova et Hedin, 2020

*Microhexura montivaga* Crosby et Bishop, 1925 (F. Coyle det., 1980)

1 ♀ (CAS 0137) — USA, North Carolina, Yancy Co., Mt Mitchel, near start of Commissary R. Tr., 6600', 10.IX.1978, F. Coyle.

#### Aranei: Araneomorphae

Anapidae Simon, 1895

*Comaroma simoni* Bertkau, 1889

1 ♂ (ZMMU) — Austria, Hieflau, 4.X.1988, C. Kropf.

*Taphiassa castanea* Rix et Harvey, 2010

1 ♂ (ZMMU) — Australia, Tasmania, Mt Field N.P., Lady Barroni Falls, 21.XII.2015, K. Eskov.

Austrochilidae Zapfe, 1955

*Austrochilus* sp.

1 ♀ (ZMMU) — Chile, N.P. Puyehue, Anticura Sector, 19.I.2014, K. Eskov.

Malkaridae Davies, 1980

*Chilenodes australis* Platnick et Forster, 1987

1 ♂ (ZMMU) — Chile, Chiloe Isl., Senda Darwin Biological Station (15 km E of Ancud), 3–4.I.2014, K. Eskov.

#### Amblypygi

Charinidae Quintero, 1986

*Charinus* sp.

1 subad. (ZMMU) — Peru: Junin Region, Pichiquia, 11°23'07"S 74°06'05"W, 500 m, 26.IX.2017, K. Eskov.

#### Thelyphonida

Thelyphonidae Lucas, 1835

*Thelyphonus* (?) sp.

1 ♀ (ZMMU) — Vietnam, 5 km N of Ankhe, 21.X.1979, V.V. Yanushev.

#### Schizomida

Hubbardiidae Cook, 1899

*Trithyreus* (?) sp.

1 ♀ (ZMMU) — Peru, Junin Region, 16 km NW from Satipo, Rio Venado, 1120 m, 14.IX.2017, K. Eskov.

## Results and discussion

General outline of Tetrapulmonata phylogeny is accepted according to Selden *et al.* [1991]. Trigonotarbita are considered the basalmost lineage of tetrapulmonates, and two sister lineages are recognized. The Pedipalpi clade comprises whip spiders (Amblypygi), whip scorpions (Thelyphonida), and schizomids (Schizomida); the latter two form the supraordinal sister group Uropygi *s.l.* The ‘non-pedipalpi’ lineage comprises Uraraneida and chimerarachnids, and culminates in the ‘true spiders’ (Aranei). *Idmonarachne* Garwood *et al.*, 2016, “where the preserved morphology is enigmatic” [Wang *et al.*, 2018: 621], and Haptopoda, whose phylogenetic position remains controversial, were not included in our comparative analysis.

### 1. Prosoma

#### 1.1. Carapace

The consolidated carapace of *Chimerarachne* is flattened, lacking both a raised head region and a distinct central fovea (Fig. 2A, D; Wang *et al.* [2018: fig. 2a]; Wunderlich [2023: fig. 29]). A deep transverse depression visible in the specimen figured by Huang *et al.* [2018: fig. 2f] is undoubtedly an artefact caused by carapace deformation.

In spiders, “The fovea represents the attachment point of two groups of muscles — medially the fovea is the dorsal attachment point of the muscles of the sucking stomach; the lateral arms of the fovea and carapace anterior to it are joined by muscles to the lower angles of each chelicera” [Raven, 1985: 19]. The carapace of Amblypygi, another arachnid order whose members possess the sucking stomach [Shear *et al.*, 1987: 13], bears several shallow pits as attachment point of such muscles (Fig. 7A).

Shear *et al.* [1987: 12] interpreted the pair of dimple-like depressions on the carapace of the Devonian trigonotarbid *Gelasinotarbus reticulatus* Shear, Selden et Rolfe, 1987, as a variant of a fovea for muscle attachment to operate a sucking stomach. However, this interpretation is not convincing. First, these two lateral depressions [Shear *et al.*, 1987: fig. 63] are distinctly different from the always unpaired, median fovea of spiders. Second, and more importantly, similar structures have not been recorded in any other trigonotarbid species.

Regarding uraraneids, the carapace of *Attercopus* Selden et Shear in Selden *et al.*, 1991 is represented by

only a few isolated fragments [Selden *et al.*, 1991: 257], and the prosoma of *Permarachne* Eskov et Selden, 2005 is visible only ventrally [Eskov, Selden, 2005: figs 2–3]. Thus, there is no evidence of a fovea in Uraraneida, but it is not yet possible to confirm its absence.

A deep, rounded or transverse, fovea is present in basal spider lineages: Liphistiomorphae, Mygalomorphae, and Filistatidae Ausserer, 1867, and was further transformed into the longitudinal thoracic groove of araneomorphs. This structure appears to have been necessary, primarily, for the attachment of muscles operating the enlarged orthognathous chelicerae. Therefore, a carapace lacking a fovea is a symplesiomorphy of trigonotarbid (and probably uraraneids) with chimerarachnids, consistent with their relatively weak chelicerae.

## 1.2. Eyes

A distinct eye tubercle on the anterior edge of carapace in *Chimerarachne* bears a compact group of six eyes (Fig. 2B–D; Huang *et al.* [2018: fig. 2f]; Wunderlich [2023: fig. 3]). Our observations do not support the suggestion by Wang *et al.* [2018: 619] that the carapace “appears to have both medial and lateral eye tubercles”. The evolution of the eye pattern in Tetrapulmonata was studied by Miether & Dunlop [2016], who emphasized fundamental differences between arachnid median and lateral eyes based on the presence or absence of a tapetum and whether the retina is inverse or evert.

Trigonotarbida, a basalmost lineage of tetrapulmonates, possess a pair of median eyes and two lateral eye tubercles. Each lateral tubercle bears three major lateral lenses accompanied by three to seven minor lateral lenses [Shear *et al.*, 1987: figs 63, 52, 127]. In *Aculeatarbus depressus* Shear, Selden et Rolfe, 1987, however, the median eye pair and the lateral eyes (with a 3+4 arrangement of major/minor lens) are grouped onto a single antero-median ocular tubercle [Shear *et al.*, 1987: figs 141–142]. Miether & Dunlop [2016: 111] noted that “The condition in *A. depressus* is actually quite reminiscent of many spiders, where the eyes are also all often on a single tubercle”. On the other hand, in *Gelasinotarbus bonamoe* Shear, Selden et Rolfe, 1987 eye number is reduced to eight through the loss of the minor lateral lenses, resulting in an arrangement of a median pair and two lateral triads [Shear *et al.*, 1987: fig. 94]. This set of eyes (but not the pattern of eyes) is fundamental for spiders.

Regarding Uraraneida, the eyes are partially visible on a single carapace fragment of *Attercopus* [Selden *et al.*, 1991: 257], and these eyes are sessile on the carapace [Selden *et al.*, 1991: text-fig. 4A]. Thus, uraraneids apparently lacked a median eye tubercle, but its absence cannot yet be confirmed.

Both Amblypygi and Thelyphonida possess a pair of median eyes on the central part of carapace and two triads of lateral eyes in the antero-lateral regions (Fig. 7A; Miether, Dunlop [2016: fig. 5A–K]). In thelyphonids, each triad of major lateral lenses is accompanied by two minor lenses. This ancestral eye pattern appears to be directly inherited from Devonian trigonotarbids. In the third order of pedipalpians, Schizomida, the eyes

are almost completely reduced: “Median eyes absent; sometimes with pale eye spots or a single pair of lateral eyes” [Miether, Dunlop, 2016: 104].

Regarding spiders, Miether & Dunlop [2016: 103] suggested that “There is a clear trend towards the lateral eyes consolidating into triads of three lenses. A number of early-branching spider families (e.g., Hypochilidae, Atypidae, but interestingly not Liphistiidae) retain clear evidence of triads”.

We propose the opposite polarity for this character in spiders. In our interpretation, the evolution of a prominent eye tubercle carrying all eight eyes (the median pair and two lateral triads), as observed in the basalmost spider lineage Liphistiomorphae [Haupt, 2003: fig. 9A; Miether, Dunlop, 2016: fig. 4E], represents a key synapomorphy of Aranei. This ground-plan condition is retained in the two other basal spider lineages, Mygalomorphae and Filistatidae, but has been lost in more derived araneomorphs.

The basal position of Filistatidae within Araneomorphae has long been recognized. Barrantes & Ramírez [2013: 72] noted that filistatids are long-lived spiders whose females continue to moult and grow after reaching maturity and whose copulatory posture resembles that of mesotheles and mygalomorphs. On the basis of these and other behavioural and morphological traits, several authors have suggested an exceptionally basal position for the family within Araneomorphae. Eskov & Zonstein [1990b] even explored the possibility of placing filistatids within the mygalomorph lineage. Additional evidence of their primitive status is provided by the retention of reduced posterior book lungs [Griswold *et al.*, 2005: 27], especially evident in first-instar specimens [Ramírez, 2014: fig. 97B]. The filistatid eye pattern is, therefore, consistent with, and further supports, their basal position among araneomorph spiders.

In some mygalomorphs, the compact group of eyes on the tubercle has disintegrated, leaving the lateral triads widely separated from the median eyes. Apart from the two atypid genera *Atypus* Latreille, 1804 and *Calommata* Lucas, 1837, which were figured and discussed by Miether & Dunlop [2016: 113, fig. 4G, H], this pattern is also demonstrated by several non-atypoid mygalomorph families: Actinopodidae Simon, 1892, Ctenizidae Thorell, 1887, Idiopidae Simon, 1889, and Migidae Simon, 1889 [Jocqué, Dippenaar-Schoeman, 2006: figs 5a, 27c, 50b–c, 62b, respectively].

All of these non-atypoid families form the advanced ctenizoid lineage within the non-atypoid mygalomorph branch, whereas Atypidae Thorell, 1870 is an advanced clade of Atypoidea [Opatova *et al.*, 2020: fig. 8; Eskov *et al.*, 2026]. Thus, the disintegration of the consolidated eye group on the tubercle should be considered a derived condition resulting from reversion, a trait that has evolved within Mygalomorphae at least twice independently.

It is important to emphasize that Hexurellidae Hedin et Bond, 2019, being the basalmost family of atypoids [Opatova *et al.*, 2020: fig. 8], possesses the most compact eye group [Gertsch, Platnick, 1979: figs 72–75]. The three genera of Atypidae demonstrate a remarkable sequence of eye group disintegration: from quite consolidated in

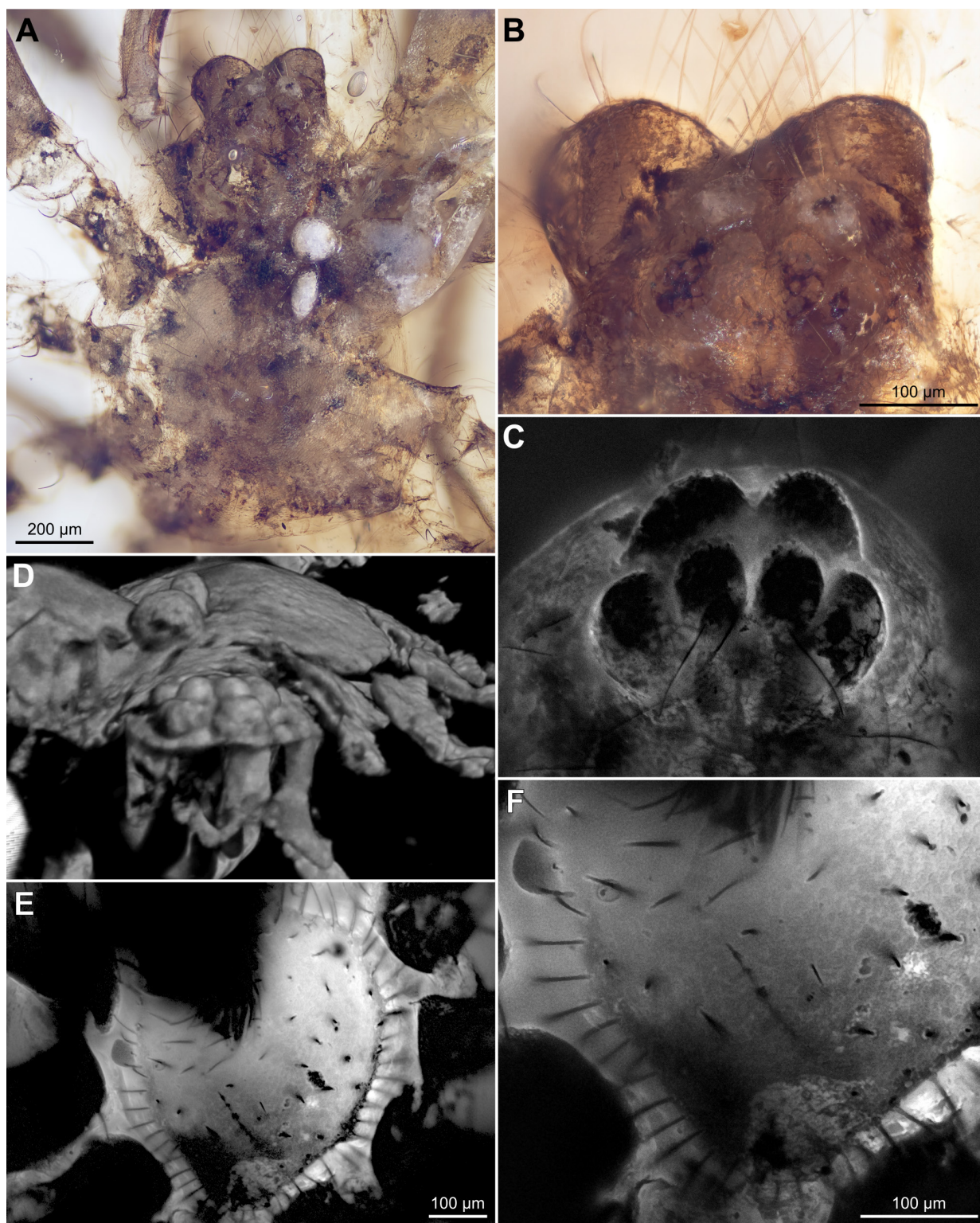


Fig. 2. Prosoma of *Chimerarachne* cf. *patrickmueller*: A — carapace, dorsally; B — anterior portion of carapace, dorsally; C — eye area; D — carapace and chelicerae, dorsofrontally; E — coxosternal region; F — the same, enlarged. A, B — reflected/transmitted light; C, E, F — CLSM; D — microtomography.

Рис. 2. Просома *Chimerarachne* cf. *patrickmueller*: A — карапакс, дорсально; B — передняя часть карапакса, дорсально; C — глазная область; D — карапакс и хелицеры, дорзофронтально; E — кокостеральная область; F — то же, увеличено. A, B — отраженный/прошедший свет; C, E, F — конфокальная лазерная сканирующая микроскопия; D — микрофотография.

*Sphodros* Walckenaer, 1835, to completely disintegrated in *Calommata*, with *Atypus* representing an intermediate condition [Gertsch, Platnick, 1980: fig. 21, Miether, Dunlop, 2016: fig. 4H and G, respectively]. This disintegration sequence can even be observed within a single genus *Atypus*, ranging from a relatively consolidated eye group in *A. snetsingeri* Sarno, 1973 [Gertsch, Platnick, 1980: fig. 13] to a partially disintegrated one in *A. affinis* Eichwald, 1830 [Miether, Dunlop, 2016: fig. 4G].

In the most advanced spider lineage, Araneomorphae, the eye tubercle has been lost, and all eyes are sessile on the carapace. The ancestral eye pattern — a pair of median eyes and two triads of lateral ones — persists only in basal four-lunged Hypochilidae Marx, 1888 [Forster *et al.*, 1987: fig. 3; Miether, Dunlop, 2016: fig. 4A]. From this basal condition, the pattern has been transformed in two principal directions.

First, in the majority of families, the median eyes have migrated anteriorly, leading to the most common araneomorph pattern of eight eyes arranged in two transverse rows (which are sometimes strongly curved). Second, within the Haplogynae (= the clade Synspermiata), the median eyes have been lost entirely. The remaining six lateral eyes are arranged in three dyads, a configuration derived from the two ancestral triads.

The dyads can be quite widely spaced, as in Orsolobidae Cooke, 1965 and Scytodidae Blackwall, 1852 [Jocqué, Dippenaar-Schoeman, 2006: figs 73A, 88C], sometimes extending to the very edges of the carapace, as in Drymusidae Simon, 1893 and Periegopidae Simon, 1893 [Jocqué, Dippenaar-Schoeman, 2006: figs 36A, 78A]. In other families, such as Segestriidae Simon, 1893 and Tetrablemmidae O. Pickard-Cambridge, 1873, they are arranged more compactly [Jocqué, Dippenaar-Schoeman, 2006: figs 89B, 101C–D]. Notably, in the advanced synspermiate family Dysderidae C.L. Koch, 1837 [Wheeler *et al.*, 2017] the six eyes are consolidated on an eye tubercle [Jocqué, Dippenaar-Schoeman, 2006: fig. 36b; Miether, Dunlop, 2016: fig. 4D]. However, this structure appears not to be homologous to the eye tubercles of the basal spider lineages discussed above and, instead, represents a putative autapomorphy of Dysderidae.

In all tubercle-bearing basal lineages (liphistiomorphs, mygalomorphs and filistatids) the eye number never reduces from eight to six due to the loss of the anterior median eyes (AME). This contrasts with the numerous independent AME reductions observed in various araneomorph taxa (e.g., Lopardo, Hormiga [2015: char. 88]).

Although the AME in these lineages can be significantly reduced in size, as in the filistatid genus *Microfilistata* Zonstein, 1990 [Zonstein, 2009: figs 1–2] and extant Liphistiidae [Haupt, 2003: fig. 9A], they never disappear completely. Wunderlich [2017: 92] considered the extinct liphistiomorph *Burmathela* Wunderlich, 2017 to be six-eyed. However, given that the AME in Liphistiomorphae are so minute and inconspicuous, their absence cannot be reliably recognized in this fossil [Wunderlich, 2017: photo 32]. In fact, some Paleozoic liphistiomorphs retain eyes of equal size (e.g., Selden *et al.* [2014: fig. 2]).

Therefore, we consider the presence of a single median eye tubercle to be a synapomorphy of ‘chimerarachnid + araneid lineage’, secondarily lost in the derived lineages of ‘true spiders’ (Aranei). Meanwhile, the compact group of six eyes in *Chimerarachne*, resulting from the loss of the AME, appears to represent an apomorphic condition that evolved in parallel with some advanced araneomorphs of the Synspermiata clade.

### 1.3. Coxosternal region

The prosoma of *Chimerarachne* exhibits ventral arrangement of movable coxae and a consolidated, broad sternum, narrowed posteriorly (Fig. 2E; Huang *et al.* [2018: fig. 1g]). Wunderlich [2023] noted the absence of sternal sigilla, which we confirm (Fig. 2F).

Shear *et al.* [1987: 13], discussing this character in tetrapulmonates, stated: “Araneae and Trigonotarbida have a broad consolidated prosomal sternum, but in the other arachnid orders the prosomal sternum is much smaller, divided, and evidently of less functional importance. In these three orders [Amblypygi, Thelyphonida, and Schizomida], the ventral surface of the prosoma is formed mostly by the coxae.” Based on both morphological and ontogenetic evidence, they concluded that movable coxae with a broad sternum are plesiomorphic, whereas the small, tripartite sternum is a synapomorphy of the Pedipalpi clade.

It should be emphasized that the coxosternal region of Uraraneida appears spider-like. The Permian *Permarachne* has a consolidated, broad sternum and movable coxae [Eskov, Selden, 2005: figs 2–3].

“In the Mesothelae, the sternum is narrow and appears as a plateau with steep edges (fig. 10). It is so narrow that the labium, at its widest, is at least as wide as the sternum. <...> In the Opisthothelae, the sternum is wider than the labium and, in profile, is quite low to domed — never is it so elevated and narrow as in the Mesothelae. The most parsimonious hypothesis explaining the different sternum types in spiders is that the presence of a sternum is another autapomorphy for the Araneae, the elevated sternum is an autapomorphy of the Mesothelae, and that the wide, low sternum of the Opisthothelae is their autapomorphy” [Raven, 1985: 8–9].

However, this narrow, elevated sternum appears to be a familial autapomorphy of the extant Liphistiidae rather than a subordinal autapomorphy of Mesothelae. This is because all extinct liphistiomorphs visible ventrally exhibit a wide, low sternum [Wunderlich, 2017: figs 6, 8], as well as in Opisthothelae and in *Chimerarachne*.

“The fourth coxae of both *Liphistius* and *Heptathela* have peculiar invaginations at their posteromedian corners (fig. 5); so far as we are aware these invaginations are found neither in other spiders nor in amblypygids, and their presence is considered autapomorphic for the Liphistiidae” [Platnick, Gertsch, 1976: 9]. These invaginations are present not only in extant Liphistiidae but also in fossil liphistiomorph families [Wunderlich, 2017: fig. 8]. Therefore, this feature is interpreted as an infraordinal autapomorphy (for the Liphistiomorphae). In contrast, the unmodified fourth coxa in *Chimerarachne* (Fig. 2E; Wang

*et al.* [2018: figs 1c–d, 2c–d]) is a plesiomorphic character state common to all non-liphistiomorph tetrapulmonates.

Therefore, *Chimerarachne* shares the plesiomorphic condition of the coxosternal region with trigonotarbid and uraneids on the one hand, and with ‘true spiders’ (Aranei) on the other. Furthermore, the absence of sternal sigilla appears to be a symplesiomorphy of chimerarachnids and liphistiomorph spiders. This supports the longstanding hypothesis that the presence of sigilla is an apomorphy of Opisthothelae, retained in various early-branching spider lineages such as mygalomorphs, filistatids, and some ‘hypochilids’, and lost in all higher Araneomorphae [Raven, 1985: 10; Eskov, Zonstein, 1990b: 131].

In spiders, “The ventral basal corners of each coxa have fields of proprioceptive setae (‘hair plates’), which are deflected by the folding of the pleural membrane” [Ramírez, 2014: 75]. The coxosternal region of *Chimerarachne* has the same hair plates (cf. Fig. 2E–F and Ramírez [2014: fig. 44F]), and this appears to be a synapomorphy of chimerarachnids and ‘true spiders’.

## 2. Prosomal appendages

### 2.1. Chelicerae

The chelicerae of *Chimerarachne* are relatively small and of the jackknife type, with a naked (hairless) fang, making them essentially spider-like (Fig. 3A–B; Wang *et al.* [2018: fig. 3d]; Huang *et al.* [2018: fig. 2g]). On the other hand, they closely resemble chelicerae present in the uraneids *Attercopus* [Selden *et al.*, 1991: text-fig. 4C] and *Permarachne* [Eskov, Selden, 2005: figs 4–5]. Thus, these two cheliceral features — jackknife configuration and naked fang [Selden *et al.*, 1991] — appear to be strongly correlated, and should be considered as synapomorphies of this tetrapulmonate lineage.

A key cheliceral feature of *Chimerarachne*, as emphasized by Wang *et al.* [2018: 619], is that “They lie in an orthognathous position, but point down at an angle of about 45°”; Wunderlich [2023: 164] considered “basal cheliceral articles directed down-wards” to be a diagnostic character of the chimerarachnids. The fangs are directed at an angle to each other (Fig. 3B; Wang *et al.* [2018: fig. 3d]; Huang *et al.* [2018: fig. 2g]).

Consequently, we argue that the chelicerae of *Chimerarachne*, as well as of *Attercopus* and *Permarachne*, should be considered plagiognathous (according to Kraus & Kraus [1993]) rather than orthognathous. While Shultz [2007: char. 19] treated plagiognathy merely as a variety of orthognathy, we follow Zonstein [2004] in distinguishing these two states and consider plagiognathy to be the ancestral state in spiders.

According to this hypothesis, labidognathous chelicerae cannot be derived directly from orthognathous ones. As Zonstein [2004: 362] stated: “The cheliceral configuration found in the Devonian *Attercopus* represents possibly the only version that appears suitable to be a prototype to all the recent spider groups.”

This morphology subsequently evolved in two distinct directions (Fig. 4). First, toward the labidog-

nathous chelicerae of higher Araneomorphae, via the plagiognathous condition in basal araneomorphs such as Hypochilidae [Zonstein, 2004: figs 29, 32]. Second, toward the orthognathous chelicerae of Liphistiomorphae and Mygalomorphae.

We agree with Zonstein [2004] that the shift of the chelicerae into a biomechanically disadvantageous orthognathous position was likely driven by a dramatic enlargement of their basal joints. Zonstein attributed this enlargement to the burrowing habits of these spiders. We suggest, instead, that it was related to the emergence of endocheliceral venom glands, which required additional internal space within the basal joint. Endocheliceral glands are confined to the basal spider groups: liphistiomorphs, mygalomorphs, and hypochilids. In all higher araneomorphs, including the ‘hypochilids’ more derived than Hypochilidae, venom glands have migrated into the cephalothorax [Marples, 1968; Forster *et al.*, 1987].

In the plagiognathous chelicerae of both uraneids and chimerarachnids, which we consider precursors of chelicerae of ‘true spiders’ (Fig. 4), the non-enlarged basal joints probably did not yet contain venom glands. Selden *et al.* [2008: 20784] concluded: “The preponderance of the evidence now suggests that poison glands were also absent in *Attercopus*”. This interpretation is consistent with the observation by Wang *et al.* [2018: 619] that “The preservation [of the studied specimens of *Chimerarachne*] does not reveal whether the fang had an opening for a venom gland”.

Therefore, it is plausible that chimerarachnids, unlike ‘true spiders’, lacked a venomous apparatus altogether, and this plesiomorphic condition is inherited from the Paleozoic uraneids.

### 2.2. Pedipalps

The highly modified male pedipalps of *Chimerarachne*, apparently adapted for sperm transfer, represent one of the two key characters, together with the spinnerets, that unite chimerarachnids with ‘true spiders’ [Wang *et al.*, 2018; Huang *et al.*, 2018; Wunderlich, 2023]. The pedipalp terminates in a bifurcate tarsus, interpreted by these authors as a cymbium enclosing a bulb with a long, needle-shaped embolus (Fig. 5B–E). Wunderlich [2023: figs 12–13, 24] additionally illustrated structures of the bulb, termed a ‘questionable conductor’ and a ‘translucent shield’, associated with the embolus. These details of the palp structure seem to be best distinguished in the *C. alexbeigel* Wunderlich, 2023 (Fig. 5E; Wunderlich [2023: photo 34]).

Five species of *Chimerarachne* are recognized currently (*C. yingi* Wang *et al.*, 2018, *C. longiflagellum* (Wunderlich et Müller, 2022), *C. patrickmueller* Wunderlich, 2023, *C. alexbeigel* Wunderlich, 2023, and *C. spiniflagellum* Wunderlich, 2023). The morphology of the male palp appears to be a key diagnostic character at the species level.

In our male specimen of *Chimerarachne* (PIN 5608/475), only part of the tarsus is visible (Fig. 5A–B). Its tentative identification as *C. cf. patrickmueller* is based mainly on the structure of the flagellum (see be-

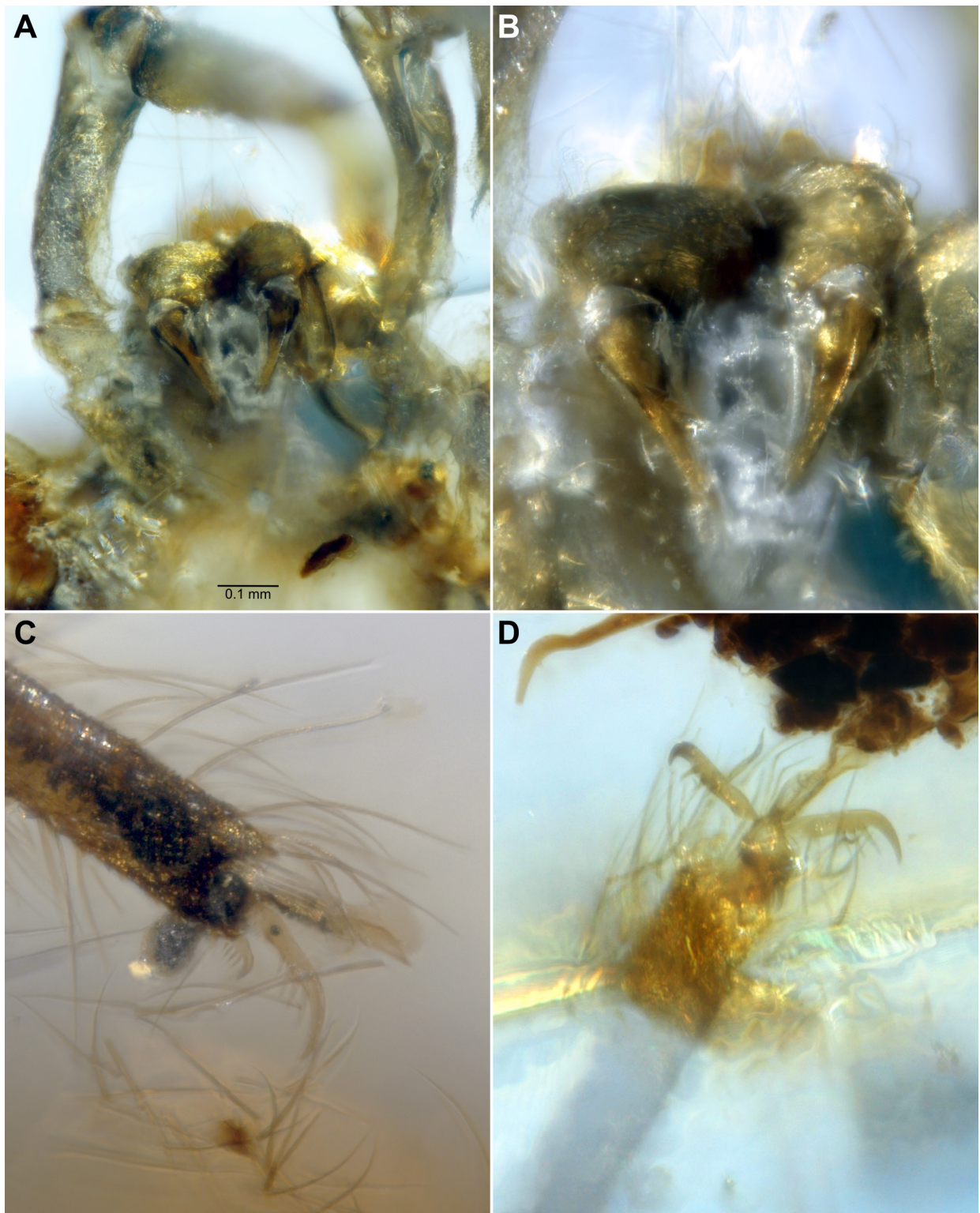


Fig. 3. Morphology of *Chimerarachne yingi* (NIGP166870): A — chelicerae, ventrally; B — the same, enlarged; C — claws and pseudopulvillus, tarsus II; D — claws and pseudopulvillus, tarsus IV.

Рис. 3. Морфология *Chimerarachne yingi*: A — хелицеры, вентрально; B — то же, увеличено; C — коготки и псевдопульвилла, тарзус II; D — коготки и псевдопульвилла, тарзус IV.

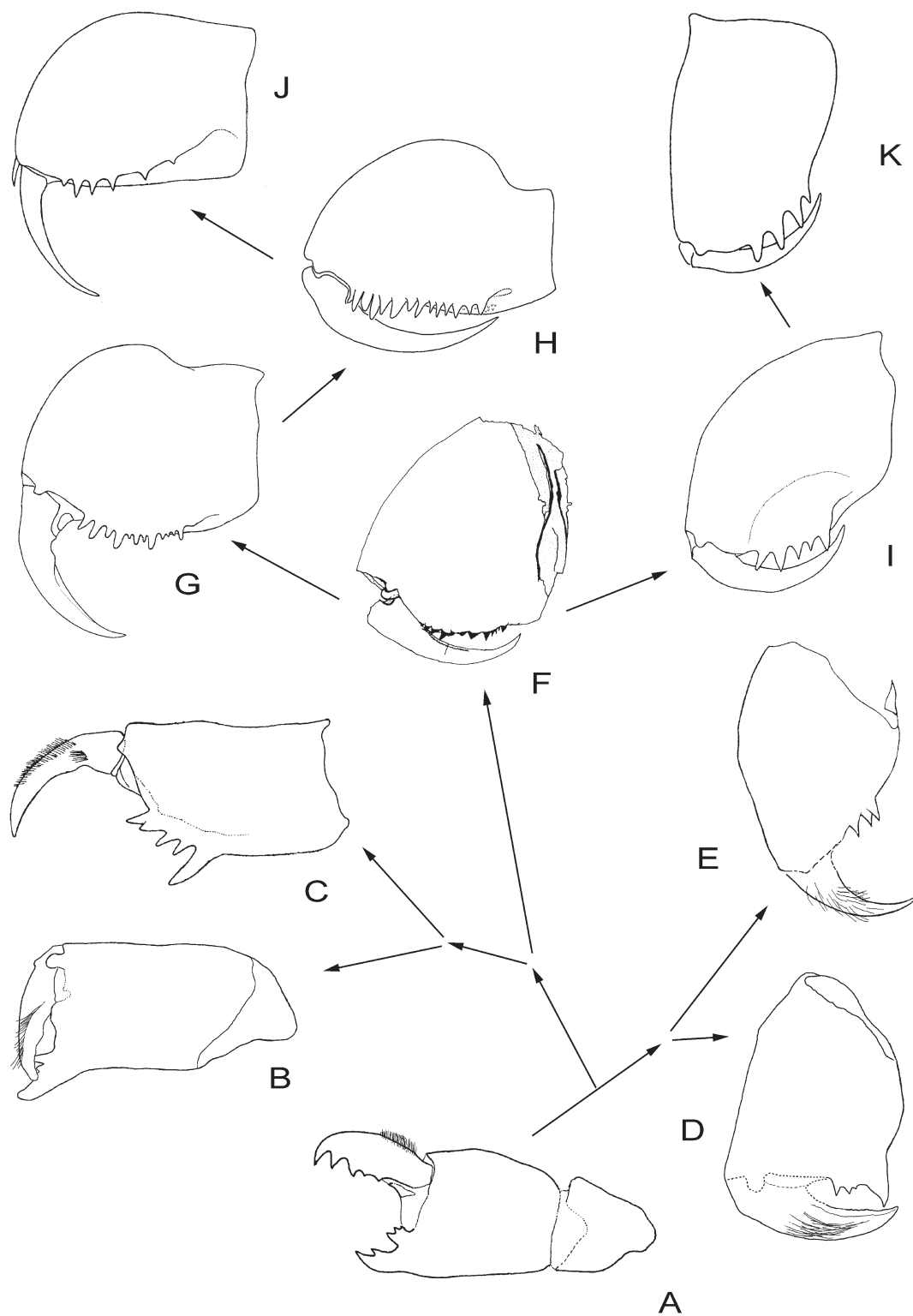


Fig. 4. Presumed evolution of chelicerae in main lineages of tetrapulmonate arachnids (courtesy Sergei Zonstein): A — lower arachnids (Scorpiones); B — schizomid *Stenochrus*; C — whip spider *Charinus*; D — some Trigonotarbida; E — trigonotarbid *Gelasinotarbus reticulatus*; F — *Attercopus*; G — *Liphistius*; H — mecicobothriid *Megahexura*; I — *Hypochilus*; J — nemesiid *Nemesia*; K — majority of Araneomorphae.

Рис. 4. Предполагаемая эволюция хелицер в главных группах Tetrapulmonata (любезно предоставлено С. Зонштейном): А — низшие арахниды (Scorpiones); В — схизомид *Stenochrus*; С — фрин *Charinus*; D — некоторые таксоны Trigonotarbida; E — тригонотарбида *Gelasinotarbus reticulatus*; F — *Attercopus*; G — *Liphistius*; H — мецикоботриид *Megahexura*; I — *Hypochilus*; J — немезида *Nemesia*; K — большинство таксонов Аранеоморфае.



Fig. 5. Male palps of *Chimerarachne*: A — *C. cf. patrickmueller* (PIN 5608/475), dorsally; B — the same, dorsoanteriorly; C — *C. yingi*, para-type (NIGP166871), laterally; D — *C. yingi*, holotype (NIGP166870), laterally; E — *C. alexbeigel*, ventrally (courtesy J. Wunderlich & A. Beigel).

Рис. 5. Пальпы самцов *Chimerarachne*: А — *C. cf. patrickmueller* (PIN 5608/475), дорсально; В — то же, дорсоантериально; С — *C. yingi*, паратип (NIGP166871), латерально; D — *C. yingi*, голотип (NIGP166870), латерально; E — *C. alexbeigel*, вентрально (любезно предоставлено Й. Вундерлихом и А. Бейгелем).

low), which appears to be species-specific [Wunderlich, 2023]. Moreover, the shape of the visible portion of the palp — namely, branches of unequal length in the bifurcate tarsus — is consistent with that of *C. patrickmueller* (cf. Fig. 5B and Wunderlich [2023: fig. 13]).

Three specimens have been assigned to the type species of *Chimerarachne*, *C. yingi* [Wang *et al.*, 2018; Huang *et al.*, 2018]. However, two of them — the paratype NIGP166871 and the specimen NIGP167161 examined by Huang *et al.* [2018] — appear not to be conspecific with the holotype NIGP166870, based on the morphology of both the male palps and the flagella.

In the holotype NIGP166870, the branches of the bifurcate tarsus are equal in size and lack spines; the embolus is thin and needle shaped; and the ‘questionable conductor’ and ‘translucent shield’ (*sensu* Wunderlich [2023]) are large and clearly visible (Fig. 5D; Wang *et al.* [2018: fig. 3e]). In the paratype NIGP166871, the outer branch of the bifurcate tarsus is somewhat shorter than the inner one and terminates in a cluster of stout spines; the embolus is thick and tube-shaped; and additional bulb structures are indistinct (Fig. 5C; Wang *et al.* [2018: fig. 3f]). Wang *et al.* [2018: 620] also noted: “There is a distinct difference in the flagella of these two specimens [paratype and holotype]” (see below for details).

The third specimen referred to *C. yingi*, NIGP167161 [Huang *et al.*, 2018], appears instead to belong to *C. longiflagellum*, based on the shape of the flagellum (see below) and the morphology of the male palp, which exhibits a thin embolus and a broad, suboval ‘translucent shield’ (cf. Huang *et al.* [2018: fig. 1d]; Wunderlich [2023: figs 18–19]).

Regarding the ground plan of the chimerarachnid palp, we find it remarkably similar to that of liphistiomorph spiders, the basalmost lineage of Aranei. The bilobed cymbium of liphistiomorphs is here interpreted as a clear homologue of the bifurcate tarsus of chimerarachnids (Fig. 6A–B). Particularly notable in this respect are species of *Heptathela* Kishida, 1923, in which the paracymbium and cymbium are nearly equal in size and shape [Haupt, 2003: fig. 49A–D]. Complex bulb sclerites accompanying the embolus in liphistiomorphs (Fig. 6A–B; Logunov, Vahtera [2017: figs 7–13]) appear to correspond to the chimerarachnid ‘questionable conductor’ and ‘translucent shield’, although precise homologies remain uncertain.

The shared ground plan of the male palp in both chimerarachnids and the basalmost ‘true spiders’ (i.e., a modified bipartite tarsus and a bulb bearing an embolus with associated structures) appears too complex to have arisen by convergence. This supports the view that the complex organization of the palp in Liphistiomorphae represents the ancestral condition for Aranei and was secondarily simplified in theraphosoid Mygalomorphae and haplogyne Araneomorphae [Kraus, 1978].

The origin of pyriform palpal bulbs with secondarily fused elements in Mygalomorphae may be reconstructed stepwise [Eskov, Zonstein, 1990a: fig. 40]. “So we face two lines in the evolution of the mygalomorph palp <...> Also the atypoid palp seems to be much more archaic than the theraphosoid one in the majority of the characters, we

conclude the practical impossibility of derivation of the second type from the first one. The atypoid and theraphosoid lineages of palpal evolution seems to be completely independent; their divergence should have arisen yet at a level of the common mygalomorph ancestor with its palp retaining all the characteristic elements of the liphistiomorph one” [Eskov, Zonstein, 1990a: 359–361].

The diagnosis of the basalmost family of Araneomorphae, Hypochilidae, includes a “spine-bearing paracymbium and complex bulb attached subdistally” [Forster *et al.*, 1987: 6]. The bilobed cymbium of hypochilids [Kraus, 1978: fig. 14] is similar to that of liphistiomorphs (Fig. 6A–B); on the other hand, their ‘spine-bearing paracymbiums’ resemble the bifurcate tarsus of *Chimerarachne*, in which the outer branch bears a cluster of stout spines (Fig. 5B; Wang *et al.* [2018: fig. 3f]).

The basalmost tetrapulmonates, Trigonotarbida, retained unmodified, leg-like pedipalps (e.g., Shear *et al.* [1987: figs 83–84, 91]). This ancestral morphology subsequently evolved in two distinct directions: first, toward the complex male pedipalps adapted for sperm transfer in chimerarachnids and ‘true spiders’; and second, toward the enlarged, raptorial pedipalps of the three orders of Pedipalpi. Therefore, both modifications are unquestionable synapomorphies of these two major branches of Tetrapulmonata.

## 2.3. Walking legs

### 2.3.1. Segmentation

Leg segmentation in *Chimerarachne* is spider-like: leg I is not antenniform, and tarsi II–IV are not segmented. The legs are moderately long (femur I approximately equal in length to the carapace) and moderately thick (tibia I as long as 6.5 diameters of the joint). The metatarsi are approximately one and a half times longer than the tarsi (Fig. 1B–C).

Shear *et al.* [1987: 13] noted: “Amblypygi, Uropygi, and Schizomida share large, raptorial pedipalps and antenniform first legs <...> Antenniform first legs are not found in any other orders. <...> We take these facts as suggestive that such characters were present in a common ancestor not shared with Trigonotarbida and Araneae, where the palps are leg-like and the first legs, while clearly very important sensorily in spiders, are not at all antenniform”.

These three orders, in addition to having drastically thinned and elongated metatarsi and pseudosegmented tarsi of leg I, possess three-jointed tarsi II–IV (Fig. 7B–C; Van der Hammen [1989: figs 260A, 261A, 262A]). These clearly correlated characters are unquestionable synapomorphies of the Pedipalpi clade. Consequently, the unmodified leg segmentation of *Chimerarachne* represents a plesiomorphic condition, shared with Aranei on the one hand and with Trigonotarbida and Uraeidea on the other.

The dwarfish (less than 6 mm long) Cretaceous whip scorpion *Mesothelyphonus xiaoae* Wu *et al.*, 2025 is of particular interest, because it lacks the key apomorphy of Pedipalpi, namely antenniform first legs. Although tarsus I of *M. xiaoae* consists of eight tarsomeres, versus three in tarsi II–IV, the tarsus-basitarsus of the first leg

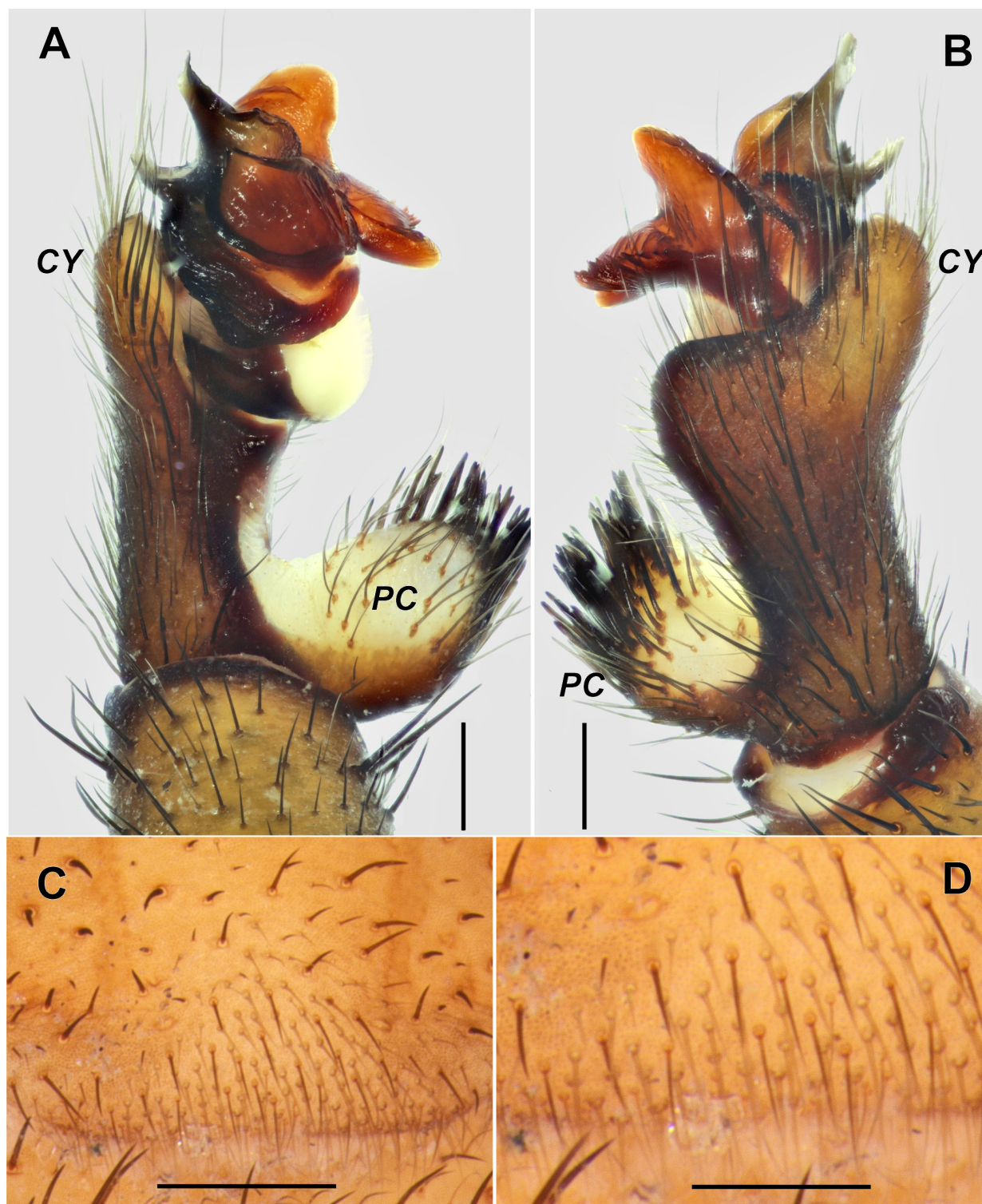


Fig. 6. Morphology of extant liphistiomorph spider *Vinathela nahang* (courtesy D.V. Logunov): A — male palp, ectal view; B — the same, mesal view; C — epandrous area; D — the same, enlarged. Abbreviations: CY — cymbium; PC — paracymbium.

Рис. 6. Морфология современного паука-лифистиоморфа *Vinathela nahang* (любезно предоставлено Д.В. Логуновым): А — пальпа самца, эктально; В — то же, мезально; С — эпиандрозная область; D — то же, увеличено. Сокращения: CY — цимбиум; PC — парацимбиум.

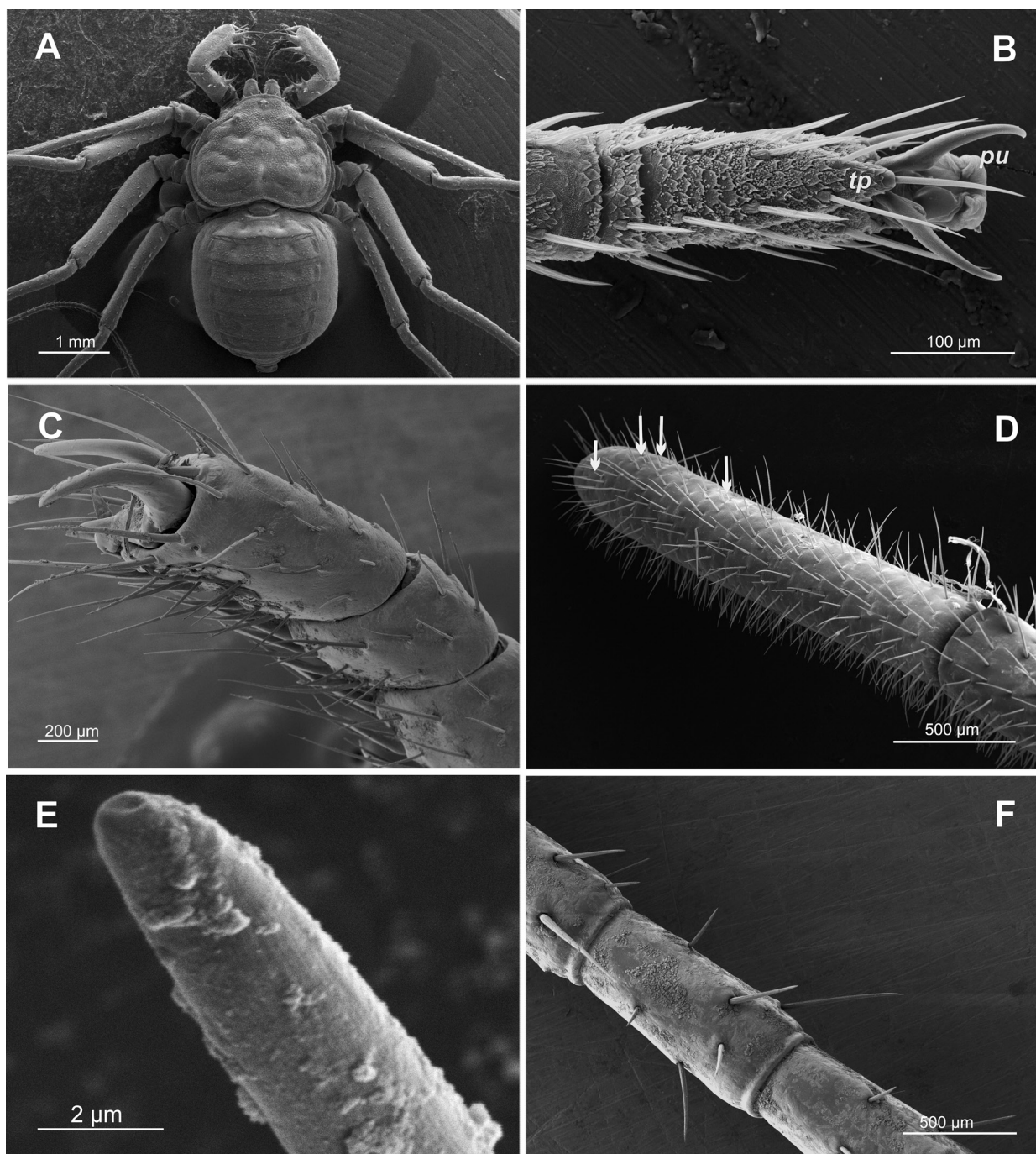


Fig. 7. Morphology of extant amblypygian *Charinus* sp. (A–B) and thelyphonid *Thelyphonus* (?) sp. (C–F): A — general appearance; B — tarsus II; C — tarsus IV; D — tarsus of antenniform leg I (arrows show ‘club setae’); E — the same, enlarged ‘club seta’; F — flagellum joints. Abbreviations: *pu* — pulvillus; *tp* — tarsal processus.

Рис. 7. Морфология современных фринов *Charinus* sp. (A–B) и телифонов *Thelyphonus* (?) sp. (C–F): A — общий вид; B — тарзус II; C — тарзус IV; D — тарзус антеннообразной ноги I (стрелками показаны «булавовидные щетинки»); E — то же, увеличенная «булавовидная хета»; F — членики флагеллюма. Сокращения: *pu* — пульвилла; *tp* — тарзальный отросток.

was correctly considered by Wu *et al.* [2025: 4] to be “unmodified”, and the length and thickness of leg I are almost equal to those of legs II–IV [Wu *et al.*, 2025: fig. 1A–B]. In our opinion, such a condition of leg I in *M. xiaoae* represents the antenniform leg *in statu nascendi*, and this dwarfish species may be interpreted as a relict

of a basalmost lineage of the Thelyphonida, or even of Pedipalpi as a whole.

A unique synapomorphy of Aranei is the patella–tibia joint with the ‘CZY’, a posterior emargination occupied by lightly sclerotized cuticle, which S.M. Manton termed the ‘compression zone Y’ (CZY) [Selden *et al.*, 1991;

Table 1. Characters of four types of tactile hairs in *Chimerarachne*.  
Таблица 1. Признаки четырех типов тактильных волосков у *Chimerarachne*.

|                         | Appressed/<br>Protruding | Smooth/<br>Pubescent           | Straight/ Curved               | Cylindrical/ Conical               | Thin/ Thick                        | Long/ Short       |
|-------------------------|--------------------------|--------------------------------|--------------------------------|------------------------------------|------------------------------------|-------------------|
| Type 1<br>Fig. 10A, B   | Protruding               | Smooth                         | Slightly curved                | Cylindrical, filiform              | Thin (2.5–3 µm)                    | Long, > joint d)  |
| Type 2<br>Fig. 10A, E–F | Appressed                | Smooth                         | Straight                       | Cylindrical, filiform              | Very thin (1.5 µm,<br><< socket d) | Short, < joint d) |
| Type 3<br>Fig. 10A, E–F | Appressed                | Pubescent with<br>microtrichia | Slightly curved                | Conical, terminally<br>pointed     | Thick (6–8 µm at<br>the base)      | Long, > joint d)  |
| Type 4<br>Fig. 10C–D    | Protruding               | Pubescent with<br>microtrichia | Slightly to strongly<br>curved | Cylindrical,<br>terminally rounded | Thick (3.5–6 µm)                   | Short, < joint d) |

Shultz, 2007: char. 73]. “The condition of this joint [in the uraraneid *Attercopus*] is of great interest: the rocking articulation is present but CZY is absent. Functionally, this suggests substantially less mobility at this joint than in <...> spiders, but more than in trigonotarbid” [Selden *et al.*, 1991: 255]. In spiders, “The area of the retrolateral indentation [CZY] is distorted by the movement, coincident with the placement of the lyriform proprioceptor organs” [Ramírez, 2014: 75]. The patella of all three pedipalpal orders lacks this structure (Fig. 8D–E; Ruiz, Valente [2023: fig. 12E]).

The CZY was found on the distal edge of the *Chimerarachne* patella. It forms a semicircular unsclerotized notch (Fig. 9A–D), in contrast to the spider CZY, which represents an unsclerotized strip [Ramírez, 2014: fig. 44D], that sometimes appears like a suture, almost dividing the segment longitudinally (Fig. 8A–C; Kropf [1998: fig. 12]). Thus, in the evolutionary trend toward increasing patellar mobility, *Chimerarachne* occupies a transitional position between Uraraneida and the ‘true spiders’ (Aranei).

### 2.3.2. Setation

The leg setation in *Chimerarachne* is highly diverse. According to the classifications of Foelix [2011] and Ramírez [2014] for ‘true spiders’ several types of tactile hairs, macrosetae, and trichobothria can be recognized in *Chimerarachne*.

(1) Tactile hairs, usually referred to simply as ‘hairs’, are the most frequent and widespread kind of setae. The hair shaft arises from a simple rounded socket of cuticle. We designated four types of tactile hairs in *Chimerarachne*.

Hairs of types 2 and 3 are numerous and appear along the entire length of the leg (Fig. 10A, E–F). Hairs of types 1 and 4 are few and localized only on distal leg joints (the tarsus and the end of the metatarsus) and on basal joints (the femur and patella), as well as on the first tergite (Fig. 10A–B and C–D, respectively). Wang *et al.* [2018: 617, fig. 4b] misidentified the long protruding tarsal setae of type 1 (Fig. 10A–B; Wunderlich [2023: photo 31]) as trichobothria (see below).

(2) Macrosetae, also known as “spines”, are the largest setae, with a thick, long conical shaft and a robust asymmetrical socket. Spines can be erected hydraulically by an increase in hemolymph pressure; their asymmetrical

socket allows only up-and-down movement of the shaft [Foelix, 2011: 86]. The leg macrosetae of spiders are arranged in stereotyped patterns [Ramírez, 2014: 122].

Macrosetae of *Chimerarachne* consist of a strongly protruding hood-shaped socket and a conical but blunt shaft, long (1.5–2 times longer than the diameter of the joint) and thick (almost 0.2 of the joint diameter) (Figs 10A, 11A–B). Two remarkable features of chimerarachnid macrosetae should be noted in comparison with those of spiders. First, the shaft is covered with microtrichia arranged spirally (Fig. 11C–D), whereas the shafts of spider macrosetae are smooth (e.g., Ramírez [2014: figs 86A–D, 88A–B]). Second, the apical surface of a macroseta facing a joint bears a short longitudinal row of two or three tubercles (Fig. 11E–F).

Wunderlich [2023: 165] listed “a single row of 3–6 ventral bristles [i.e. spines] on tibia I–II” as a chimerarachnid apomorphy. However, the spines are arranged in longitudinal rows on all tibiae of *Chimerarachne*, both ventrally and laterally (Fig. 11A), and they form a terminal rosette on all metatarsi (Fig. 11B; Wang *et al.* [2018: fig. 4d]).

(3) Trichobothria, or ‘filiform hairs’, are extremely fine hairs nested within special sockets called bothria; the trichobothrial pattern and bothrial morphology in *Chimerarachne* are discussed in detail below.

Thus, the leg setation in chimerarachnids is highly diverse and comprises various hairs, macrosetae, and trichobothria, as in Aranei. In contrast, the leg joints of all pedipalpal orders bear only uniform tactile hairs — flattened in Amblypygi and smooth, conical in Uropygi and Schizomida (Fig. 8D–F; Ruiz, Valente [2023: fig. 12D–H]) — and lack hydraulically movable macrosetae with an asymmetrical socket [Wolff, 2015; pers. observations].

On the other hand, *Chimerarachne* lacks several types of leg setae that are characteristic of ‘true spiders’. Spider “tenent setae” are specialized for adhesion to smooth surfaces. They have a defined patch of barbs with expanded tips, which make contact with the substratum and produce adherence through molecular forces, and form the claw tufts and scopulae [Ramírez, 2014: fig. 85C–D]. “Scales” are drastically widened and flattened setae, which are bent at an angle immediately after insertion, so that they lie parallel to the cuticle surface. They may occur in a wide diversity of shapes, from leaf-shaped to feather-shaped [Ramírez, 2014: figs 92C, 93A and 92F, I, respectively].

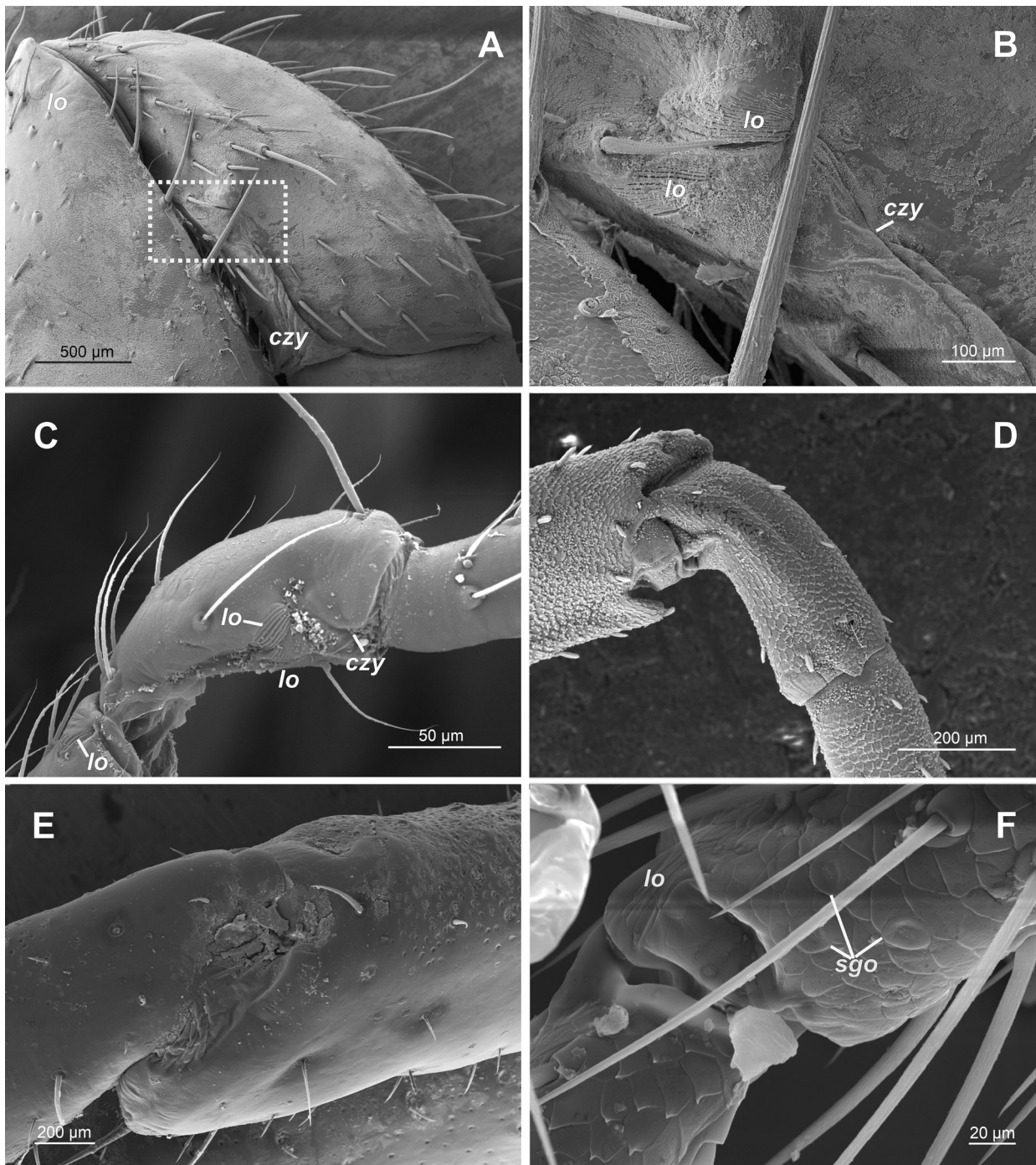


Fig. 8. Leg joints of extant spiders and pedipalpians — patella (A–E) and distal end of metatarsus (F): A — *Liphistius* sp. (Mesothelae), patella III (white box shown in more detail in B); B — the same, posterior end of unsclerotized CZY and pair of lyriform organs; C — *Taphiassa castanea* (Araneomorphae), patella I, CZY and pair of lyriform organs; D — *Charinus* sp. (Amblypygi), patella II; E — *Thelyphonus* (?) sp. (Thelyphonida), patella-tibia juncture II; F — *Trithyreus* (?) sp. (Schizomida), metatarsus-tarsus juncture II. Abbreviations: czy — ‘compression zone Y’, CZY; lo — lyriform organs; sgo — slit-like gland openings.

Рис. 8. Членики ног современных пауков и педипальпов — колено (A–E) и дистальный конец метатарзуса (F): A — *Liphistius* sp. (Mesothelae), колено III (белый прямоугольник показан более подробно на рисунке B); B — то же, задний конец несклеротизированной зоны компрессии Y и пара лировидных органов; C — *Taphiassa castanea* (Araneomorphae), колено I, зона компрессии Y и пара лировидных органов; D — *Charinus* sp. (Amblypygi), колено II; E — *Thelyphonus* (?) sp. (Thelyphonida), сочленение колена и голени II; F — *Trithyreus* (?) sp. (Schizomida), сочленение метатарзуса и тарзуса II. Сокращения: czy — «зона компрессии Y», CZY; lo — лировидные органы; sgo — щелевидные отверстия кутикулярных желез.

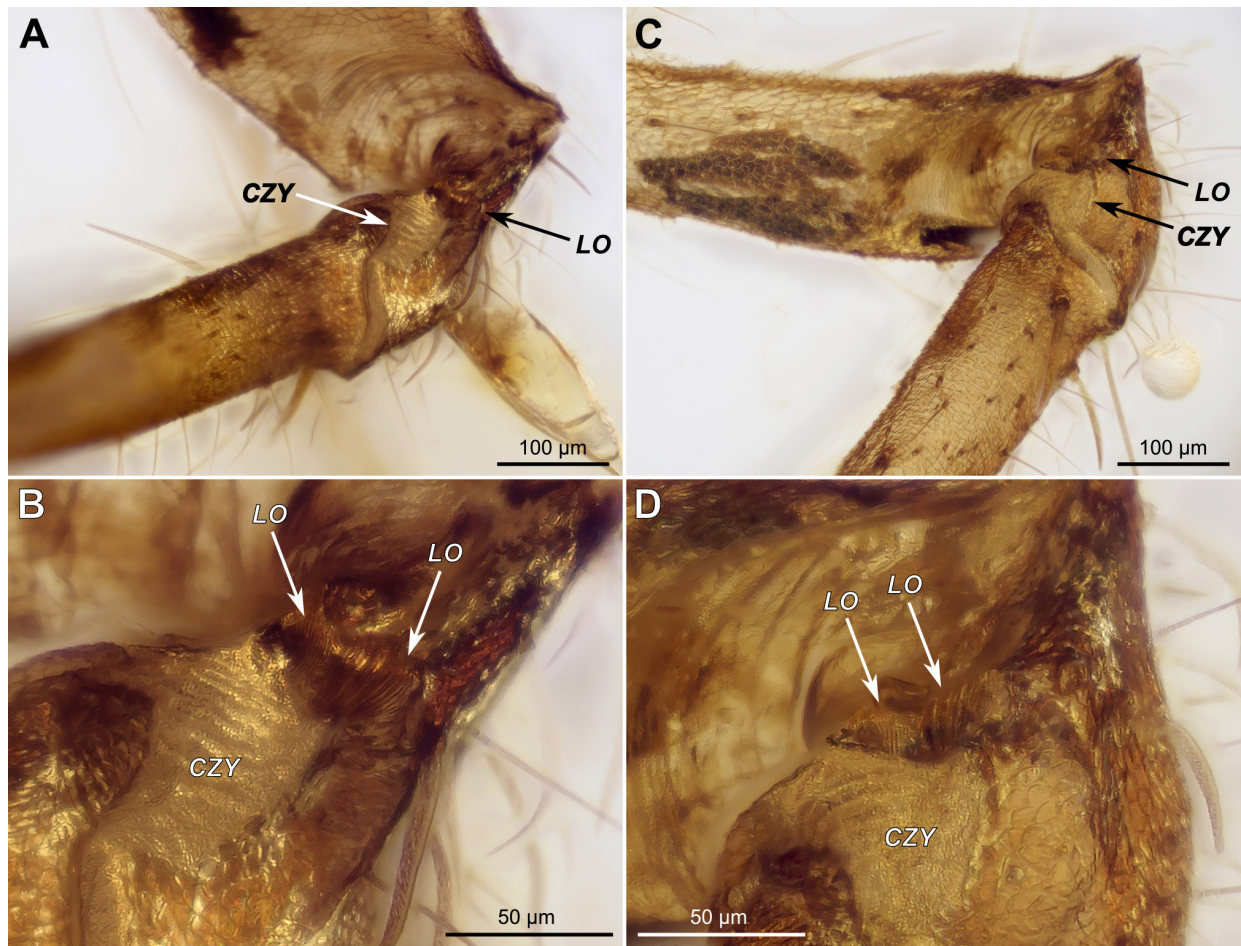


Fig. 9. Patellae of *Chimerarachne* cf. *patrickmuelleri*: A — patella IV, anteriolaterally; B — the same, enlarged; C — patella III, anteriolaterally; D — the same, enlarged. Abbreviations: *czy* — ‘compression zone Y’, CZY; *lo* — lyriform organs.

Рис. 9. Колени *Chimerarachne* cf. *patrickmuelleri*: A — колено IV, переднелатерально; B — то же, увеличено; C — колено III, переднелатерально; D — то же, увеличено. Сокращения: *czy* — «зона компрессии Y», CZY; *lo* — лировидные органы.

Spider chemosensory setae, or “terminal-pore sensilla”, have characteristic features such as an S-shaped profile and a blunt tip with a pore [Foelix, 2011: fig. 4.15a–b; Ramírez, 2014: figs 84E, 85B], so it is fairly certain that *Chimerarachne* does not possess them. These setae are present in various spider lineages, including both basal ones: Liphistiomorphae [Haupt, 2003: fig. 13C; Foelix *et al.*, 2012: fig. 8A–B] and Mygalomorphae [Foelix *et al.*, 2013: fig. 1b–d]. Therefore, these chemosensory organs should be regarded as an important synapomorphy of the order Aranei, distinguishing ‘true spiders’ from chimerarachnids.

The leg joints of Devonian Trigonotarbida are covered with appressed tactile hairs: more or less uniform, as in *Gelasinotarbus* Shear, Selden et Rolfe, 1987 [Shear *et al.*, 1987: figs 85–89; 117–118], or of two sharply different types, as in *Gilboarachne* Shear, Selden et Rolfe, 1987 [Shear *et al.*, 1987: figs 46–47].

The leg setation of the uraraneid *Attercopus* is of particular interest due to the presence of flattened, slightly curved macrosetae (Fig. 13A; Shear *et al.* [1987: figs 132–133]; Selden *et al.* [1991: Pl. 5, fig. 3]), in addition to

two types of appressed tactile hairs (Fig. 13B–C; Selden *et al.* [1991: Pl. 6, figs 1–2, 4–5]). Such diverse setation was correctly considered a diagnostic feature: “The metatarsus is well clothed with setae, some of which are long and thin, and macrosetae are present inferiorly and inferodistally. The macrosetae are very prominent <...> The tarsus <...> is similarly profusely clothed with two sizes of setae, and macrosetae occur inferiorly” [Selden *et al.*, 1991: 272]. It should be noted that macrosetae of *Attercopus* are situated at the distal ends of metatarsi [Shear *et al.*, 1987: figs 132–133], just like the rosettes of macrosetae in *Chimerarachne* (Fig. 11B).

The legs of the uraraneid *Permarachne* are “clothed in fine setae. At least tibia and metatarsus of all legs with macrosetae arranged in parallel rows of  $\geq 4$  pairs on presumed inferior surface of tibia and metatarsus” [Eskov, Selden, 2005: 113]. The ventral rows of macrosetae on the tibiae of *Permarachne* [Eskov, Selden, 2005: figs 2–3; Selden *et al.*, 2008: fig. 3A–B] are very similar to those of *Chimerarachne* (Fig. 11A).

Therefore, a diverse leg setation in both Aranei and *Chimerarachne*, comprising macrosetae and at least two

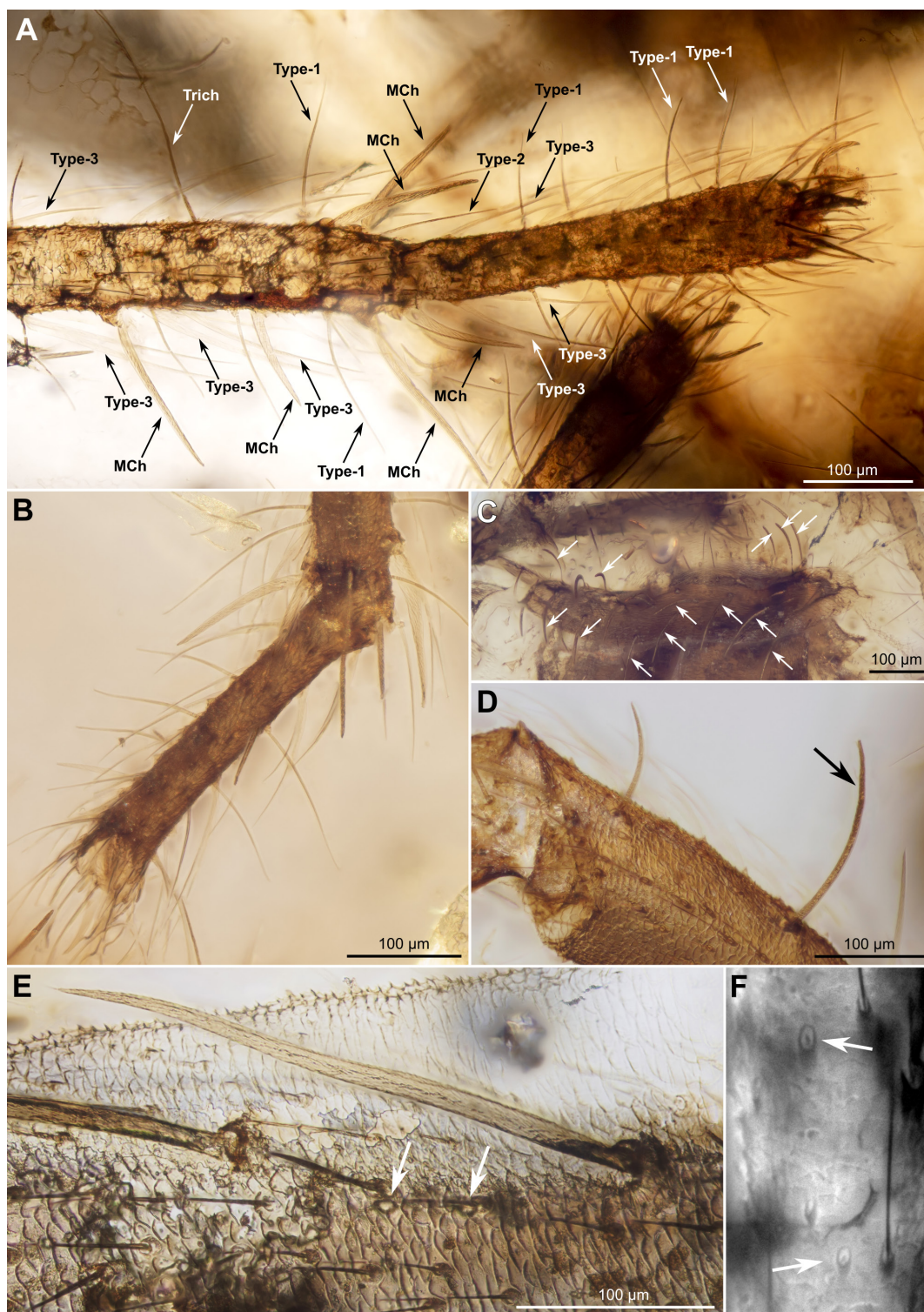


Fig. 10. Leg setation of *Chimerarachne* cf. *patrickmueller*: A — metatarsus-tarsus juncture III, setal types 1–3, macrosetae and trichobothrium; B — metatarsus-tarsus juncture III, setal type 1 and macrosetae; C — first tergite, setal type 4 (arrows); D — femur IV, setal type 4 (arrow); E — femur IV, setal types 2 and 3, enlarged (arrows — slit-like gland openings); F — the same, setal type 2, enlarged (arrows — slit-like gland openings). A–E — reflected/transmitted light; F — CLSM. Abbreviations: *Type-1* – *Type 4* — four setal types (Table 1); *MCh* — macroseta; *Trich* — trichobothrium.

Рис. 10. Хеты ног *Chimerarachne* cf. *patrickmueller*: A — сочленение метатарзуса и тарзуса III, хеты типов 1–3, макрохеты и трихоботрия; B — сочленение метатарзуса и тарзуса III, хеты типа 1 и макрохеты; C — первый тергит, хеты типа 4 (стрелки); D — бедро IV, хета типа 4 (стрелка); E — бедро IV, хеты типов 2 и 3, увеличенные (стрелки — щелевидные отверстия желез); F — то же, щетинка типа 2, увеличенная (стрелки — щелевидные отверстия желез). A–E — отраженный/прошедший свет; F — конфокальный лазерный сканирующий микроскоп. Сокращения: *Type-1* – *Type 4* — четыре типа щетинок (табл. 1); *MCh* — макрохеты; *Trich* — трихоботрия.

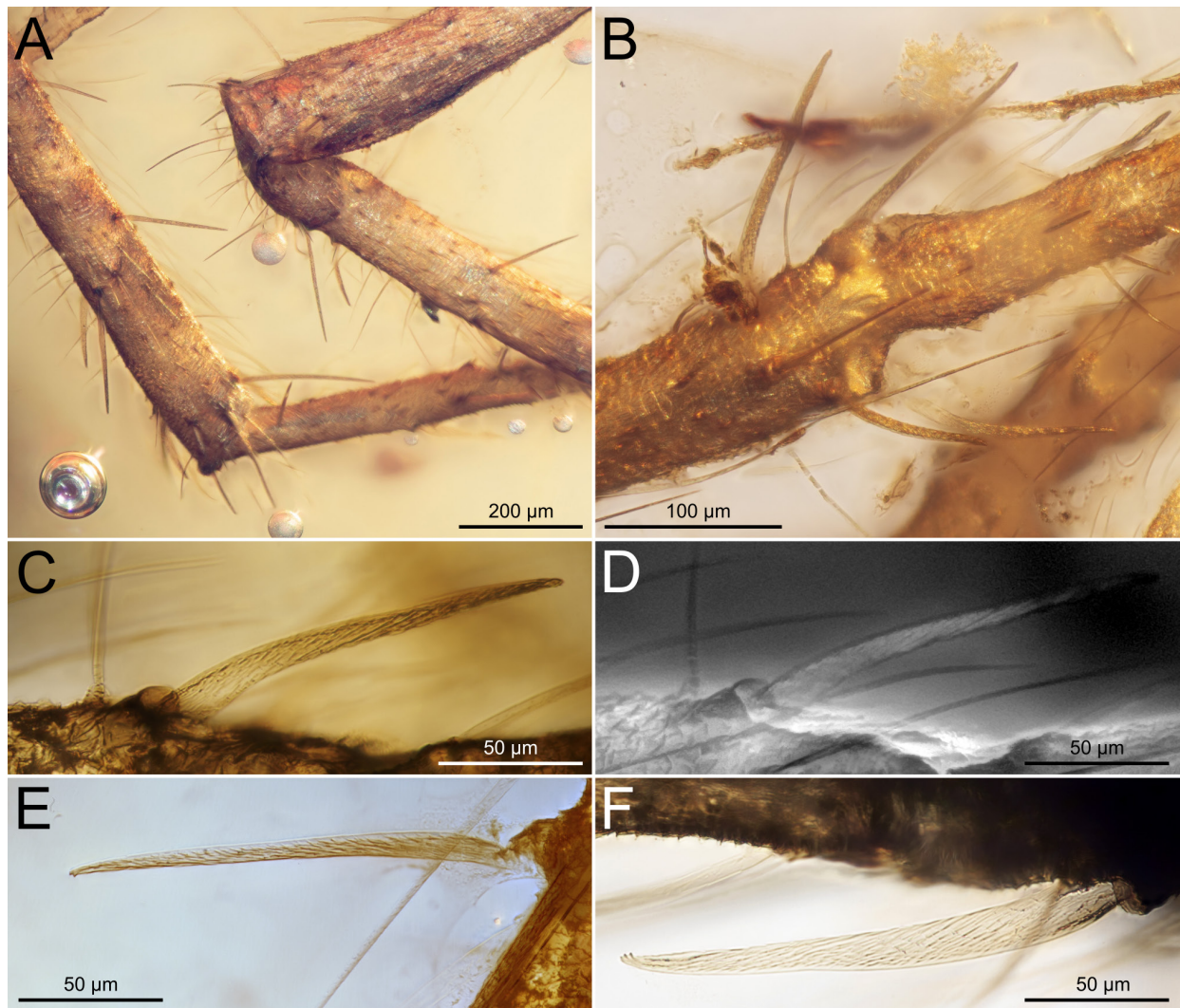


Fig. 11. Macrosetae of *Chimerarachne* cf. *patrickmueller*: A — tibia IV, ventral row of macrosetae; B — metatarsus–tarsus juncture IV, rosette of macrosetae; C — metatarsus III, hood-shaped socket and shaft microtrichia of macrosetae; D — the same; E — tibia IV, apical surface of a macroseta with two tubercles; F — tibia IV, apical surface of a macroseta with three tubercles. A–C, E–F — reflected/transmitted light; D — CLSM.

Рис. 11. Макрохеты *Chimerarachne* cf. *patrickmueller*: A — голень IV, вентральный ряд макрохет; B — сочленение метатарзуса и тарзуса IV, розетка макрохет; C — метатарзус III, капюшонное гнездо и микротрихии стержня макрохеты; D — то же самое; E — голень IV, апикальная поверхность макрохеты с двумя бугорками; F — голень IV, апикальная поверхность макрохеты с тремя бугорками. A–C, E–F — отраженный/прошедший свет; D — конфокальный лазерный сканирующий микроскоп.

types of tactile hairs, is inherited from trigonotarbid and uraraneids, and represents an ancestral condition in Tetrapulmonata. In contrast, the simplified uniform setation of the pedipalpans appears, surprisingly, as a synapomorphy of this lineage. The further increase in diversity of setae in ‘true spiders’, in particular the appearance of chemosensory setae, represents a synapomorphy of the order Aranei, separating it from chimerarachnids.

### 2.3.3. Tarsal (apotele) structures

The tarsi of *Chimerarachne* end in a set of paired major claws and a median minor claw (superior tarsal claws and inferior tarsal claw by Griswold *et al.* [2005]), all gently curved and strongly combed (pectinate), and an anteriorly directed, spatulate appendage of the empod-

dium — ‘pseudopulvillus’ (Figs 3C–D, 12A–F; Wang *et al.* [2018: figs 3i–j, 4c–d]).

#### 2.3.3.1. Tarsal claws

The combed claws appear to be an undoubted synapomorphy of *Chimerarachne* and Aranei, including the basalmost lineage of the latter: Liphistiomorphae [Foelix, 2011: fig. 1.6a; Wunderlich, 2017: figs 9, 12]. In all extant arachnid orders [Van der Hammen, 1989], including their extinct members (e.g., Wunderlich [2015]), the claws are smooth. Smooth claws are a diagnostic character of the order Trigonotarbida [Shear *et al.*, 1987: figs 48, 87; Selden *et al.*, 1991: 255].

These smooth claws are occasionally provided with additional small denticles, as in Opiliones–Laniatores

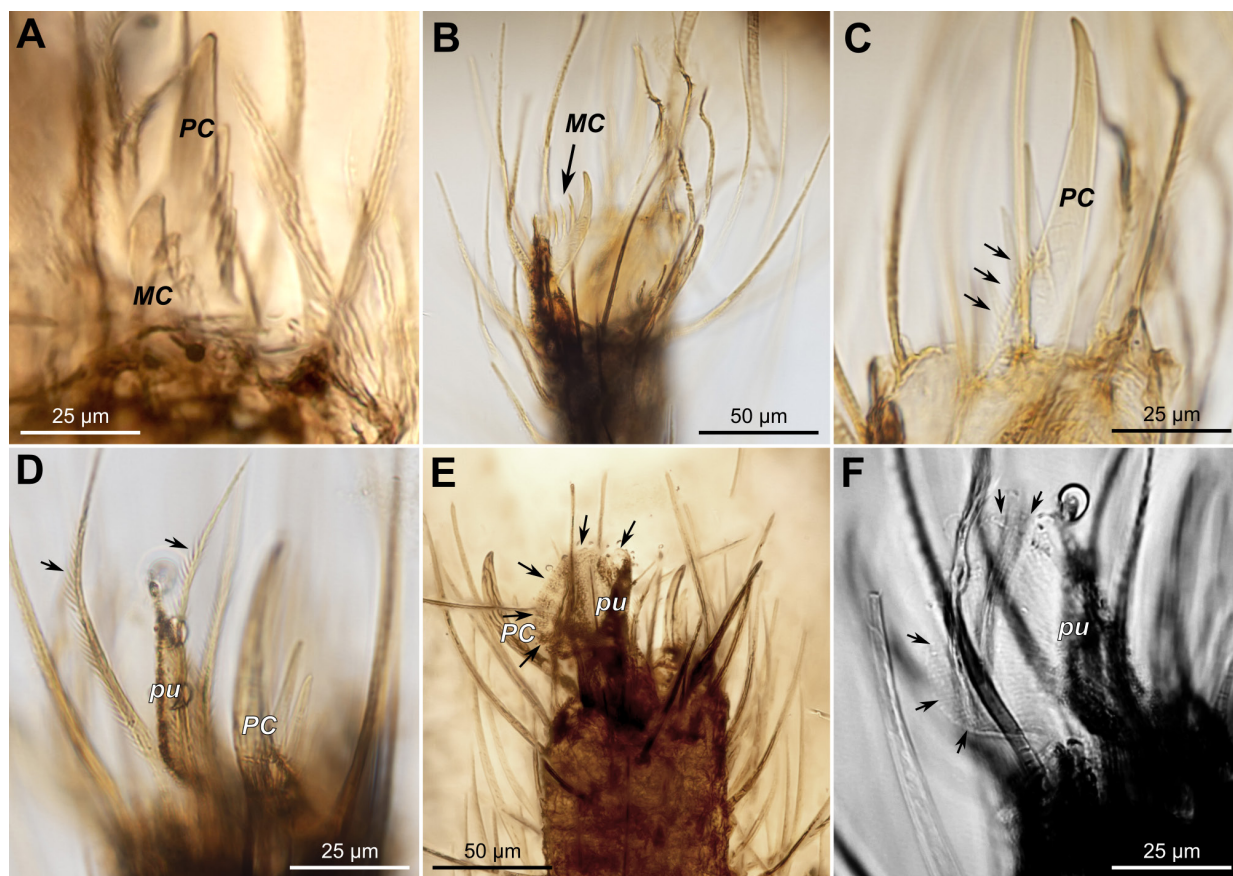


Fig. 12. Tarsus of *Chimerarachne* cf. *patrickmueller*: A — tarsus II, focused on claws (*pc*, one of the paired claws; *mc*, medial claw); B — tarsus III, focused on medial claw; note the bifurcate ventral spine (arrow); C — the same tarsus III, focused on the paired claw; note the fine serration or microtrichia along the side of the claw (arrows) in addition to three ventral spines; D — tarsus IV, focused on the pseudopulvillus and serrate accessory setae (arrows); E — tarsus III, focused on pseudopulvillus; arrows point to the lobe of the pseudopulvillus; F — tarsus IV, focused on the transparent thin lobe of the pseudopulvillus (arrows). A–E — reflected/transmitted light; F — CLSM.

Рис. 12. Тарзус *Chimerarachne* cf. *patrickmueller*: A — тарзус II, сфокусировано на коготках (*pc*, один из парных коготков; *mc*, срединный коготок); B — тарзус III, сфокусировано на срединном коготке, обратите внимание на раздвоенную вентральную хету (стрелка); C — тот же тарзус III, сфокусировано на парном коготке, обратите внимание на тонкую зазубренность или микротрихии вдоль боковой стороны коготка (стрелки) в дополнение к трем вентральным хетам; D — тарзус IV, сфокусировано на псевдопульвилле и зазубренных дополнительных хетах (стрелки); E — тарзус III, сфокусировано на псевдопульвилле, стрелки указывают на лопасть псевдопульвиллы; F — тарзус IV, сфокусировано на прозрачной тонкой лопасти псевдопульвиллы (стрелки). A–E — отраженный/прошедший свет; F — конфокальный лазерный сканирующий микроскоп.

[Wolff, 2015: fig. 2.10A; Ramin *et al.*, 2016: fig. 2A] and oribatid mites [Pfungstl, 2023: figs 11d, 13f], or with a ventral row of microsetae, as in several unrelated families of trombidiform mites [Walter *et al.*, 2009: figs 13.1E–F, 13.19A–D, 13.56D]. However, all of these structures are sharply distinct from the combed claws of chimerarachnids and spiders.

The tarsal claws of the uraraneid *Attercopus fimbriunguis* [Shear *et al.*, 1987], which possesses ‘proto-spinnerets’ (see below), are of particular interest. They cannot be referred to as combed, but they have a fimbriate structure composed of fine cuticular extensions (Fig. 13A–C; Shear *et al.* [1987: figs 138–139]). These fimbriate claws gave the species its name and were one of the reasons for excluding *Attercopus* from Trigonotarbida, where it was originally placed [Shear *et al.*, 1987: 65; Selden *et al.*, 1991: 255]. It should be noted that the combed *Chimerarachne* claws are provided, besides large

teeth, a ventrolateral fine serration or microtrichia along the side of the claw (Fig. 13C) similar to the *Attercopus* ones (cf. Fig. 13A–B; Shear *et al.* [1987: fig. 139]). So, a dentation on the claws of chimerarachnids and spiders could have occurred in parallel with the *Attercopus* fimbriate structure.

To test the hypothesis on some correlation/connection of tarsal claws shape with the spinning activity, let us consider the tarsi of Tetranychidae, or spider mites—the only group of arachnids besides spiders that may spin protective silk webs. Several trombidiform lineages possess a row of microsetae on the ventral surface of the tarsal claws (see above), and it is in tetranychids that this structure reaches its highest degree of development. Approximately a dozen long and stout microsetae, termed ‘tenent hairs’, form a comb superficially similar to the pectinated claws of some spiders [Foelix, 2011: fig. 1.6b]. It should be emphasized that this comb-shaped structure

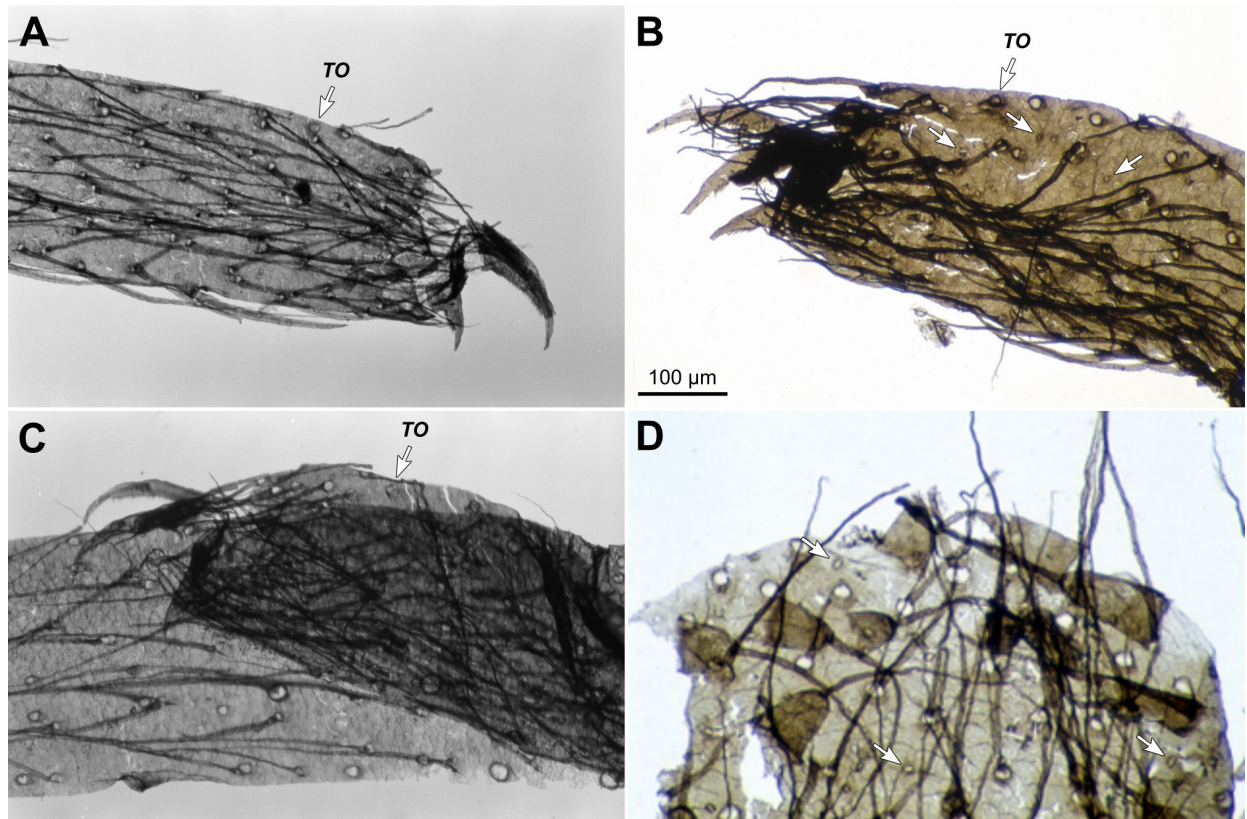


Fig. 13. Morphology of uraneid *Attercopus fimbriunguis*: A — tarsus: setation, serrate macroseta, tarsal process, tarsal organ, and arrangement of paired and median fimbriate claws (specimen 334.1 a.4.), x 165; B — tarsus: setation, serrate macroseta and tarsal organ (arrows — slit-like gland openings) (specimen SM 1-11-5.); C — tarsus: claw fimbriae and tarsal organ (specimen 411.02.12M.6.), x 154. D — piece of cuticle from corner of opisthosomal ventral plate showing setae and spigots (arrows — slit-like gland openings) (specimen SM 1.11.4.). Abbreviations: TO — tarsal organ.

Рис. 13. Морфология уранеиды *Attercopus fimbriunguis*: A — тарзус: хеты, зазубренные макрохеты, тарзальный отросток, тарзальный орган и расположение парных и срединного бахромчатых коготков (экземпляр 334.1 a.4.), x 165; B — тарзус: хеты, зазубренные макрохеты и тарзальный орган (стрелки — щелевидные отверстия желез) (экземпляр SM 1-11-5.); C — тарзус: бахромчатые коготки и тарзальный орган (экземпляр 411.02.12M.6.), x 154. D — фрагмент кутикулы из угла вентральной пластинки опистосомы, показывающий хеты и спиготы (стрелки — щелевидные отверстия желез) (экземпляр SM 1.11.4.). Сокращения: TO — тарзальный орган.

appears in tetranychids in at least two different ways: either directly on the claws [Walter *et al.*, 2009: fig. 13.74F] or as a specialized outgrowth of the empodium [Walter *et al.*, 2009: fig. 13.74E].

Therefore, it seems that if an arachnid lineage develops spinning activity, a comb-shaped tarsal structure tends to evolve as well. Moreover, such comb-shaped structures have arisen convergently at least three times: once in the ‘chimerarachnid + araneid lineage’ and twice within Tetranychidae. The uraneid *Attercopus*, which possesses both a spinning apparatus *in statu nascendi* and combed claws *in statu nascendi* (see above), can be recognized as an initial point of this evolutionary trend.

It should be noted, however, that the functional basis of this correlation is not entirely clear. In spiders, only the median (inferior) claw with the ‘serrated accessory setae’ (see below) interact directly with a silk thread, whereas the paired (superior) combed claws are not typically involved in seizing or grasping threads [Foelix, 2011; Eberhard, 2020]. The observations on the filistatid *Kukulcania hibernalis* (Hentz, 1842) demonstrate that web

lines are sometimes snagged on the teeth of paired claws [Eberhard, 2020: fig. 2.18g], but such events, at least in *Kukulcania*, seem to be incidental and occasional rather than the rule (Eberhard, pers. comm.).

Nevertheless, the interaction between combed claws with web lines may represent a relict behavior of basal spider lineages, which had yet not developed ‘serrated accessory setae’ (see below) as, for example, filistatids. In this scenario, the notches between the teeth of combed claws can perform a function analogous to the slits of belay devices for climbing, as the ‘Sticht belay plate’ and its derivatives.

### 2.3.3.2. Serrate accessory claw setae, SAS

“Serrate accessory claw setae <...> Many three clawed spiders that hang beneath webs have modified setae beneath the STC [superior tarsal claw] and near the ITC [inferior tarsal claw]. These setae are serrate along the lower margin, and may be flattened. They may function to grasp and release the silken line (see Foelix [2011: fig. 2.12b]; Eberhard [2020: fig. 2.16]), and for this

reason are sometimes called “false claws.” [Griswold *et al.*, 2005: 49].

SAS are absent in the Liphistiomorphae and Mygalomorphae [Foelix *et al.*, 2010: figs 8 and 11, respectively] and represent a synapomorphy of Araneomorphae. They appear in the basal araneomorph lineage ‘hypochiloids’, but are absent in the basalmost Hypochilidae [Griswold *et al.*, 2005: figs 133A–D and 132A, respectively]. Interestingly, SAS persist in some webless hunters, such as Archaeidae C.L. Koch et Berendt, 1854, but have been lost in some groups that hang beneath webs, such as Stiphidiidae Dalmat, 1917 [Griswold *et al.*, 2005: figs 134F, 132B, respectively].

The origin of SAS may be traced in Filistatidae — the other basal araneomorph lineage. In the majority of filistatid genera, evenly pubescent ‘ciliated setae’ accompany claws instead of the strongly ventrally serrated SAS (e.g., Magalhaes, Ramírez [2017: fig. 6D]). However, at least in *Kukulcania*, this even pubescence is replaced on the ventral surface of the seta by a row of small denticles, which appears to correspond to the serration of SAS [Magalhaes, Ramírez, 2019: fig. 13D]. Ciliated setae, instead of serrated SAS, are retained in several unrelated araneomorph lineages, such as Cycloctenidae Simon, 1898 [Ramírez, 2014: fig. 62A].

The tarsi of *Chimerarachne* lack SAS but possess several distinctive ciliated setae (Fig. 12D). These ciliated setae are slenderer than those in araneomorphs, for instance in filistatids, but they may be considered, with some reservations, as a precursor to the latter, and, subsequently, the SAS. Their presence indirectly indicates a well-developed spinning activity in chimerarachnids.

### 2.3.3.3. ‘Pseudopulvillus’

The spatulate empodium appendage was referred to by Wang *et al.* [2018] as a ‘pulvillus’. However, Selden [2021] preferred Wunderlich’s [2017: 91] term ‘pseudopulvillus’, because a ‘pulvillus’ in the generally accepted sense is a fleshy pad outgrowth of the empodium, which replaces the median claw (‘empodial claw’) in Amblypygi (Fig. 7B) and some other arachnids [Dunlop, 2002].

The function of this structure remains unknown. The morphology of the pseudopulvilli appears to differ among *Chimerarachne* species and may therefore represent a species-specific character (cf. Figs 3C–D and 12D–F).

Pseudopulvilli were recorded and figured in several liphistiomorph spider fossils, in both amber [Wunderlich, 2017: figs 16, 19, 21] and imprint [Selden, 2021: fig. 14E–F] preservation. Selden [2021: 336] concluded: “Interestingly, tarsi of the spider-relative *Chimerarachne* bear elongate, toothed, paired claws, a toothed median claw, and a spatulate structure (called a pulvillus by Wang *et al.*, 2018). <...> The tarsal structures of [extinct liphistiomorph genera] *Geralycosa*, *Parvithela*, *Pulvillothela*, and *Chimerarachne* are probably homologous and, because of their presence in *Chimerarachne*, are likely plesiomorphic for Araneae.”

Pseudopulvilli are absent both in Trigonotarbita and in all Pedipalpi, and are a synapomorphy of the

chimerarachnids and ‘true spiders’. They were later lost in more advanced spider lineages, including the extant liphistiomorphs, Liphistiidae [Foelix, 2011: fig. 1.6a]. The homology of pseudopulvilli with the tarsal structures recognized by Labarque *et al.* [2017] in extant spiders remains unclear.

### 2.3.3.4. The tarsal process

In some arachnid orders tarsi are provided with a particular structure of unknown function named by Wolff [2015] the ‘tarsal process’: an anteriorly directed protuberance above the paired claws, equipped with a long stout macroseta. This structure is a synapomorphy of the order Amblypygi (Fig. 7B; Dunlop [2002: fig. 2c]; Wolff [2015: fig. 3.6. B–E]), and has been recorded in Trigonotarbita [Shear *et al.*, 1987: figs 51, 109], Uraraneida (Fig. 13A–C; Selden *et al.* [1991: plate 5, figs 1–3]), as well as in the non-tetrapulmonate groups Scorpiones [Wolff, 2015: fig. 3.2. C, E] and Opiliones–Laniatores [Ramin *et al.*, 2016: fig. 2A].

In *Chimerarachne* (Fig. 10A–B) and Aranei the ‘tarsal process’ is absent. Tarsi of the fossil amber liphistiomorph *Burmathele* Wunderlich, 2017 are provided with a distinct anteriorly directed outgrowth [Wunderlich, 2017: fig. 11]. However, this outgrowth bears several setae instead of the sole robust terminal macroseta, and we do not consider it homologous to the ‘tarsal process’.

Two interpretations may be proposed: (1) the ‘tarsal process’ evolved as parallel autapomorphies in the listed arachnid lineages; (2) the ‘tarsal process’ is the plesiomorphic condition that was independently lost in the remaining arachnid lineages. The latter hypothesis seems more convincing.

First, this structure is present in scorpions and harvestmen; therefore, it must have arisen at the pre-tetrapulmonate stage of arachnid evolution. Second, within Pedipalpi, the evolutionary sequence can be traced from the process-bearing Amblypygi to Schizomida, which completely lack the process [Ruiz, Valente, 2023: fig. 14D], via Thelyphonida, in which a robust macrochaeta sits on a slightly protruding tubercle (Fig. 7C; Wolff [2015: fig. 3.4.D]). During postembryonic development in thelyphonids, the initial tarsal process is lost at the protonymph stage [Wolff, 2015: 74]. In contrast, in Opiliones, a non-tetrapulmonate order, the tarsal process may grow gradually with each molt, and is fully developed only in adults [Ramin *et al.*, 2016: 331].

Therefore, the absence of the tarsal process in *Chimerarachne* represents an apomorphic condition, as it is in Aranei. However, the loss of this structure may be not a synapomorphy of these two lineages, but rather a parallel autapomorphy of each.

### 2.3.4. Trichobothrial pattern

The trichobothrial pattern in *Chimerarachne* is represented by a single, extremely long trichobothrium on metatarsi I–IV (Figs 10A, 15A; Huang *et al.* [2018: fig. 1e]).

Wang *et al.* [2018: 617] stated: “Trichobothrium present on all metatarsi at the 0.6 position. Cluster of at least

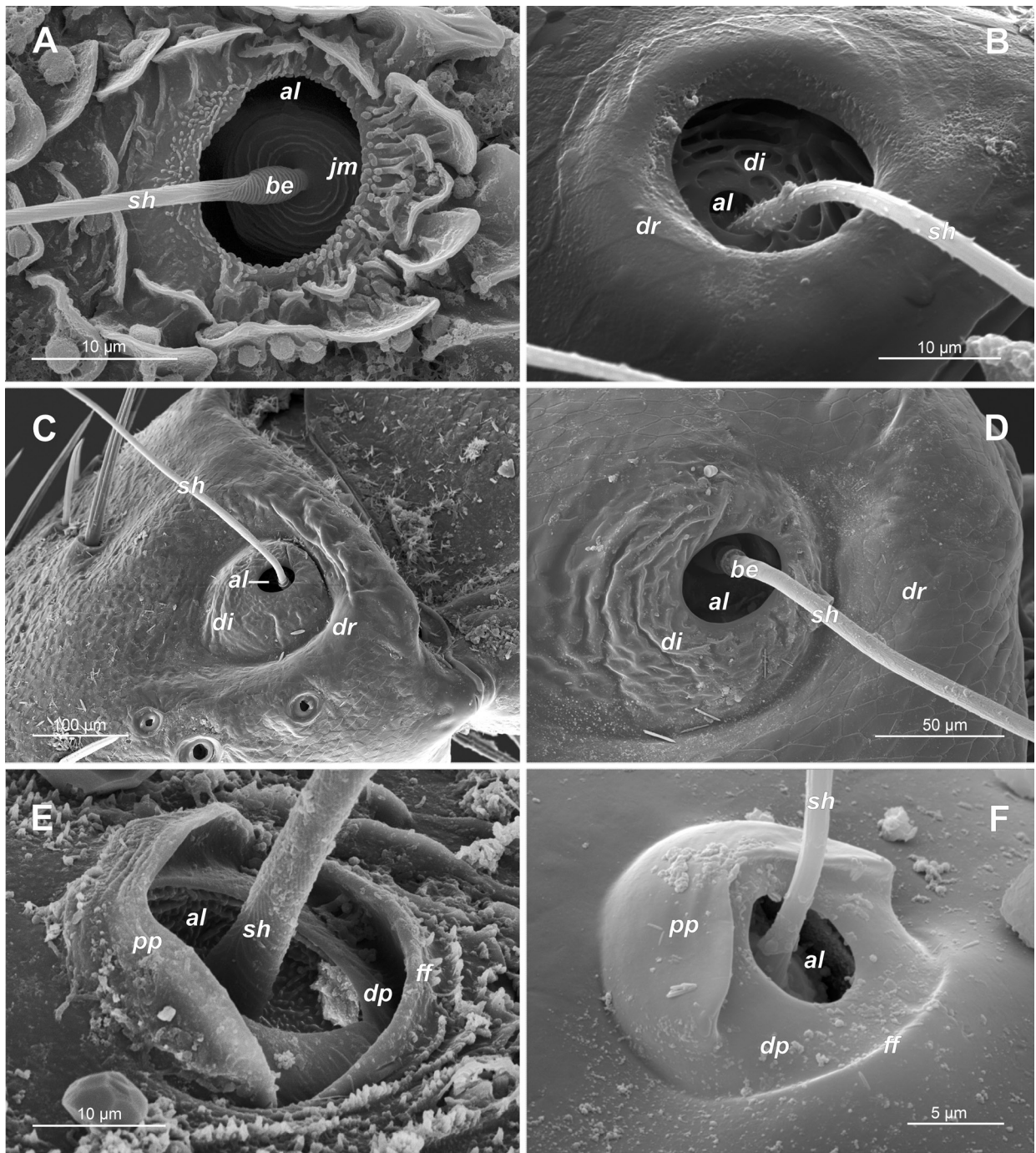


Fig. 14. Bothria of extant pedipalpians and spiders: cup-shaped, diaphragm-less (A), diaphragmed (B–D), and with transformed diaphragm and rim (E–F). A — *Charinus* sp. (Amblypygi), tibia II; B — *Trithyreus* (?) sp. (Schizomida), tibia II; C — *Thelyphonus* (?) sp. (Thelyphonida), tibia II; D — the same, enlarged; E — *Liphistius desultor* (Mesothelae), tibia III; F — *Chilenodes australis* (Araneomorphae), tibia III. Abbreviations: *al* — alveolus; *be* — basal expansion of setal shaft; *di* — diaphragm; *dp* — distal plate (homologue of diaphragm); *dr* — doughnut-shape rim; *ff* — frontal fold (homologue of anterior portion of rim); *jm* — joint membrane; *pp* — proximal plate (homologue of posterior portion of rim); *sh* — setal shaft.

Рис. 14. Ботрии современных педипальпий и пауков: чашевидные, без диафрагмы (А), с диафрагмой (В–Д) и с трансформированной диафрагмой и ободком (Е–Ф). А — *Charinus* sp. (Amblypygi), голень II; В — *Trithyreus* (?) sp. (Schizomida), голень II; С — *Thelyphonus* (?) sp. (Thelyphonida), голень II; Д — то же, увеличено; Е — *Liphistius desultor* (Mesothelae), голень III; Ф — *Chilenodes australis* (Araneomorphae), голень III. Сокращения: *al* — альвеола; *be* — базальное расширение стержня щетинки; *di* — диафрагма; *dp* — дистальная пластинка (гомолог диафрагмы); *dr* — ободок в форме пончика; *ff* — фронтальная складка (гомолог передней части ободка); *jm* — соединительная мембрана; *pp* — проксимальная пластинка (гомолог задней части ободка); *sh* — стержень хеты.

five trichobothria at the distal end of at least tarsus II.” However, the presence of tarsal trichobothria in chimerarachnids was later refuted by Wunderlich [2023: 166], and we concur with this assessment. Evidently, Wang *et al.* [2018: fig. 4b] misidentified non-homologous tarsal setae of type 1 — which are protruding and slightly curved (Fig. 10A–B; Wunderlich [2023: photo 31]) — as trichobothria. The true trichobothrial shaft is straight and, as far as is known, never curved.

Wunderlich [2023: 166] listed the absence of tarsal trichobothria and the reduction of other trichobothria to a single, extremely long metatarsal one as apomorphies of chimerarachnids. This interpretation closely corresponds to Shultz’s [1990: 21] description: “A unique pattern of trichobothria occurs on the walking legs of Thelyphonida and Schizomida [2-1-1 terminal tibial trichobothria] <...>. Similar trichobothria are present in certain Trigonotarbita [Shear *et al.*, 1987].” Fossil thelyphonids exhibit the same pattern [Cai, Huang, 2017: 101]. In contrast, in the remaining tetrapulmonate orders (Aranei and Amblypygi) trichobothrial patterns are sharply dissimilar, with numerous trichobothria (e.g., Eskov *et al.* [2024]).

A pattern with a single, extremely long (*c.* five diameters of the joint) distal trichobothrium per leg is shared by *Chimerarachne* and *Uropygi s.l.* (Thelyphonida + Schizomida), as is the similar bothrial morphology in these groups (see below). However, this trichobothrium is located on the metatarsi in chimerarachnids, *versus* on the tibiae in uropygids. Thus, the question arises: are these patterns homologous, or merely superficially similar?

Let us consider the trichobothrial patterns in the basalmost tetrapulmonates, the Trigonotarbita, mentioned in this context by Shultz [1990: 21]. The reconstruction of *Gelasinotarbus bonamoae* [Shear *et al.*, 1987: fig. 94] depicts a single trichobothrium per leg, all located on the tibia; however, the actual situation is considerably more complex.

The main difficulty is that the Devonian trigonotarbitids from Gilboa were recovered from the siltstone matrix by maceration with hydrofluoric acid (HF), resulting in specimens that are highly fragmented, although their cuticular microstructures are perfectly preserved. Six complete legs, attributed to two trigonotarbitid species, are available, but only two of them are attached to a prosoma in a certain position [Shear *et al.*, 1987: fig. 91]. Because the arrangement of trichobothria varies among these legs, the lack of information on the numbering of detached legs renders any conclusion regarding the trigonotarbitid trichobothrial pattern preliminary.

Trichobothria were recorded and figured on the six complete legs of four specimens belonging to the two trigonotarbitid species [Shear *et al.*, 1987].

*Gelasinotarbus bonamoae* Shear, Selden et Rolfe, 1987:

Specimen # 411-7-AR74(a): legs II and III attached to a prosoma, both with a single trichobothrium on the tibiae [Shear *et al.*, 1987: figs 91, 111, 112];

Specimen # 411-7-AR74(b): detached, unnumbered leg, with paired trichobothria on the metatarsus [Shear *et al.*, 1987: figs 105, 106];

Specimen # 2002-6-AR7: detached, unnumbered leg, with a single trichobothrium on the metatarsus [Shear *et al.*, 1987: figs 108, 110];

In addition, specimen # 2002-12-AR28: fragment of a detached, unnumbered leg, probably a metatarsus, with paired trichobothria [Shear *et al.*, 1987: fig. 113].

*Gelasinotarbus bifidus* Shear, Selden et Rolfe, 1987:

Specimen # 411-7-AR37: detached, unnumbered leg, with paired trichobothria on the tibia (Fig. 16C–D; Shear *et al.* [1987: figs 115, 116]), and a detached, unnumbered leg, with a single trichobothrium on the tibia (Fig. 16A–B; Shear *et al.* [1987: figs 117, 119, 120]).

Thus, three conclusions can be drawn with confidence:

(1) Only a single leg joint bears trichobothria in Trigonotarbita [Shear *et al.*, 1987: figs 105, 108, 115, 117].

(2) This joint may be the tibia or metatarsus, the trichobothria may be paired or single, and all four possible combinations are represented: (a) tibia with a single trichobothrium (Fig. 16A–B; Shear *et al.* [1987: figs 111, 112, 119, 120]); (b) tibia with paired trichobothria (Fig. 16C–D; Shear *et al.* [1987: fig. 116]); (c) metatarsus with a single trichobothrium [Shear *et al.*, 1987: fig. 110]; (d) metatarsus with paired trichobothria [Shear *et al.*, 1987: figs 106, 113].

(3) All single trichobothria are placed at the terminal end of a joint, whether tibia (Fig. 16A–B; Shear *et al.* [1987: figs 111, 112, 119, 120]) or metatarsus [Shear *et al.*, 1987: fig. 110], whereas all paired trichobothria are placed more or less longitudinally in the distal third of a joint, whether tibia (Fig. 16C–D; Shear *et al.* [1987: fig. 116]) or metatarsus [Shear *et al.*, 1987: figs 106, 113].

The exact and complete trichobothrial arrangement in Trigonotarbita cannot yet be reconstructed owing to the absence of sufficiently many legs attached to the prosoma and therefore confidently numbered. Nevertheless, the patterns observed in chimerarachnids (all metatarsi with a single trichobothrium) and *Uropygi s.l.* (tibiae with 2-1-1 trichobothria) appear to represent symplesiomorphies shared with the basalmost tetrapulmonate lineage, Trigonotarbita (one or two trichobothria on either the tibia or metatarsus).

Therefore, the multiplication of trichobothria in Amblypygi and Aranei should be considered the autapomorphies of these lineages. This conclusion is supported by the multiplication of trichobothria during the postembryonic development of liphistiomorph spiders. Their number increases with each of the eight molts, from a single one on the metatarsus in nymphal stage I up to 6–7 on the tarsus and 8–9 on the metatarsus in the adult female [Haupt, 2003: fig. 33]. Amblypygi is the only tetrapulmonate order that has a trichobothrium on the patella (Fig. 8D), alongside with numerous irregularly arranged trichobothria on tibia.

The opposite evolutionary trend could be the loss of trichobothria in the uraraneid *Attercopus*: “A major surprise in the present study was to find no evidence of trichobothria on any of the leg segments” [Selden *et al.*, 1991: 256]. It was regarded as the *Attercopus* autapomorphy: “Somewhat worrisome, but a potential third autapomorphy, is the absence of trichobothria. It may be that

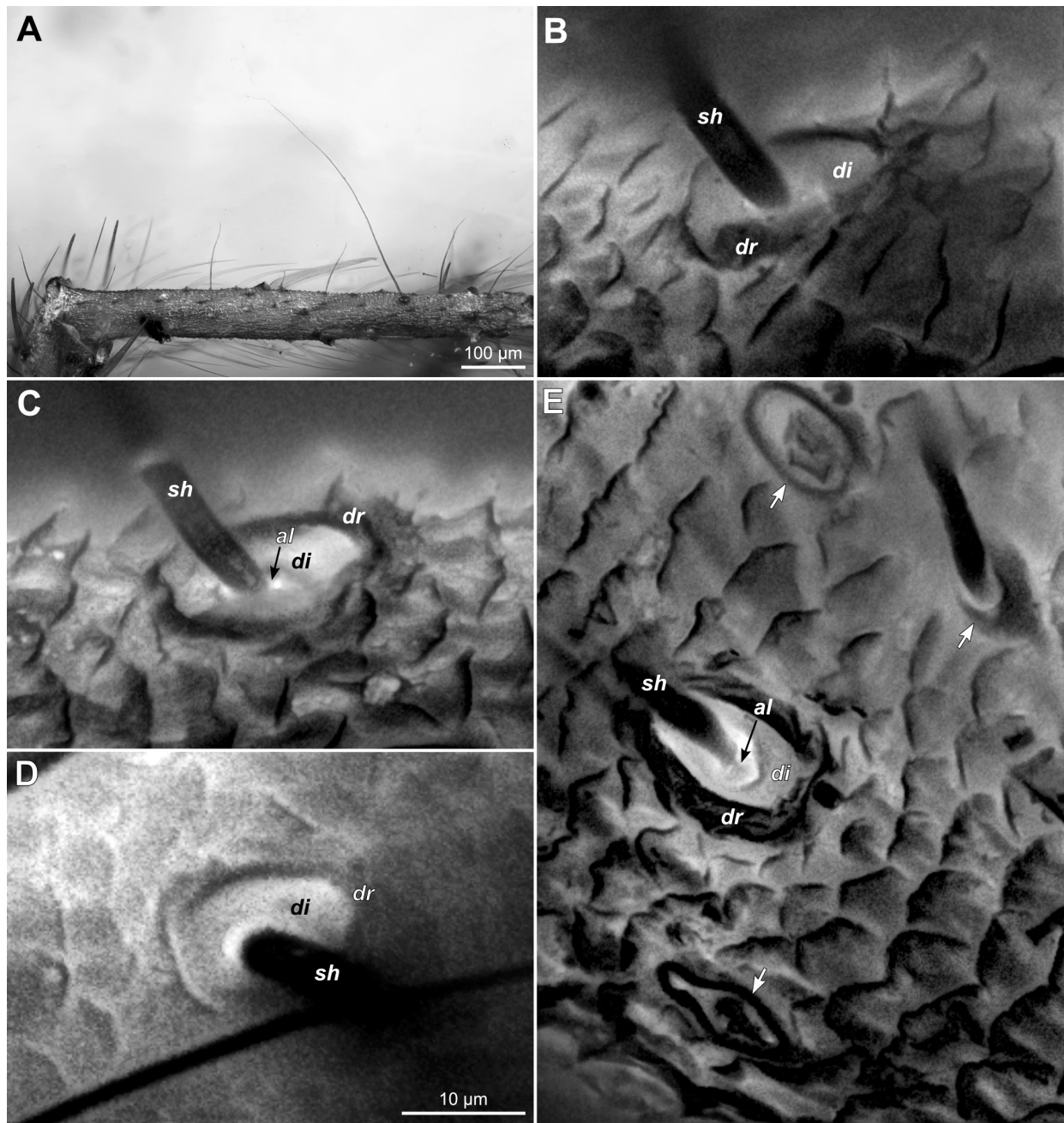


Fig. 15. Trichobothria and slit-like gland openings of *Chimerarachne* cf. *patrickmueller*: A — metatarsus III, trichobothrium; B — metatarsus III, bothrium; C — metatarsus IV, bothrium; D — metatarsus II, bothrium; E — metatarsus II, bothrium (arrows — ‘slit-like gland openings’ and setal socket). A — reflected/transmitted light; B–E — CLSM. Abbreviations: *al* — alveolus; *di* — diaphragm; *dr* — doughnut-shape rim; *sh* — setal shaft.

Рис. 15. Трихоботрии и щелевидные отверстия желез у *Chimerarachne* cf. *patrickmueller*: A — метатарзус III, трихоботрия; B — метатарзус III, ботрия; C — метатарзус IV, ботрия; D — метатарзус II, ботрия; E — метатарзус II, ботрия (стрелки — «щелевидные отверстия желез» и гнездо для хеты). A — отраженный/прошедший свет; B–E — конфокальный лазерный сканирующий микроскоп. Сокращения: *al* — альвеола; *di* — диафрагма; *dr* — ободок в форме пончика; *sh* — стержень хеты.

they are present and we have not found them, but given our close examination of the material, this is extremely unlikely” [Selden *et al.*, 1991: 255].

### 2.3.5. Trichobothrial bases (bothria)

Eskov *et al.* [2024: 108] emphasized that the bothria of schizomids and thelyphonids differ drastically from those

of amblypygians and spiders, while being unexpectedly similar to those of Devonian trigonotarbid. They further noted: “Unfortunately, nothing is known about the bothria of *Chimerarachnida* <...>, whereas it should be an important piece of information, which would clarify the relationships of these controversial arachnids with other tetrapulmonate lineages”.

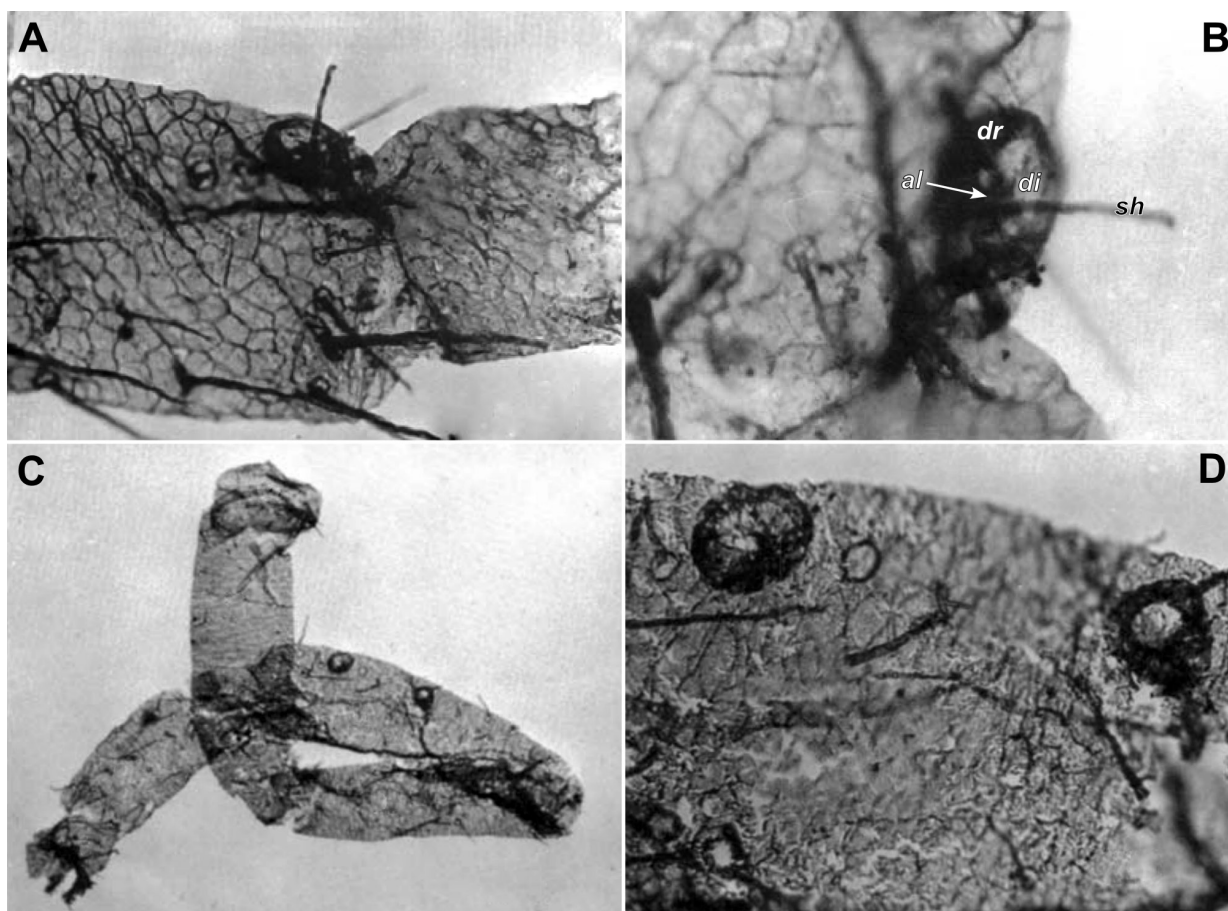


Fig. 16. Trichobothrial bases of trigonotarbid *Gelasinotarbus bifidus* (A–D): A — unnumbered leg, with a single trichobothrium on the tibia; B — the same, enlarged; C — paired trichobothria on the tibia (specimen 411-7-AR37); D — the same, enlarged. Abbreviations: *al* — alveolus; *di* — diaphragm; *dr* — doughnut-shape rim; *sh* — setal shaft.

Рис. 16. Базы трихоботрий тригонотарбиды *Gelasinotarbus bifidus* (A–D): A — нога без номера, с одной трихоботрией на голени; B — то же, увеличено; C — парные трихоботрии на голени (экземпляр 411-7-AR37); D — то же, увеличено. Сокращения: *al* — альвеола; *di* — диафрагма; *dr* — ободок в форме пончика; *sh* — стержень хеты.

The structure of the bothria of *Chimerarachne*, studied here for the first time (Fig. 15B–E), proves to be shared with *Uropygi s.l.* (Thelyphonida + Schizomida), on the one hand, and with Trigonotarbida, on the other. This result is not surprising, given the existing data on the unity of the trichobothrial pattern in these tetrapulmonate lineages (see above).

The typical arachnid bothrium is a cup-like setal socket, the bottom of which is lined by a membranous, wrinkled cuticle ('joint membrane' *sensu* Messlinger [1987: fig. 15]). Such a simple cup-shaped bothrial structure is characteristic of all trichobothria-bearing non-tetrapulmonate arachnids: Scorpiones, Pseudoscorpiones, Palpigradi, and Acari [Eskov *et al.*, 2024: fig. 7A–F].

In the clade Tetrapulmonata, bothrial structures are much more diverse. Only Amblypygi retain (or perhaps recapitulate) the ancestral state with simple cup-shaped bothria (Fig. 14A; Platnick, Gertsch [1976: fig. 7]). In the remaining three extant tetrapulmonate orders, i.e. Aranei, Thelyphonida, and Schizomida, the bothria are modified in various ways.

The structure of spider trichobothria and the names of their parts are given here following Ramírez [2014: 122–125] and Eskov & Marusik [2024a: figs 3A–F, 4A–F]. The initial bothrial type in Aranei appears in its basal-most lineage, Mesothelae, as two short crescentic outgrowths of the bothrial cup margin (anterior and posterior), framing a horizontal diaphragm with a rounded opening for the setal shaft, which overlaps the central alveolus of the bothrium (Fig. 14E). This diaphragm (the 'dome' of Platnick & Gertsch [1976]) was recognized by Eskov *et al.* [2024: 105] as homologous to the bothrial "distal plate" of Opisthothelae, which also has a rounded opening for the shaft (Fig. 14F; Ramírez [2014: fig. 84D]).

Trichobothria of Schizomida and Thelyphonida appear at first glance to be sharply different (cf. Fig. 14B and Fig. 14C–D, respectively). However, the bothrial ground plan in both lineages of *Uropygi s.l.* is, in fact, the same; the differences result from the development of gigantic trichobothria in whip scorpions, which reach approximately 200  $\mu\text{m}$  in bothrial diameter (*versus* the typical arachnid bothrial diameter of 5–20  $\mu\text{m}$ ) and about

2 mm in shaft length. Due to this, Eskov *et al.* [2024: 105] confused the dome-shaped diaphragm of the thelyphonid bothria, which reach *ca.* 100 µm in diameter (Fig. 14D), with the bothrium as a whole (Fig. 14C).

The uropygid bothrium is an alveolus overlapped by a horizontal diaphragm with a rounded opening for the setal shaft and bordered by a doughnut-shape rim. The doughnut-shape rim is circular and uniform in Schizomida (Fig. 14B; Eskov *et al.* [2024: fig. 8A]), while in Thelyphonida it is suboval and reduced posteriorly (Fig. 14C). The diaphragm is flattened and honeycomb-sculptured in Schizomida (Fig. 14B; Ruiz, Valente [2023: fig. 14B]), while in Thelyphonida it is dome-convex and rugose (Fig. 14D).

The diaphragms of uropygids (Fig. 14B–D) and liphistiomorph spiders (Fig. 14E; Eskov *et al.* [2024: fig. 5A–F]) differ in surface sculpture and in the size of the opening, but are similar in general structure: in both cases, the basal extension of the setal shaft lies below the diaphragm plane, at the depth of the alveolus. As regards the origin of this structure, the concentrically arranged ‘bothrial lamellae’ of Scorpiones [Messlinger, 1987: figs 2–4, 7, 15; Eskov *et al.*, 2024: fig. 7A] were proposed by Eskov *et al.* [2024: 106] as probable homologues.

“One characteristic feature of scorpion trichobothria is the lamellated interior wall of the bothrium. The innermost lamellae which surround the basal opening like a collar <...>, are supposed to limit (unphysiological) movements of the hair” [Messlinger, 1987: 55]. The tetrapulmonate diaphragm appears to have arisen as a broadened ancestral bothrial lamella — not the innermost one, but rather one of the outer lamellae.

All these features are clearly observed in the bothria of *Chimerarachne*: they are suboval, encircled by a rim, and possess a flattened central diaphragm with a rounded opening for the setal shaft (Fig. 15B–E). The same features can be recognized in the bothria of Devonian Trigonotarbid (Fig. 16A–D). In ‘true spiders’, the diaphragm is transformed into the bothrial ‘distal plate’, whereas the posterior and anterior portions of the rim correspond to the ‘proximal plate’ and ‘frontal fold’, respectively (Fig. 14E–F); this complication is an undoubted synapomorphy of the order Aranei.

Therefore, the development of a bothrial diaphragm overlapping the alveolus of a primary cup-shaped setal socket should be recognized as a synapomorphy of Tetrapulmonata. The ancestral bothria, observed in trigonotarbids, were directly inherited by both chimerarachnids and uropygids, along with the ancestral trichobothrial pattern (see above). In the remaining tetrapulmonate lineages, the ancestral bothria were modified: in ‘true spiders’ they became highly complex, whereas in amblypygians they were secondarily simplified to the pre-tetrapulmonate, diaphragm-less state. In addition, the basal uraraneid *Attercopus*, as stated by Selden *et al.* [1991: 256], completely lost trichobothria.

### 2.3.6. Lyriform organs

‘Lyriform’ or ‘compound slit sense organs’ are readily recognized by the very close, parallel, side-by-side

arrangement of two or more slits. Surprisingly, these mechanoreceptors have not previously been recorded in chimerarachnids. We discovered at least two distinct lyriform organs (LOs) on the legs of *Chimerarachne*, located laterally on the patella and dorsally at the distal end of the metatarsus (Figs 9C–D and 17A–B).

The metatarsal type of LO has been distinguished as a special case, termed the “metatarsal vibration sense organ” (VSO) [Ramírez, 2014: 77]. “In all spiders, the metatarsal organ is situated behind a cuticular ridge at the distal end of the metatarsus. Two features distinguish it from all other lyriform organs and slit sensilla: its position in the middle of the dorsal surface and the orientation of its slits, which are perpendicular to the long axis of the leg” [Barth, 2002: 73].

The lateral LO on the *Chimerarachne* patella consists of a pair of lyriform patches, the slit sensillae of which are oriented at an angle to each other. Such bipartite patellar LOs are otherwise known only in Aranei (Fig. 8A–C; Kropf [1998: fig. 12]; Ramírez [2014: fig. 45E]). “The retrolateral distal margin of the patella is indented in an unsclerotized area [‘CZY’], leading to one or two closely grouped lyriform organs” [Ramírez, 2014: 75].

Leg slit sense organs in Aranei differ from those of all other arachnid orders in the proportions of single slits, slit groups, and lyriform organs. “Whereas in the spiders there are 15 lyriform organs on each leg, in the other arachnids there are none, or only one or two. Where spiders have lyriform organs, the scorpion and whip scorpion have groups of single slits” [Barth, 2002: 41]. Barth & Stagl [1976] reported two LOs in Amblypygi, both located on the trochanter, and one LO in Thelyphonida, positioned retrolaterally on the metatarsus.

A single LO on the leg of Schizomida is of particular interest. It is located dorsally at the distal end of the metatarsus, in the same position as the VSO of Aranei. However, the slits of the schizomid LO are oriented parallel to the long axis of the joint, whereas those of the spider VSO are oriented perpendicular to it (Fig. 8F; Ruiz, Valente [2023: fig. 13B]). Thus, no extant arachnid order other than Aranei possesses a true VSO.

Various ‘true slit sense organs’ have been documented on different leg joints of the uraraneid *Attercopus*. “They may occur singly, at the distal end of the tarsus for example, in groups, such as those adjacent to the distal articulations of the femur, or in lyriform organs, examples of which can be seen at the distal ends of the patella, the tibia and the metatarsus” [Selden *et al.*, 1991: 257]. The distribution of LOs on the generalized leg of *Attercopus* is illustrated in the reconstruction by Selden *et al.* [1991: fig. 2].

The metatarsal LO of *Attercopus* [Selden *et al.*, 1991: figs 8C, 9A, 12D–F] is characterized by its dorsal position at the distal margin of the joint and by “crescentic slits arranged transverse to the long axis of the podomere” [Shear *et al.*, 1987: 63], both features being correctly recognized as diagnostic for the taxon. All joints except the metatarsi bear lateral LOs with slits oriented parallel to the long axis of the podomere: femur [Selden *et al.*, 1991: fig. 5A, D], patella [Selden *et al.*, 1991: figs 6C, E–F, 9B,

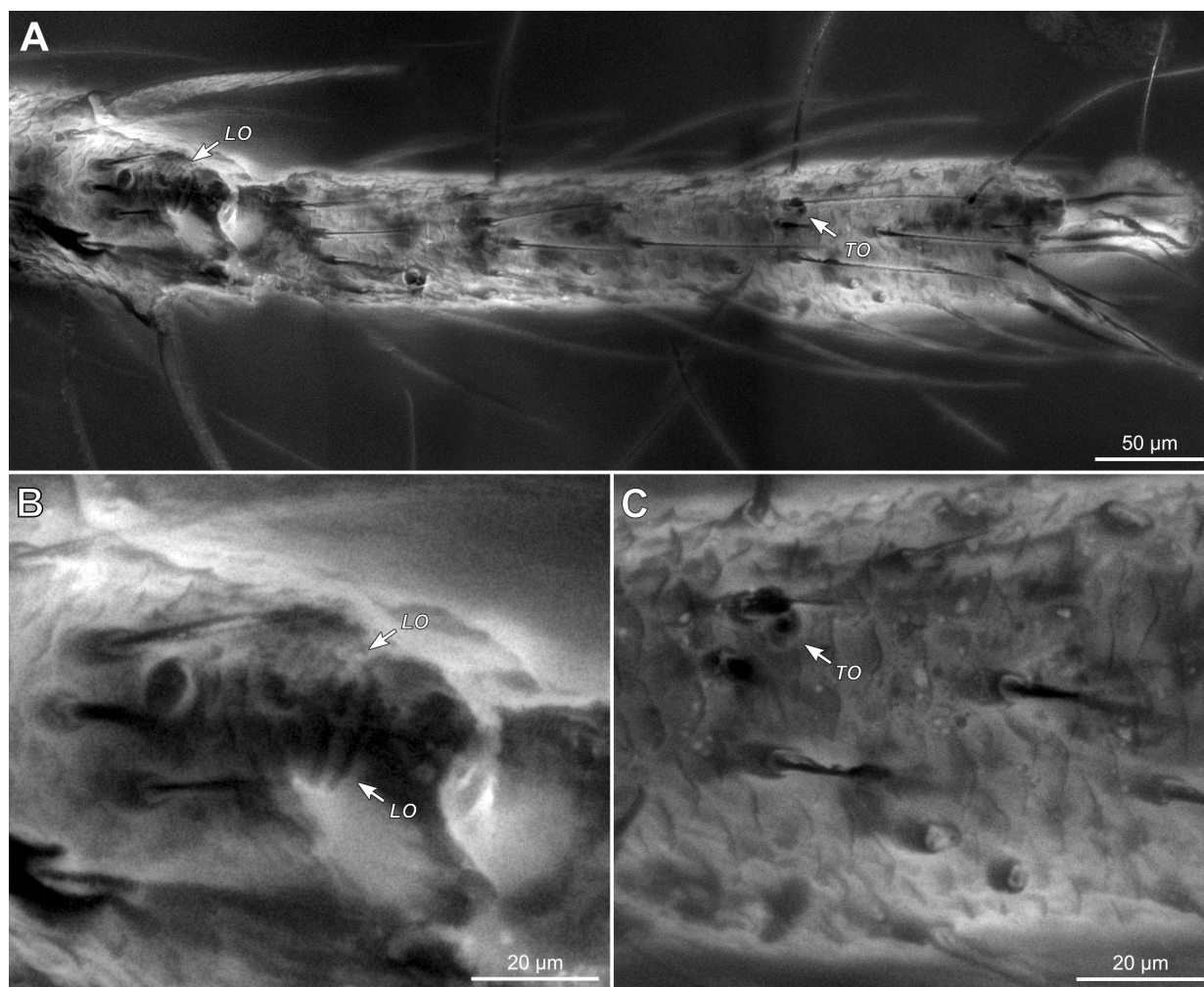


Fig. 17. Tarsal (TO) and lyriform (LO) organs of *Chimerarachne* cf. *patrickmueller*: A — end of metatarsus and tarsus III (arrows — lyriform VSO and tarsal organ); B — the same, enlarged (arrow — lyriform VSO); C — the same, enlarged (arrow — tarsal organ). A–C — CLSM.

Рис. 17. Тарзальные (TO) и лировидные (LO) органы *Chimerarachne* cf. *patrickmueller*: A — конец метатарзуса и тарзус III (стрелки — лировидный VSO и тарзальный орган); B — то же, увеличено (стрелка — лировидный VSO); C — то же, увеличено (стрелка — тарзальный орган). A–C — конфокальный лазерный сканирующий микроскоп.

12A–B], and tibia [Selden *et al.*, 1991: fig. 7A–B, E–F]. The patella is of particular interest, bearing three LOs, with slits oriented at angles to one another.

The uraraneid *Attercopus fimbriunguis* was initially described as Trigonotarbida [Shear *et al.*, 1987]. It was later temporarily relocated to Aranei [Selden *et al.*, 1991], and features of the LO were an important argument for this relocation: “It should also be recognized that <...> transversely oriented metatarsal lyriforms, and the presence of lyriforms on podomeres other than metatarsi, are probable autapomorphies of Araneae, joining the better known features of cheliceral poison glands, opisthosomal silk glands and spinnerets, and the palpal intromittent organ in mature males” [Selden *et al.*, 1991: 256]. Indeed, the metatarsal lyriforms of Trigonotarbida are oriented longitudinally rather transversely [Shear *et al.*, 1987: figs 46, 76].

Thus, there are three unique, apparently correlated, characters shared by *Attercopus*, *Chimerarachne*, and all ‘true spiders’: (1) the presence of several lateral LOs

on joints other than the metatarsi; (2) a dorso-distal VSO on the metatarsi with transversely oriented slits; (3) a patella with more than one LO, whose slits are oriented at an angle to each other. This triad should be regarded as synapomorphies of the Uraraneida + Aranei lineage.

The general trend toward the aggregation of individual slit sensilla into compound lyriform organs is much more clearly expressed in this lineage than in other arachnids, including the remaining Tetrapulmonata orders.

### 2.3.7. Tarsal organs

Tarsal organs (TOs) are hydrosensors located dorsally on each terminal segment (tarsus) of the spider leg and palp [Foelix, 2011]. These receptors have not been previously recorded in chimerarachnids; the “questionable tarsal organ” noted by Wunderlich [2023: fig. 22] is certainly not a TO. We have identified a TO on the tarsi of *Chimerarachne* in position 0.7 (Fig. 17A, C).

Tarsal organs of spiders were divided by Forster [1980] into two major types: ‘exposed TOs’, in which

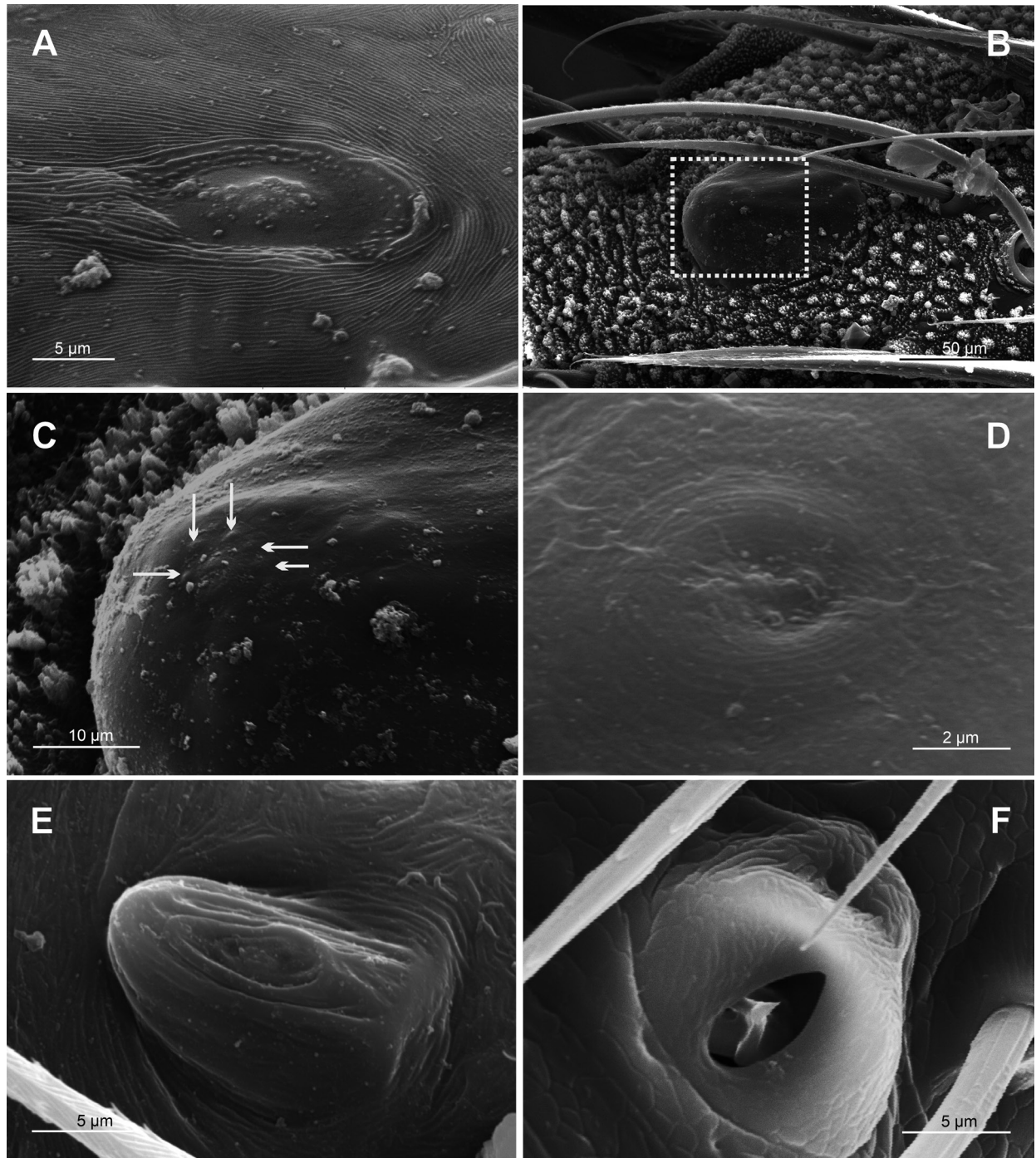


Fig. 18. Tarsal organs (TO) of extant spiders: exposed TO of the pit subtype (A), exposed TO of the lobulated subtype (B–E) and capsulated TO (F). A — *Austrochilus* sp. (Araneomorphae: 'Hypochoiloidea'), tarsus III; B — *Liphistius* sp. (Mesothelae), tarsus III (white box shown in more detail in C); C — the same, enlarged receptor area (arrows show receptor mounds); D — *Antrodiaetus montanus* (atypoid Mygalomorphae), tarsus III, encircled receptor area; E — *Microhexura montivaga* (non-atypoid Mygalomorphae), tarsus III; F — *Comaroma simoni* (Araneomorphae), tarsus II.

Рис. 18. Тарзальные органы (ТО) современных пауков: открытый ТО ямочного подтипа (А), открытый ТО выступающего подтипа (В–Е) и капсулированный ТО (F). А — *Austrochilus* sp. (Аранеоморфае: 'Гипохилоида'), тарзус III; В — *Liphistius* sp. (Мезотелает), тарзус III (белый прямоугольник показан более подробно на С); С — то же, увеличенная рецепторная область (стрелками показаны бугорки рецептора); D — *Antrodiaetus montanus* (атипоидные Мугаломорфае), тарзус III, рецепторная область околнурена; E — *Microhexura montivaga* (неатипоидные Мугаломорфае), тарзус III; F — *Comaroma simoni* (Аранеоморфае), тарзус II.

the receptors are directly exposed on the surface (Fig. 18A–E), and ‘capsulate TOs’, in which the receptors are protected by a domed cuticular hood with an aperture (Fig. 18F). This distinction is still widely accepted (e.g., Griswold *et al.* [2005: char. 2]). Capsulate TOs are restricted to more derived labidognathan groups (all Entelegynae and a few haplogyne families), whereas all basal spider lineages (Orthognatha and the majority of Haplogynae) possess various forms of exposed TOs.

The ‘pit tarsal organ’ (term of Foelix *et al.* [1975]) is a simple, shallow depression in which several low mounds on the floor indicate receptor nodes. This type of TO is found in all ‘hypochiloid’ families (Fig. 18A; Forster *et al.* [1987: figs 17–18, 99–102, 381–383]), as well as in several families of Haplogynae–Synspermiata [Forster, Platnick, 1985: figs 858–862].

As noted by Forster *et al.* [1987: 107–108]: “Outgroup comparison with the Amblypygi, which have similar tarsal organs [Forster, 1980: fig. 4; Forster *et al.*, 1987: fig. 378], suggests that this form of tarsal organ [the ‘pit TO’] is plesiomorphic for spiders as a whole. However, this hypothesis faces the difficulty that the liphistiids and some mygalomorphs possess an entirely different, smooth, lobulated organ instead”.

This alternative subtype of the exposed TO may be termed the ‘lobulated TO’. In this form, the low mounds indicating receptor nodes are situated not on the floor of a depression (as in the pit TO), but on the convex surface of a more or less prominent lobe. This subtype of exposed TO is characteristic of the basalmost spiders, the Orthognatha.

“A comparable structure [the ‘pit TO’] has not yet been located in the Orthognatha despite <...> intensive examination in recent years. By contrast, considering the Orthognatha as a whole, it would be logical to nominate the Liphistiid type of tarsal organ as the plesiomorphous form. This is a smooth prominent lobe <...> but no clear indication of the position of receptors can be ascertained by SEM examination. <...> In Atypoidea and [other] Mygalomorphae we find a series of tarsal organs where receptor nodes are progressively delineated; perhaps the localization series involved is directed towards the localization of these structures” [Forster, 1980: 272].

However, detailed examination shows that the apparently smooth surface of the liphistiid lobulated TO bears an unencircled receptor area with weakly differentiated receptor mounds (Fig. 18B–C) that can easily be overlooked. For example, the TOs of antrodiaetid mygalomorphs appear as smooth as those of liphistiids [Gertsch, Platnick, 1979: figs 6, 8, 10], yet they also bear a weakly encircled receptor area (Fig. 18D).

Thus, orthognathan lobulated TOs indeed represent the “series of progressively delineated receptor areas” recognized by Forster [1980]. This series ranges from a smooth protruding lobe (Fig. 18B–C; Gertsch, Platnick [1979: figs 6, 8, 10, 12, 14]), through a lobe with fine striation encircling only the receptor area (Fig. 18D; Gertsch, Platnick [1979: fig. 22]; Gertsch, Platnick [1980: fig. 12]), to strongly developed concentric ridges occupying the entire lobe surface (Fig. 18E; Gertsch, Platnick [1979: figs 29–32]).

Of particular interest are the smooth lobulated TOs of some basal mygalomorphs, in which the receptor area forms a clearly delimited depression [Gertsch, Platnick, 1979: figs 19–20, 28]. Surprisingly, the TO of *Chimerarachne* appears to belong to this type: it consists of a domed structure with a distinct rounded depression (Fig. 17C), and is in any case strongly dissimilar to the pit TO (Fig. 18A).

This finding reinforces the doubts raised by Forster *et al.* [1987: 107–108]: is the ‘pit TO’, which first appears only in Labidognatha, truly ancestral for the order Aranei, given that basal Orthognatha and, as now shown, chimerarachnids possess a different type of exposed TO? The hypothesis of pit TO ancestral state in spiders was based entirely on its similarity to the ‘pit organs’ of Amblypygi; however, the homology of these structures is questionable.

Neither Amblypygi nor Uropygi *s.l.* possess TOs on the tarsi of non-antenniform legs II–IV (Fig. 7B–C). Only the tarsus of the antenniform leg I of Amblypygi bears six types of sensory organs [Foelix *et al.*, 1975: fig. 1b]. One of these, termed the ‘pit organ’, at first glance resembles spider exposed TOs [Foelix *et al.*, 1975: figs 26–28; Forster, 1980: fig. 4; Forster *et al.*, 1987: fig. 378].

In contrast, the antenniform legs I of Uropygi *s.l.* lack any structure comparable to the pit organ (Fig. 7D; Ruiz, Valente [2023: fig. 13A]). They bear only two types of sensory organs: the ‘rosette-shaped glandular openings’ synapomorphic for schizomids and thelyphonids [Santos, Pinto-da-Rocha, 2009: figs 13–16 and 17–19], and the ‘club setae’ (Fig. 7D–E; Ruiz, Valente [2023: fig. 13A–D]) similar to that of Amblypygi (cf. Fig. 7E and Foelix *et al.* [1975: figs 8–9]).

The amblypygian pit organ differs from the spider pit TO in several important characters: the depression is poorly delimited, the mounds on its floor are larger, and, most importantly, each mound bears a distinct pore [Foelix *et al.*, 1975: figs 27–28]. Thus, the pit organ of the antenniform leg I appears to represent an autapomorphy of Amblypygi, comparable to various tarsal sensilla found in several non-tetrapulmonate arachnid orders (e.g., the pore-bearing ‘tarsal organ’ of harvestmen).

Tarsal organs are absent in Trigonotarbitida [Shear *et al.*, 1987] but present in the uraraneid *Attercopus* [Selden *et al.*, 1991]. In the latter, the TO appears as a small dorsodistal mound with a rounded depression (Fig. 13A–C; Selden *et al.* [1991: fig. 8A–B, D]) and most likely corresponds to a lobulated TO of *Chimerarachne* (Fig. 17C). Thus, this type of tarsal organ appears to be a symplesiomorphy of chimerarachnids and basal lineages of ‘true spiders’, inherited from uraraneids. This ancestral type was subsequently transformed in more advanced spider lineages into the autapomorphic pit TO and capsulate TO.

### 3. Opisthosoma

#### 3.1. General appearance

The opisthosoma of *Chimerarachne* is divided into two morphologically distinct regions: a wide mesosoma and a narrowed metasoma (post-abdomen, pygidium), compris-

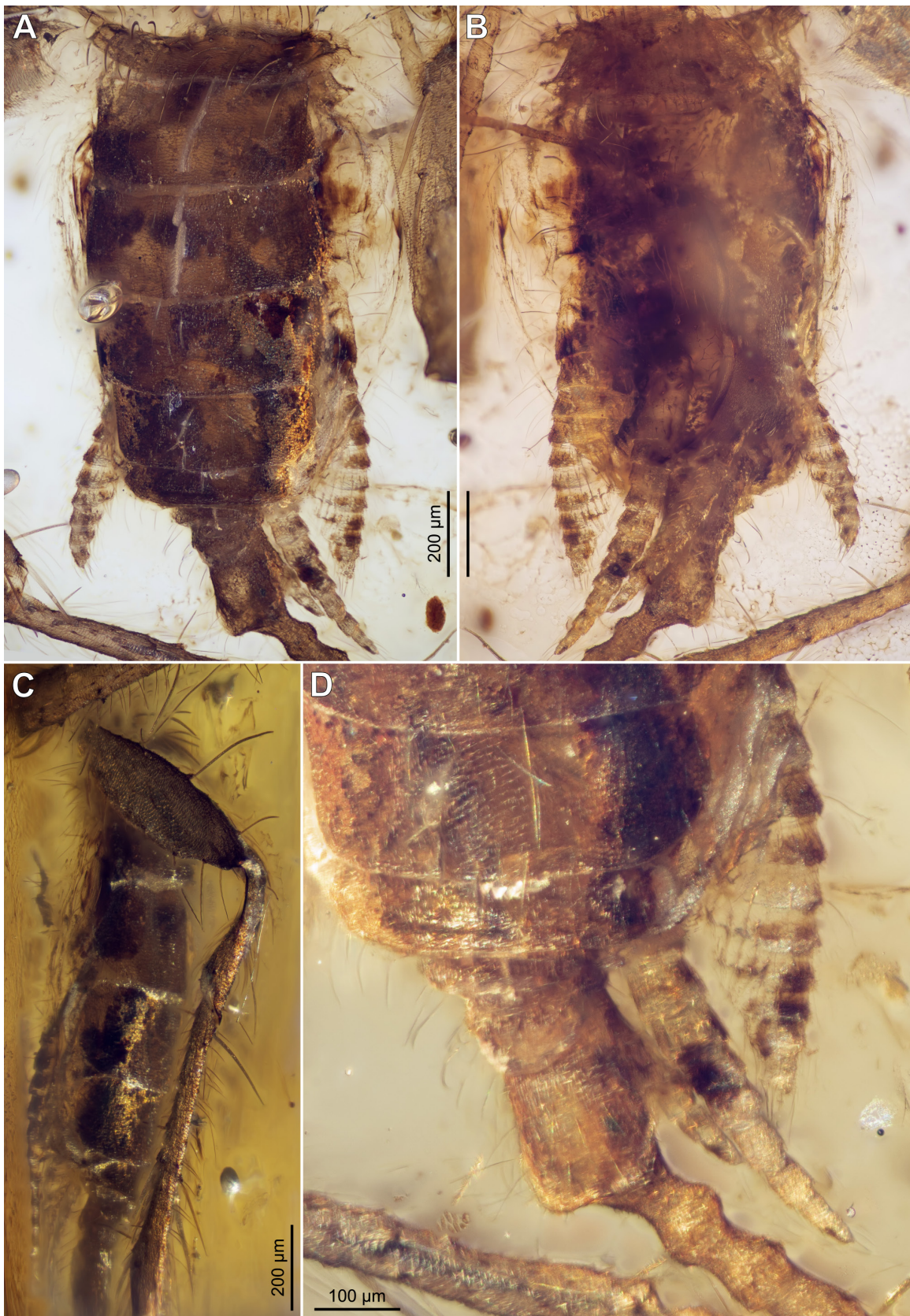


Fig. 19. Opisthosoma of *Chimerarachne cf. patrickmuelleri*: A — dorsally; B — ventrally; C — laterally; D — pygidium dorsally.

Рис. 19. Опистосома *Chimerarachne cf. patrickmuelleri*: A — дорсально; B — вентрально; C — латерально; D — пигидий дорсально.

ing segments VIII–XIV and XV–XVIII, respectively. The metasoma terminates in a long, multiarticulated flagellum (telson) (Fig. 22A; Wang *et al.* [2018: fig. 1b, d]).

The mesosoma of *Chimerarachne* is dorsoventrally flattened, subelliptical in dorsal outline, and completely segmented (Fig. 19A–C; Wang *et al.* [2018: fig. 4e–g]; Huang *et al.* [2018: fig. 2a, d]). The segmentation of the opisthosoma is regarded as an undoubtedly plesiomorphic character of chimerarachnids [Wang *et al.*, 2018; Huang *et al.*, 2018; Wunderlich, 2023].

Wang *et al.* [2018: 617] noted: “Dorsal surface of opisthosoma bears seven visible tergites (segments VIII–XIV) with straight anterior and posterior borders and rounded lateral borders”. As a result, in their proposed reconstruction of *Chimerarachne* [Wang *et al.*, 2018: fig. 3a–b] the mesosoma acquires an excessive similarity to the subglobular opisthosoma of liphistiomorph spiders: “Each [segment] consists of a dorsal tergite and ventral sternite. Both parts are connected by the pliable pleurae, which are not segmented, but form a continuous band on each side [of abdomen] (fig. 2.26a)” [Foelix, 2011: 39].

However, as far as can be observed, the lateral borders of the *Chimerarachne* tergites are not rounded, and the lateral pleural folds do not form a continuous, unsegmented band on each side of the abdomen (Fig. 19C; Huang *et al.* [2018: fig. 2a, d]). “It is well known that extant mesothel spiders retain traces of external abdominal segmentation (clearly visible as plate-like tergites) <...>, but opisthosomal segmentation is only visible dorsally, while in *Chimerarachne* segmentation occurs throughout the opisthosoma <...>, including ventrally and laterally” [Huang *et al.*, 2018: 626].

The flattened, completely segmented opisthosoma of *Chimerarachne*, which retains a distinct four-segmented postabdomen (Fig. 19D), is therefore sharply distinct from that of liphistiomorph spiders. On the contrary, it closely resembles those of trigonotarbid [Shear *et al.*, 1987], uraneids [Selden *et al.*, 2008] and *Idmonarachne*, a tetrapulmonate *incertae sedis* [Garwood *et al.*, 2016: fig. 4]. Consequently, complete opisthosomal segmentation in chimerarachnids appears to represent an ancestral, ‘pre-spider’ condition within Tetrapulmonata.

The pygidium and the flagellum are discussed below.

### 3.2. Prosoma–opisthosoma juncture

Wang *et al.* [2018: 619] stated that in *Chimerarachne* the “body is divided into a prosoma and opisthosoma connected by a narrow waist, or pedicel”. However, it should first be clarified what a ‘pedicel’ is in general.

A drastic constriction of the first opisthosomal segment evolved in spiders to increase abdominal mobility during spinning activity and is correlated with this unique synapomorphy of the order. As noted by Van der Hammen [1989: 490]: “Araneida <...> with a distinct constriction at the border of prosoma and opisthosoma, due to the modification of the first opisthosomatic segments into a narrow pedicel”.

Shultz [2007: char. 97] divided pedicels (where present within an order) into an “aranean type” and a “ricinuleid type” and further clarified:

“The body narrows at or near the prosoma–opisthosoma juncture in several arachnid lineages (i.e. Solifugae, Palpigradi, Amblypygi, Araneae, Ricinulei) and this ‘waist’ has often been used as character at the interordinal level <...>. However, this interpretation is rejected here for being subjective and for uniting non-homologous conditions. For example, Araneae and Amblypygi are often grouped on the basis of a ‘pedicel’, yet it is a highly specialized structure in Araneae and its parts are not readily homologized with those of Amblypygi. In contrast, the condition in Amblypygi is a slightly narrower version of the highly moveable prosoma–opisthosoma juncture in Uropygi, which is not generally considered a ‘pedicel’” [Shultz, 2007: 255].

In our opinion, the prosoma–opisthosoma junction in *Chimerarachne* (Figs 10C, 19A–B; Wang *et al.* [2018: fig. 4e–g]; Huang *et al.* [2018: fig. 1g–h]), as well as in the uraneid *Permarachne* [Eskov, Selden, 2005: figs 2–3] cannot be classified as a ‘pedicel of the aranean type’ and is instead more similar to the above-mentioned ‘pedipalpal’ junction. Apparently, spinning activity in chimerarachnids was achieved through the mobility of their extremely elongated, multi-articulated spinnerets, rather than through mobility of the abdomen as a single unit, as in ‘true spiders’ (including liphistiomorphans).

### 3.3. Spinning apparatus

Wang *et al.* [2018: 619] described *Chimerarachne* spinnerets as follows: “Ventrally, the third opisthosomal segment bears a pair of prominent multi-articled spinnerets (Figs 3g–h and 4g), which we interpret as equivalent to the anterior lateral spinnerets [ALS] of spiders, plus a pair of less developed spigot-bearing mounds in a median position, which may be equivalent to the anterior median spinnerets [AMS]. The fourth segment again has prominent spinnerets, equivalent to the posterior lateral spinnerets [PLS], but no corresponding median structures [PMS]”. Surprisingly, the descriptions and interpretations of the spinning apparatus of chimerarachnids given by other authors differ sharply.

Huang *et al.* [2018: 624] insisted on the presence in *Chimerarachne* of two pairs (not one pair) of median spinnerets: “*Chimerarachne yingi* can be distinguished from other arachnids by <...> opisthosoma ventrally bearing two pairs of lateral, long multi-articulated spinnerets with spigots [ALS and PLS], two pairs of small non-articulated median spinnerets [AMS and PMS]”, and repeat further: “The spinnerets and spigots of extant mesothel spiders and our fossil species nonetheless are remarkably similar, both having two long pairs of lateral, multi-articulated, distally tapering-off spinnerets [ALS and PLS] and two pairs of median spinnerets that are very small in comparison and not articulated [AMS and PMS]” [Huang *et al.*, 2018: 625].

Wunderlich [2023] agreed with Wang *et al.* [2018] regarding the existence in *Chimerarachne* of three pairs of spinnerets, in contrast to four pairs reported by Huang *et al.* [2018]. However, he interpreted the median spinnerets in another way, as PMS: “Three pairs of opisthosomal spinnerets: two pairs of multi-segmented laterals (about

equal in length) as well as a posterior median pair [PMS]” [Wunderlich, 2023: 165], and repeated further: “I think (see fig. A) that the anterior median spinnerets [AMS] — most probably — got lost in the Chimerarachnida as well as in the Opisthothelae; in the Mesothelae they exist basically” [Wunderlich, 2023: 166].

Our data demonstrate that the Wang *et al.* [2018] conclusions are correct, while both the Huang *et al.* [2018] and Wunderlich’s [2023] interpretations are erroneous. *Chimerarachne* indeed possesses three pairs of spinnerets: the prominent multi-articled ALS and PLS on the third and fourth opisthosomal segments, and the small non-articulated AMS on the third segment (cf. Figs 19B, 21A and Wang *et al.* [2018: fig. 3h]).

It is necessary to emphasize that Huang *et al.*’s [2018] assertion concerning the “two pairs of median spinnerets” contradicts their own illustrations (micro computed tomography reconstructions of *C. yingi*), which exhibit only three pairs of spinnerets in total: “Fig. 2h, Detail of the proximal region of the spinnerets (anterior median, green arrows; anterior lateral, red arrows; posterior lateral, blue arrows)”.

The spinning apparatus of chimerarachnids turns out to be almost an exact copy of that of extant Mesothelae spiders. It is represented by several typical spigots that have a broad base and a slender distal part, which are arranged along the entire length of the long multi-articulated lateral spinnerets (Fig. 20A–E; Huang *et al.* [2018: fig. 1f]; Wunderlich [2023: photo 31]).

In contrast, spinnerets of all Opisthothelae are few-segmented. In mygalomorphs, PLS consist of 3 or 4 segments which have the spigots along much of the ventral surface and at the tip [Foelix, 2011: fig. 5.9a; Murphy, Roberts, 2015: pls. 3–28]. In araneomorphs, PLS consist of only two segments which bear spigots only on the terminal segment [Foelix, 2011: fig. 5.11].

“The lateral spinnerets of adult mesothelid specimens are long and conical and made up of 9–12 articles which decrease in diameter to the distal end of the spinnerets (fig. 29b). <...> All spigots are located on the inner ventral surface of the spinnerets. They are arranged in rows on the distal margins of the articles (fig. 28D), except for the basal one. While articles of the anterior lateral spinnerets bear up to 10 spigots, there are only about six on the articles of the posterior lateral spinnerets” [Haupt, 2003: 41]. See also Murphy & Roberts [2015: pls. 1–2].

Chimerarachnid ALS and PLS consist of 11 and 14 articles, respectively (Fig. 19B; Huang *et al.* [2018: fig. 1f–h]). They differ from mesothelae lateral spinnerets only in the number of spigots per article: “Like in mesothelae, *Chimerarachne* has mesoventrally placed spigots — at least one per spinneret article in the section of the posterior lateral spinnerets where this character is discernible” [Huang *et al.*, 2018: 625]. The number of spigots per article decreases from ALS to PLS in both chimerarachnids (three to one or two, respectively: Fig. 20A, E) and in mesothelae (ten to six, respectively: see above).

It should be noted that the shape of the prominent multi-articulated lateral spinnerets varies among species of *Chimerarachne*. For instance, in *C. yingi* both ALS and

PLS are similarly sized and distally tapering [Huang *et al.*, 2018: figs 1h, 2c], whereas in *C. cf. patrickmueller* and *C. patrickmueller* the ALS are conical and thick at the base, while the PLS are nearly cylindrical and approximately twice as slender (Fig. 19B; Wunderlich [2023: photo 30]).

The median spinnerets are reduced to varying degrees in both lineages, mesothelae and chimerarachnids. “In *Liphistius*, there are functioning AMS and PMS, albeit with only a single spigot each. In *Heptathele kikuyai*, the AMS are reduced to a pair of coluli and the PMS are completely absent. In some *Heptathele*, the PMS are fused and represented by a single midline colulus” [Murphy, Roberts, 2015: 41].

In *Chimerarachne*, the AMS are represented by a pair of spigot-bearing non-articulated mounds on the third opisthosomal segment (Fig. 21A, D–E; Wang *et al.* [2018: fig. 3h]), whereas PMS on the fourth segment are completely lost; Wang *et al.* [2018: 619] recorded: “Median posterior border of sternite 4 [visible only in the specimen NIGP166870] bears a V-shaped, colulus-like structure”, but we interpret this as an artifact. Notably, the AMS of *Chimerarachne* bear a pair of spigots (Fig. 21D–E; Wang *et al.* [2018: fig. 3h]), whereas the mesothelae median spinnerets bear a single spigot, or are spigot-less, clearly non-functional.

The numerous features of the spinning apparatus in both chimerarachnids and the basalmost ‘true spiders’, Mesothelae, exhibit a remarkable unity, as well as the same evolutionary trends toward reduction of median spinnerets in both lineages. In our opinion, it clearly indicates a common origin of these organs rather than their convergent development.

“The different articles [in Mesothelae] are supplied by muscles (fig. 29a, b) which allow these spinnerets a remarkable flexibility e.g., during the construction of the burrow” [Haupt, 2003: 40]. If the internal anatomy of the multi-articulated spinnerets in *Chimerarachne* is the same (and there is no reason to assume otherwise), this arachnid was likely capable of various types of silk use. However, the range of such behaviors was probably more limited than in mesothelae due to the more limited mobility of the non-pedicellate chimerarachnid abdomen (see above).

Shultz [1987] reasonably suggested that silk in spiders evolved for reproductive needs, such as sperm transfer or egg protection; this mode of weaving activity should be considered ancestral in the ‘chimerarachnids + true-spiders’ lineage. Most likely, *Chimerarachne* retained this primary weaving style, and used silk only for constructing sperm webs and, possibly, for wrapping eggs.

Based on the presence of a flagellum, Huang *et al.* [2018] considered *Chimerarachne* to belong to the Uraraneida. This order was established to comprise two Paleozoic ‘tailed arachnids’, *Attercopus* and *Permarachne* [Selden *et al.*, 2008]. Devonian *Attercopus* was described as the earliest known silk-producing arachnid due to the presence of spigots consisting of a bell-shaped base, supporting a narrow shaft (Fig. 13D; Selden *et al.* [2008: figs 1C, 2A]). It was even initially considered a spider, but further study stated that its fragment, first interpreted as a ‘spinneret’ [Shear *et al.*, 1989: figs 1–2; Selden *et*

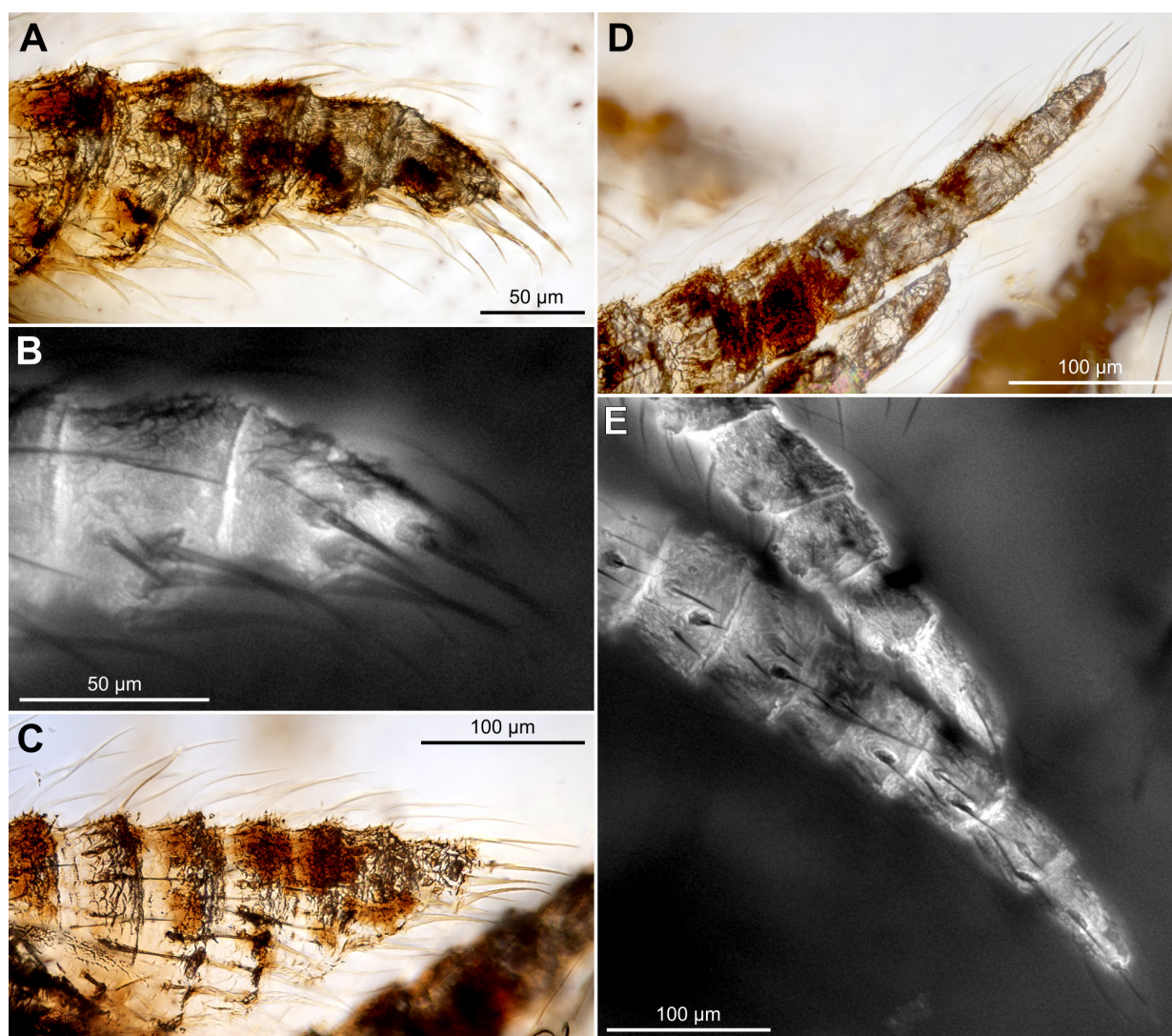


Fig. 20. Lateral spinnerets of *Chimerarachne* cf. *patrickmueller* (PIN 5608/475): A — left ALS, laterally; B — tip of left ALS, ventrally; C — right ALS laterally; D — right PLS, dorsally; E — right PLS, ventrally. A, C, D — reflected/transmitted light; B, E — CLSM.

Рис. 20. Боковые паутинные бородавки *Chimerarachne* cf. *patrickmueller* (PIN 5608/475): А — левая передняя латеральная паутинная бородавка (ALS), сбоку; В — кончик левой ALS, снизу; С — правая ALS, сбоку; D — правая задняя латеральная паутинная бородавка (PLS), сверху; Е — правая PLS, снизу. А, С, D — отраженный/прошедший свет; В, Е — конфокальный лазерный сканирующий микроскоп (CLSM).

*al.*, 1991: fig. 11A–C] is actually a twice-folded sheet of cuticle that bears a row of spigots along the posterior edge [Selden *et al.*, 2008: 20782]. It is hard to conclude anything with certainty about the spinning apparatus of Permian *Permarachne*, except that the spinnerets cannot be clearly distinguished in this imprint fossil [Eskov, Selden, 2005; Selden *et al.*, 2008].

Thus, we face an evolutionary sequence of the development of the spinning apparatus in the ‘tailed arachnids’, classified in one way or another as ‘uraneids’. It begins with dispersed spigots on the opisthosomal sternites in the Devonian *Attercopus* and culminates in specialized, movable spinnerets in the Cretaceous *Chimerarachne*. There is little doubt that the ‘transitional’ Permian *Permarachne* possessed spigots, but it remains unclear whether they were dispersed (as in *Attercopus*), placed on spinnerets

(as in *Chimerarachne*), or aggregated in some intermediate way. This is key to resolving whether ‘Uraneneida’ represents a clade or a grade.

### 3.4. Epigastric apparatus

The epigastric apparatus (term of Lopez, Emerit [1988]) in male *Chimerarachne* is represented by 10 epiandrous spigots with distinctly swollen basal portions, which are arranged in a single transverse row anterior to the epigastral furrow (Fig. 21A–C). Wang *et al.* [2018: fig. 3h] partially figured this structure at the uppermost edge of their photograph but did not comment on it. Furthermore, Wunderlich [2023: 165] noted: “I did not recognize epiandrous gland spigots [in chimerarachnids] although I will not exclude their existence in this suborder”.

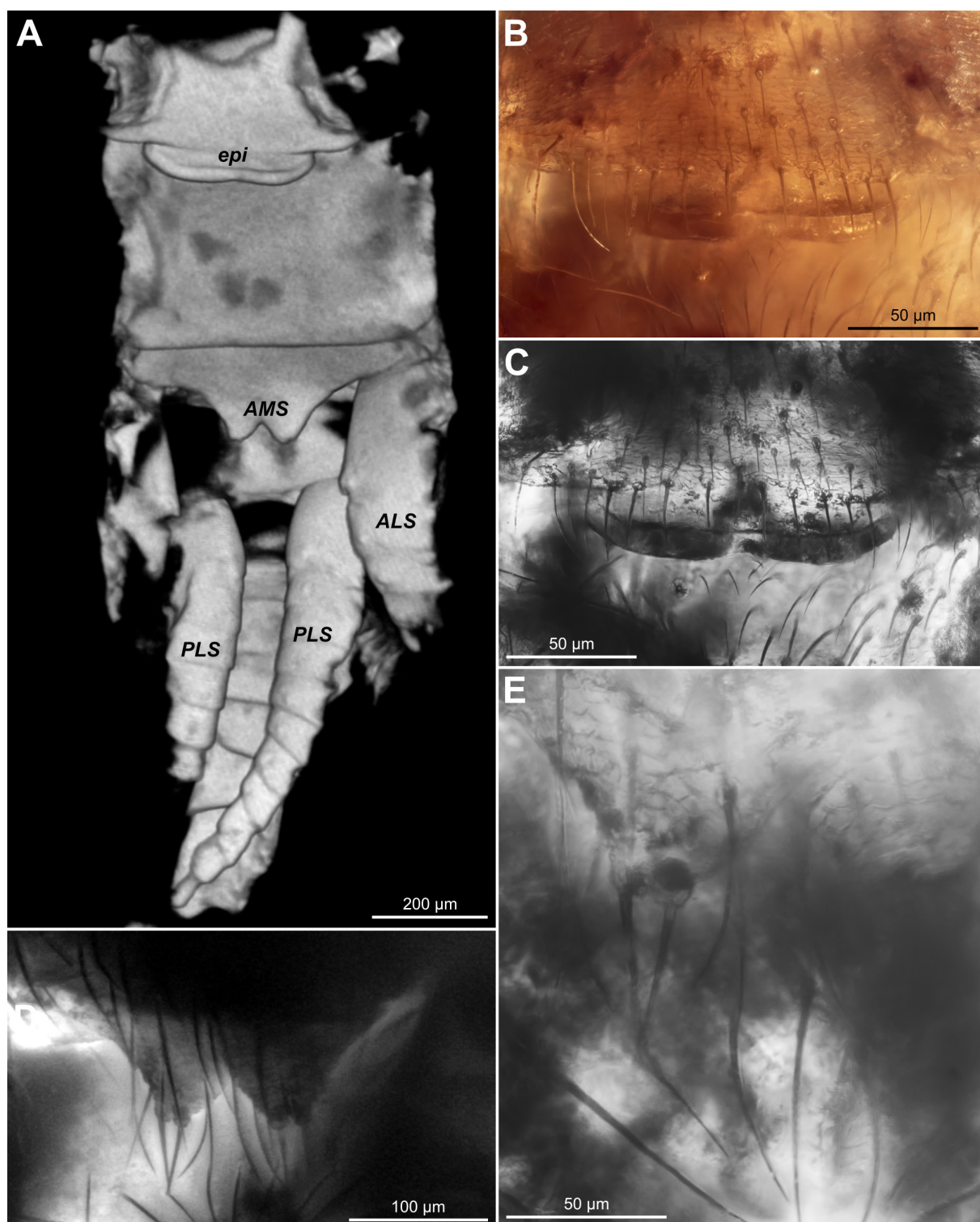


Fig. 21. Opisthosomal structures of *Chimerarachne* cf. *patrickmueller* (PIN 5608/475): A — opisthosoma ventrally; B — epiandrous spigots; C — the same; D — AMS; E — left AMS, enlarged. A — microtomography; B,C,E — reflected/transmitted light; D — CLSM. Abbreviations: *epi* — epiandrous area; *AMS* — anterior median spinnerets; *ALS* — anterior lateral spinnerets; *PLS* — posterior lateral spinnerets.

Рис. 21. Структуры опистосомы *Chimerarachne* cf. *patrickmueller* (PIN 5608/475): A — опистосома вентрально; B — эпиандрусные спиготы; C — то же; D — AMS; E — левая AMS, увеличено. A — микротомография; B, C, E — отраженный/проходящий свет; D — конфокальная лазерная сканирующая микроскопия. Сокращения: *epi* — эпиандрусная область; *AMS* — передние медиальные паутинные бородавки; *ALS* — передние латеральные паутинные бородавки; *PLS* — задние латеральные паутинные бородавки.



Fig. 22. Flagellum of *Chimerarachne* cf. *patrickmueller* (PIN 5608/475): A — opisthosoma and flagellum; B — basal portion of flagellum; C — median portion of flagellum; D — distal portion of flagellum; E — tip of flagellum.

Рис. 22. Флагеллум *Chimerarachne* cf. *patrickmueller* (PIN 5608/475): А — опистосома и флагеллум; В — базальная часть флагеллума; С — срединная часть флагеллума; D — дистальная часть флагеллума; E — кончик флагеллума.

Epiandrous spigots were first discovered and figured in haplogyne spiders by Machado [1951], who correctly homologized them with spinneret spigots. The epiandrous glands connected to these spigots produce silk for the sperm web spun by male spiders. This web serves as an intermediate structure for transferring a droplet of the semen from the male genital opening to the embolus of the pedipalp. This complex mechanism of indirect sperm transfer is one of key apomorphies of the order Aranei [Foelix, 2011], including its basalmost lineage, the Liphistiomorphae [Haupt, 2003: 56].

The problem was formulated by Eberhard [2020: 46]: “The mystery of the epiandrous glands is not the function of their silk, but why it is needed. They produce a small mat of fine lines in the “sperm web”, onto which the male deposits a droplet of the semen directly from his gonopore; he then takes up the semen into his pedipalps. But why is this tiny mat necessary?”

Indeed, in basal spider lineages, Mygalomorphae and Filistatidae, this mat of fine epiandrous silk is a minor portion of their giant sperm webs (2–10 cm, versus 2–3 mm in araneomorphs), which consist mainly of ordinary, spinneret silk [Costa, Pérez-Miles, 2002; Barrantes, Ramírez, 2013]. In several unrelated spider lineages, epiandrous spigots are absent: “How or if they construct sperm webs is unknown” [Griswold *et al.*, 2005: 56]. These spigots are so diminutive that they may, in some cases, be overlooked [Eberhard, 2020], but in other groups they are definitely lost.

The independent loss of epiandrous spigots is considered a synapomorphy of several lineages of higher araneoids: the ‘Anapidae + Symphytognathidae clade’ [Lopardo, Hormiga, 2015: char. 56], the linyphiid subfamily Erigoninae [Hormiga, 2002: 376–377], and some unrelated genera of Theridiidae [Agnarsson, 2004: char. 168]. A similar parallel loss of epiandrous spigots is recorded in several genera of the pholcid subfamilies Arteminae Simon, 1893 and Modisiminae Simon, 1893 [Huber, 2000: figs 130–141] which are phylogenetically distant from the Araneoidea. Probably, in these small or minute spiders the sperm web is reduced to a single thread, as in the haplogyne *Scytodes* Latreille, 1804 [Foelix, 2011: 234]; this thread may be produced by spinneret spigots rather than epiandrous ones.

Epigastric apparatus in basal spider lineages, Liphistiomorphae (Fig. 6C–D) and Mygalomorphae [Ferretti *et al.*, 2017: fig. 1A–B]), is represented by numerous (several dozen) epiandrous spigots dispersed over a wide area. Each spigot arises from a circular socket in the cuticle and tapers distally, but lacks the swollen basal part and narrow distal shaft typically seen in spinneret spigots [Ferretti *et al.*, 2017: fig. 2]. In more derived suborder Araneomorphae, a relatively small number of spigots is usually grouped into two clusters along the epigastric furrow (e.g. Foelix [2011: fig. 7.3]).

A special case is the epigastric apparatus of some Synspermiata, which consists of a single transverse row of a few flask-shaped epiandrous spigots. These are extremely similar to spinneret spigots, which consist of a swollen basal part (‘bulb’) and a narrowed distal part (‘shaft’)

connected by membranous ring [Eberhard, 2020: fig. 2.1c–d]. Such flask-shaped spigots have been recorded in Ochyroceratidae Fage, 1912 [Machado, 1951: figs 62–63; Brescovit *et al.*, 2018: fig. 2B], Leptonetidae Simon, 1890 [Lopez, Emerit, 1988: fig. 4] and some Pholcidae [Huber, 2000: figs 119–124].

The case of Filistatidae, a basal araneomorph lineage that shares with Mygalomorphae the presence of giant sperm webs (see above), is of particular interest. In some filistatid genera, such as *Kukulcania* Lehtinen, 1967 and *Filistatinella* Gertsch et Ivie, 1936, the epigastric apparatus appears mygalomorph-like, with tubular spigots dispersed over a wide area [Magalhaes, Ramírez, 2017: fig. 20A–B; Magalhaes, Ramírez, 2019: fig. 11B, respectively]. In other genera, such as *Wandella* Gray, 1994, the epigastric apparatus is represented by a single row of a few flask-shaped spigots [Magalhaes, 2016: fig. 7B], as in the aforementioned synspermiates. It is noteworthy that the former, mygalomorph-like condition appears to be confined to the basal part of the filistatid cladogram, whereas the latter, synspermiate-like condition is restricted to its more derived part [Magalhaes, Ramírez, 2022: fig. 5].

Surprisingly, the epigastric apparatus of *Chimerarachne* (Fig. 21B–C) is most similar to this synspermiate-like condition. On the other hand, it also closely resembles the flask-shaped spigots dispersed on the surface of the opisthosomal sternites of the uraraneid *Attercopus* (Fig. 13D; Selden *et al.* [2008: figs 1C, 2A]). Thus, it may be assumed that uraraneid spigots are the precursors not only of spinnerets [Selden *et al.*, 2008], but also of the epigastric apparatus.

Therefore, three conclusions can be drawn.

First, flask-shaped epiandrous spigots share a common origin with spinneret spigots and represent an ancestral condition in the ‘chimerarachnid + true spider’ lineage, inherited from uraraneids.

Second, the replacement of a single row of few flask-shaped spigots by numerous dispersed tubular spigots, as seen in liphistiomorphs and mygalomorphs, represents an apomorphy of Aranei, whereas the reappearance of flask-shaped spigots in some haplogyne araneomorphs can be interpreted as a reversal to the ancestral condition.

Third, both components of the complex spider mechanism of indirect sperm transfer — the specialized male pedipalp and the sperm web — appear to have arisen simultaneously at a ‘pre-spider’ evolutionary stage.

As expected, a detailed study of the epigastric area in male Schizomida by Ruiz & Valente [2023: fig. 4A, C] did not reveal any traces of epiandrous spigots.

### 3.5. Pygidium

The opisthosoma of *Chimerarachne* terminates in a narrowed four-segmented metasoma (pygidium) bearing a long, multiarticulated flagellum (Figs 19D, 22A; Wang *et al.* [2018: fig. 1b, d]). Metasomal segments form complete sclerotized rings, in contrast to mesosomal segments, in which the dorsal tergite and ventral sternite are separated by a lateral pleural fold [Van der Hammen, 1989].

Shultz [1990: 27] resurrected the largely forgotten arachnid division Megoperculata Börner, 1902, uniting

Tetrapulmonata with the non-tetrapulmonate order Palpigradi: “Orders appear to have the following relationships: (Palpigradi (Araneae (Amblypygi (Thelyphonida, Schizomida))))”. The pygidium was identified as one of the key synapomorphies of this supposedly monophyletic lineage [Shultz, 1990: fig. 4]. Among different megoperculate orders, the pygidium varies from four segments to a single segment and may either retain or lack a terminal flagellum.

Flagellum-bearing pygidia occur in: Palpigradi (four-segmented: Franz-Guess, Starck [2020: 65]); *Chimerarachne* (four-segmented: Wang *et al.* [2018: 619]); Thelyphonida and Schizomida (three-segmented: Van der Hammen [1989: 471]).

Flagellum-less pygidia occur in: Trigonotarbida (two-segmented: Shear *et al.* [1987: 15]); Aranei: Mesothelae (a two-segmented anal tubercle: Huang *et al.*, 2018: 626); Aranei: Opisthothelae (a one-segmented anal tubercle: Shultz [1990: 21]); Amblypygi (a one-segmented pygidium: Van der Hammen [1989: 485]).

“It should be noted, however, that a distinct metasoma (‘postabdomen’) composed of several posterior opisthosomal segments appears during embryonic development in certain spiders” [Shultz, 1990: 21]. “The flagellum is a diagnostic feature of Uraraneida, but the segmental composition of the pygidium remains unknown in both *Attercopus* and *Permarachne*” [Selden *et al.*, 2008: 20784].

Therefore, the following evolutionary sequence may be proposed. A multisegmented (four- to three-segmented), flagellum-bearing pygidium appears to represent the ancestral condition in Tetrapulmonata, given its presence in the non-tetrapulmonate Palpigradi as well. This condition persisted as a plesiomorphic trait in both principal tetrapulmonate lineages: in pedipalpians (Thelyphonida and Schizomida) and in the ‘chimerarachnid + true spider’ lineage (*Chimerarachne* and, most probably, *Uraraneida*).

During subsequent evolution, the flagellum was lost and the number of pygidial segments was reduced to two (in Trigonotarbida and Mesothelae), and later, independently in both lineages, to a single segment in Amblypygi and Opisthothelae. However, complete loss of the pygidium has not been observed in any tetrapulmonate order.

### 3.6. Flagellum

The four-segmented pygidium of *Chimerarachne* terminates in a long, multiarticulated flagellum; its length and the features of segmentation and setation appear to differ among species. Wunderlich [2023: 169] considered the structure of the flagellum to be one of the two main diagnostic characters, along with the structure of the male genitalia, for distinguishing the five *Chimerarachne* species that he recognized.

In our specimen of *Chimerarachne* cf. *patrickmueller* (PIN 5608/475) the flagellum is complete, retaining the terminal segments (Fig. 22A, E). It is extremely long (ca. 3.2 times longer than the body, 8.15 mm/ 2.53 mm), highly pubescent, and consists of c. 100 segments, which are ca. 1.5 times longer than wide throughout the length of the flagellum (Fig. 22A). The segments are distally widened in the basal part of the flagellum, cylindrical in

the middle part, and narrowed at both ends in the terminal part. The mid-portion of each segment bears a whorl of long bristles, each ca. 4–5 segment diameters long in the basal and terminal parts of the flagellum, and ca. 6–7 diameters long in the middle part (Fig. 22B–D).

We agree with Wunderlich [2023] that the structure of the flagellum in *Chimerarachne* appears to be species-specific. These characters distinguish our specimen from all described chimerarachnids [Huang *et al.*, 2018; Wang *et al.*, 2018; Wunderlich, Müller, 2022; Wunderlich, 2023], except probably *C. patrickmueller*. The flagellum of *C. cf. patrickmueller* (PIN 5608/475), which consists of ca. 100 segments and reaches ca. 3.2 times the body length, is dramatically longer than that of any other known chimerarachnid.

Only three other *Chimerarachne* specimens are comparable in this respect because they retain the complete flagellum with terminal segments [Wang *et al.*, 2018: fig. 3k; Wunderlich, 2023: fig. 17]. The first is the holotype of *C. longiflagellum*; the specimen of *C. yingi* Wang *et al.*, 2018 (NIGP167161), which was discussed and figured by Huang *et al.* [2018], appears in fact to belong to this species. In both specimens the flagellum is quite long (ca. 2.3–2.6 times the body length), consists of ca. 70 homonomous segments, and is covered with moderately long bristles [Huang *et al.*, 2018: fig. 1a; Wunderlich, Müller, 2022: fig. 2a–b, photo 10]. The body and prosoma in both specimens are 2.3–2.4 and 0.9–1.0 mm long, respectively; the male palps of both possess a thin ‘embolus’ and a wide suboval ‘apophysis’ [Huang *et al.*, 2018: fig. 1d; Wunderlich, 2023: figs 18–19].

The second specimen is the paratype of *C. yingi* Wang *et al.*, 2018 (NIGP166871). Its complete flagellum is only ca. 1.3 times longer than the body, the shortest in the genus, and consists of ca. 60 segments; the seven terminal segments form a unique spindle-shaped structure [Wang *et al.*, 2018: fig. 3k]. “There is a distinct difference in the flagella of these two specimens [paratype NIGP166871 and holotype NIGP166870]” [Wang *et al.*, 2018: 620]. The male palps of the paratype and holotype also show differences (see above). In addition, the paratype is the largest specimen in the genus: its body and prosoma are 2.8 and 1.3 mm long, respectively, *versus* 2.4 and 1.1 mm in the holotype. Therefore, the paratype of *C. yingi* (NIGP166871) appears to be conspecific with neither the holotype (NIGP166870) nor any of the four species of *Chimerarachne* described later [Wunderlich, Müller, 2022; Wunderlich, 2023].

Regarding the holotype of *C. yingi* (NIGP166870), it retains only a basal portion of the flagellum, “consisting of approximately 30 alternating short and long segments; long segments bear a median bulge bearing a ring of bristles” [Wang *et al.*, 2018: 619]. Such alternation of short and long segments in the flagellum [Wang *et al.*, 2018: fig. 4h] was correctly considered by Wunderlich [2023: 169] to be a unique feature that distinguishes *C. yingi* from all other species of *Chimerarachne*.

Wang *et al.* [2018: 620] attempted to explain this unique feature by taphonomic reasons: “The segments are alternately short and long. We explain these differences

by assuming that the flagellar segments were telescopic to some extent, so that the smaller segments can be hidden inside the distal end of the larger segments”. However, the existence of such supposed ‘telescopic flagellar segments’ has not received any confirmation.

A much simpler hypothesis is that each segment is subdivided into two portions by a narrow, deep constriction. The long distal portion of a segment is bulged and bears a whorl of long bristles, whereas the short basal portion is cylindrical and hairless [Wang *et al.*, 2018: fig. 4h]. A similar transverse subdivision of flagellar segments into two portions with different setation has been reported for another order of ‘tailed arachnids’, Palpigradi: “On each article, a superficial cuticular groove surrounds the article separating a proximal part with a group of sensory setae from a distal part which carries cuticular spikes” [Franz-Guess, Starck, 2020: 65].

In all other specimens of all other species of *Chimerarachne*, the flagella are preserved incompletely. However, *C. spiniflagellum* Wunderlich, 2023 clearly differs from *C. cf. patrickmueller* (PIN 5608/475) in having longer bristles in the middle part of the flagellum (*ca.* 8–10 segment diameters versus *ca.* 6–7 diameters) and shorter bristles in the basal part (*ca.* 1.5–2 segment diameters versus *ca.* 4–5 diameters) [Wunderlich, 2023: figs 25–26, photos 35–36]. A sharp difference in the pubescence of the basal and middle parts of the flagellum was noted by Wunderlich [2023] as a diagnostic character of *C. spiniflagellum*. In *C. alexbeigel*, the segments of the middle part of the flagellum are widened apically [Wunderlich, 2023: fig. 23, photo 33]. In addition, *C. alexbeigel* is the smallest member of the genus: its body and prosoma are 1.4 and 0.8 mm long, respectively, versus 2.5 and 1.1 mm in *C. cf. patrickmueller*.

As a result, only in *C. patrickmueller* do the features of the preserved basal and middle parts of the flagellum [Wunderlich, 2023: photos 28, 30], as well as the body and prosoma lengths (2.3 and 1.1 mm, respectively), closely correspond to those of our *Chimerarachne* specimen (PIN 5608/475). Thus, we attribute this specimen, with some reservations, as *Chimerarachne cf. patrickmueller*.

The presence of a flagellum is generally recognized as a key ancestral trait of *Chimerarachne*: “However, like uraraneids and uropygids, *Chimerarachne* bears a flagelliform post-anal telson. Apart from this feature *Chimerarachne* could be considered as a spider. This was the conclusion of Wunderlich [2019], who established an order Araneida that included two suborders: Chimerarachnida and Araneae” [Selden, 2021: 323].

It should be noted that all ‘tailed arachnids’, including chimerarachnids, exhibit a single pattern of flagellar pubescence: an ordered arrangement of setal whorls, one per segment. Such whorls were reported in both members of the tetrapulmonatan order Uraraneida, *Attercopus* [Selden *et al.*, 1991: tab. 5, figs 3–4] and *Permarachne* [Eskov, Selden, 2005: figs 6–7], as well as in the non-tetrapulmonatan Palpigradi [Franz-Guess, Starck, 2020: fig. 3B].

In this respect, the Uropygi are of particular interest. The uropygid flagellar segments bear either irregularly

arranged setae, as in extant thelyphonids (Fig. 7F) and in females of schizomids [Ruiz, Valente, 2023: fig. 2B], or, as in the Cretaceous whip scorpion *Mesothelyphonus parvus* Cai et Huang, 2017, long bristles that do not form whorls [Cai, Huang, 2017: figs 3H, 4G]. At first glance, this chaotic pattern appears to be primary.

However, in another Cretaceous species, the dwarfish *Mesothelyphonus xiaoae* Wu *et al.*, 2025, which undoubtedly is not a congener of the type species *M. parvus*, the long bristles of the flagellum are grouped into whorls [Wu *et al.*, 2025: figs 1A, 2A]. Most importantly, a condition of leg I in *M. xiaoae* represents the antenniform leg *in statu nascendi* (see above), and this species may be interpreted as a relict of a basalmost lineage of the Uropygi. Consequently, the ‘whorled pubescence’ of the flagellum should be considered an ancestral character within the uropygid lineage as well.

Shultz [1990: 29–30] suggested that the flagellum arose convergently in Palpigradi and Uropygi. However, the unity of the complex, highly ordered arrangement of flagellar setae in the form of ‘whorled pubescence’ in all ‘tailed’ arachnid lineages without exception contradicts this hypothesis. It rather supports a common origin of this structure, inherited by both tetrapulmonates (Uraraneida and Uropygi) and non-tetrapulmonates (Palpigradi).

Therefore, the retention of a ‘whorled-pubescent’ flagellum in *Chimerarachne* is undoubtedly an ancestral feature, reflecting not merely a ‘pre-spider’, but even a ‘pre-tetrapulmonate’ condition.

Wunderlich & Müller [2022: 126] concluded that the presence of a long flagellum in chimerarachnids would have hindered the development of such key ‘true spider’ features as capture webs and ballooning behavior, and we agree with this view. Most likely, *Chimerarachne* used silk only for constructing sperm webs and, possibly, for wrapping eggs, as well as the initial ‘true spiders’ [Shultz, 1987]. The assumption that these ‘tailed arachnids’ inhabited silken shelters (such as retreat tubes) seems even less plausible than the assumption that they used capture webs.

#### 4. Cuticle

The cuticular sculpture of the legs, carapace and tergites of *Chimerarachne* represents a peculiar case of scaly cuticle, in which the distal margin of each polygonal cell is thickened and raised (Fig. 1C, 15E). Wang *et al.* [2018: 615] noted a “cuticular ornament of fine scales.” Wunderlich [2023: 165] termed it a “finely granulate cuticle”; he listed it among the plesiomorphic characters of chimerarachnids but provided no evidence supporting the ancestral status of this trait.

A scaly (= reticulate, imbricate, squamate) cuticle occurs in all extant orders of Tetrapulmonata (Fig. 23A–D; Eskov *et al.* [2024: fig. 8A, C, E]) and in Trigonotarbida [Shear *et al.*, 1987: figs 99, 106, 118], as well as in some non-tetrapulmonate arachnids, such as ixodid ticks [Lehtinen, 1996: fig. 29]. It appears to represent the ancestral cuticular type for at least the tetrapulmonate lineage [Eskov, Marusik, 2024b]. As Hinton & Wilson [1970: 483] concluded, the primitive arthropod cuticle

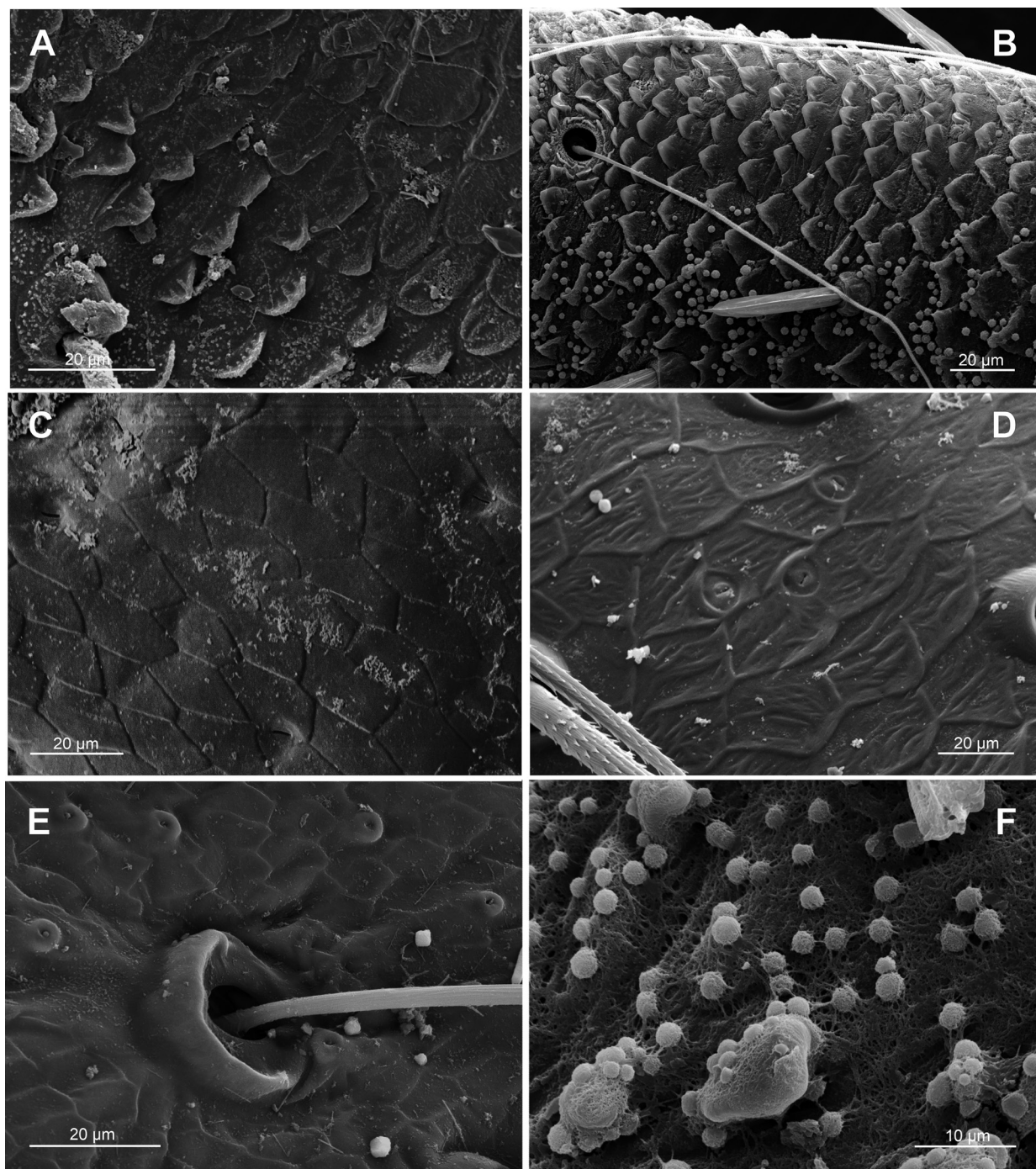


Fig. 23. Cuticular structures of extant spiders and pedipalps: 'pseudoscale' cuticle (A–B), scaly cuticle (C–E), cerotegument (F). A — *Heptathela* sp. (Mesothelae), tibia III; B — *Charinus* sp. (Amblypygi), tibia III; C — *Thelyphonus* (?) sp. (Thelyphonida), flagellum ventrally, slit-like gland openings; D — *Mecicobothrium thorelli* (Mygalomorphae), tibia II, slit-like gland openings; E — *Calommata sundaica* (Mygalomorphae), palpal tibia, slit-like gland openings; F — *Charinus* sp. (Amblypygi), carapace.

Рис. 23. Кутикулярные структуры современных пауков и педипальпий: «псевдочешуйчатая» кутикула (A–B), чешуйчатая кутикула (C–E); церотегумент (F). A — *Heptathela* sp. (Mesothelae), голень III; B — *Charinus* sp. (Amblypygi), голень III; C — *Thelyphonus* (?) sp. (Thelyphonida), флагеллум вентрально, щелевидные отверстия желез; D — *Mecicobothrium thorelli* (Mygalomorphae), II голень, щелевидные отверстия желез; E — *Calommata sundaica* (Mygalomorphae), голень пальпы, щелевидные отверстия желез; F — *Charinus* sp. (Amblypygi), карапакс.

consists of polygonal (usually hexagonal) units, each corresponding to the shape of an epidermal cell during epicuticle secretion (see also Moretto *et al.* [2015]).

The other major cuticle types, such as smooth, fingerprint, and rugose, appear to have evolved from the ancestral scaly type through transitional cuticular states [Eskov *et al.*, 2026].

A typical basal scaly cuticle (Fig. 23C–E) consists of flat polygonal plates that overlap distally and may be modified in several ways. In particular, in liphistiomorph cuticle the scales appear as protruding triangular extensions, well separated from one another (Fig. 23A; Eskov, Marusik [2024b: fig. 2A–B]). This cuticle type was recognized by Lehtinen [1996] as unique among spiders and termed ‘pseudoscale’ by Eskov & Marusik [2024b]. However, the transformation of scales of the ‘typical scaly cuticle’ into those of the ‘pseudoscale cuticle’ is directly observable in liphistiomorphs (Fig. 23A).

Similar scale modifications, undoubtedly parallel, occur in Amblypygi (Fig. 23B; Eskov, Marusik [2024b: fig. 2E–F]) and in the mygalomorph tribe Pseudonemesiini Caporiacco, 1955 [Raven, Platnick, 1981: fig. 6; Miglio, Bonaldo, 2011: fig. 18; Eskov *et al.*, 2026: fig. 22E–F].

Thus, the derived cuticular sculpture of *Chimerarachne*, with thickened and raised distal margins on every scale, appears intermediate between the typical scaly cuticle and the peculiar ‘pseudoscale’ cuticle of the basalmost spider lineage, Liphistiomorphae (cf. Figs 15E and 23A). On the other hand, the cuticular sculpture of *Chimerarachne* corresponds exactly to the description of that in uraneids: “The cuticle pattern of *Attercopus fimbriunguis* is characteristic, and readily identifiable. The surface sculpture was described in Shear *et al.* [1987, 64] as being reticulate, with one side (distal, normally) of each polygonal cell being thicker than the other sides <...>. This sculpture pattern can be confirmed here, but with added detail: first, the distal side of each polygon of the reticulum actually forms the proximal side of the distally adjacent cells” [Selden *et al.*, 1991: 257].

Selden *et al.* [1991: 257] further noted: “Most characteristic of *Attercopus fimbriunguis* is the presence of very small cuticular organs scattered across the cuticle surface (Pl. 1. fig. 1). <...> At low magnification (up to about  $\times 100$ ) these appear very much like small setal sockets: a circle or oval of dark cuticle, about 0.006 mm in diameter. At higher magnification, however, the central pore is revealed as a slit, and thus these organs are true slit sense organs”.

Similar cuticular microstructures were found in *Chimerarachne* (Figs 10E–F, 15E). In both taxa, these structures are clearly circumscribed oval pits scattered between the rounded setal sockets; notably, the long axes of the ovals are oriented at random angles relative both to one another and to the longitudinal axis of the segment (cf. Figs 10E, 15E and 13B, D). However, they clearly differ in size: in *Attercopus*, they are smaller than the setal sockets, whereas in *Chimerarachne* they are larger. It should be noted that the cuticle of Trigonotarbida also demonstrates microstructures (e.g., Shear *et al.* [1987: figs 47, 124–125, 158]) resembling those of chimerarachnids.

Currently, similar microstructures have been discovered and studied both in spiders (Fig. 23D–E; Foelix [2011: fig. 2.33b]) and in various pedipalpans (Figs 8F, 23C; Seiter *et al.* [2021: figs 4a–d, 8e–f]; Ruiz, Valente [2023: fig. 10I]). Their function appears to be secretory rather than mechanoreceptive: “Tiny slit-like pores in the cuticle represent epidermal gland openings” [Foelix, 2011: 46]. All of them share a peculiar common feature: the above-mentioned random orientation of the slits (Fig. 23D; Seiter *et al.* [2021: fig. 8e]).

The ‘slit-like gland openings’ of pedipalpans appear to be more complex structures than the ‘tiny slit-like pores’ of spiders: “Limited by a roundish elevation <...>; in the middle there is a thin membrane bearing an elongated, narrow opening” [Ruiz, Valente, 2023: 25]. Seiter *et al.* [2021: 1167] stated: “The slit-like gland openings [of all three orders of Pedipalpi] are unique structures not yet observed in other arachnids”.

However, thelyphonids also possess simple ‘tiny slit-like pores’ similar to those of spiders (Fig. 23C). On the other hand, in some spiders these structures are more elaborate, with the pores situated on hemispherical mounds (Fig. 23E), as in thelyphonids [Seiter *et al.*, 2021: fig. 4a–b].

Therefore, such cuticular glands, currently known from all tetrapulmonate orders, appear to represent a synapomorphy of this lineage. Under this interpretation, the simple ‘tiny slit-like pores’ of uraneids, chimerarachnids, spiders, and probably trigonotarbids represent the ancestral condition within Tetrapulmonata, whereas the more complex ‘slit-like gland openings’ constitute a synapomorphy of Pedipalpi. However, some pedipalpans retain the ancestral simple pores, whereas some spiders have independently acquired derived pore structures.

The cuticle of *Chimerarachne* is certainly not coated with a cerotegument (Figs 1D, 15E), unlike that of Liphistiomorphae and Amblypygi [Eskov, Marusik, 2024b]. On the other hand, the cuticle of non-tetrapulmonate Palpigradi is coated with a structure indistinguishable in appearance from the cerotegument [Seiter *et al.*, 2021: fig. 9d], especially from the cerotegument of Amblypygi (Fig. 23F; Seiter *et al.* [2021: fig. 1b]). Consequently, the cerotegument may be regarded as a synapomorphy of the arachnid lineage Megoperculata, resurrected by Shultz [1990], comprising Palpigradi + Tetrapulmonata (see above). Subsequently, it was retained as a plesiomorphic trait in liphistiomorph spiders and whip spiders, but lost in the remaining tetrapulmonates, including chimerarachnids.

The discussed results are summarized in Table 2.

## Explanations to the Table 2

**In round brackets** — the number of the paragraph in the text discussing the character.

**In square brackets** — members of a lineage exhibiting the specified character state, where the character varies within the lineage.

**In curly brackets** — an explanation of the accepted character polarity, where necessary

Table 2. Characters and character states of chimerarachnids and other tetrapulmonates.  
Таблица 2. Признаки и их состояния химерарахнид и других тетрапульмонат.

|                                 | Trig     | Urar  | Chim | Meso      | Myga      | Aran          | Ambl | Thel    | Schi |
|---------------------------------|----------|-------|------|-----------|-----------|---------------|------|---------|------|
| 1. Carapace fovea               | (-)      | (-) ? | (-)  | (+A)      | (+A)      | (+A)(+B)(-R)  | (+C) | (-)     | (-)  |
| 2. Eyes: set                    | (-) (+/) | ?     | (+)  | (+)       | (+)       | (+)           | (+)  | (-)     | (+)  |
| 3. Eyes: pattern                | (-) (+A) | ?     | (+A) | (+A)      | (+A) (-R) | (+A) (-R)     | (-)  | (-)     | (+B) |
| 4. Eyes: tubercle               | (-)      | ?     | (+A) | (+A)      | (+A)      | (+A)(+B)(-R)  | (-)  | (-)     | (-)  |
| 5. Eyes: number                 | (-)      | ?     | (+A) | (-)       | (-)       | (-) (+B) (+C) | (-)  | (-)     | (+D) |
| 6. Coxae                        | (-)      | (-)   | (-)  | (-)       | (-)       | (-)           | (+)  | (+)     | (+)  |
| 7. Coxae IV                     | (-)      | (-)   | (-)  | (+) ?     | (-)       | (-)           |      |         |      |
| 8. Sternum                      | (-)      | (-)   | (-)  | (-)       | (-)       | (-)           | (+)  | (+)     | (+)  |
| 9. Sternum width                | (-)      | (-)   | (-)  | (-) (+) ? | (-)       | (-)           |      |         |      |
| 10. Sigilla                     | (-)      | (-)   | (-)  | (-)       | (+)       | (+) (-R)      | (-)  | (-)     | (-)  |
| 11. 'Hair plates'               | (-)      | ?     | (+)  | (+)       | (+)       | (+)           | (-)  | (-)     | (-)  |
| 12. Chelicera: fang             | (-)      | (+)   | (+)  | (+)       | (+)       | (+)           | (-)  | (-)     | (-)  |
| 13. Chelicera: type             | (-)      | (+)   | (+)  | (+)       | (+)       | (+)           | (-)  | (-)     | (-)  |
| 14. Chelicera: basal joint      |          | (-)   | (-)  | (+A)      | (+A)      | (-) (+B)      |      |         |      |
| 15. Venom glands                | (-)      | (-)   | (-)  | (±)       | (±)       | (±) (+)       | (-)  | (-)     | (-)  |
| 16. Palps                       | (-)      | (-)   | (-)  | (-)       | (-)       | (-)           | (+)  | (+)     | (+)  |
| 17. Palps of male               | (-)      | ?     | (+)  | (+)       | (+)       | (+)           | (-)  | (-)     | (-)  |
| 18. Sperm-transferring palp     |          | ?     | (-)  | (-)       | (+A)      | (±) (+B)      |      |         |      |
| 19. Leg I                       | (-)      | (-)   | (-)  | (-)       | (-)       | (-)           | (+)  | (±) (+) | (+)  |
| 20. Patella                     | (-)      | (-)   | (±)  | (+)       | (+)       | (+)           | (-)  | (-)     | (-)  |
| 21. Leg setation                | (-)      | (-)   | (-)  | (-)       | (-)       | (-)           | (+)  | (+)     | (+)  |
| 22. Macrosetae                  | (-)      | (+A)  | (+B) | (+C)      | (+C)      | (+C)          | (-)  | (-)     | (-)  |
| 23. Chemosensory setae          | (-)      | (-)   | (-)  | (+)       | (+)       | (+)           | (-)  | (-)     | (-)  |
| 24. Tarsal claws                | (-)      | (±)   | (+)  | (+)       | (+)       | (+)           | (-)  | (-)     | (-)  |
| 25. SAS                         | (-)      | (-)   | (±)  | (-)       | (-)       | (±) (+) (-R)  | (-)  | (-)     | (-)  |
| 26. Pseudopulvillus             | (-)      | (-)   | (+)  | (+) (-R)  | (-R)      | (-R)          | (-)  | (-)     | (-)  |
| 27. Tarsal process              | (-)      | (-)   | (+)  | (+)       | (+)       | (+)           | (-)  | (±)     | (+)  |
| 28. Trichobothrial pattern      | (-)      | (+A)  | (-)  | (+B)      | (+B)      | (+B)          | (+C) | (-)     | (-)  |
| 29. Bothria principal structure | (+)      |       | (+)  | (+)       | (+)       | (+)           | (-R) | (+)     | (+)  |
| 30. Bothrial diaphragm          | (-)      |       | (-)  | (+)       | (+)       | (+)           |      | (-)     | (-)  |
| 31. Slits and LOs               | (-)      | (+)   | (+)  | (+)       | (+)       | (+)           | (-)  | (-)     | (-)  |
| 32. Lateral LOs                 | (-)      | (+)   | (+)  | (+)       | (+)       | (+)           | (-)  | (-)     | (-)  |
| 33. VSO                         | (-)      | (+)   | (+)  | (+)       | (+)       | (+)           | (-)  | (-)     | (-)  |
| 34. LOs on patella              | (-)      | (+)   | (+)  | (+)       | (+)       | (+)           | (-)  | (-)     | (-)  |
| 35. Tarsal organs               | (-)      | (+A)  | (+A) | (+A)      | (+A)      | (+A)          | (+B) | (-)     | (-)  |
| 36. Non-amblypygid TO types     |          | (-)   | (-)  | (-)       | (-)       | (+A) (+B)     |      |         |      |
| 37. Opisthosoma general         | (-)      | (-)   | (-)  | (±)       | (+)       | (+)           | (-)  | (-)     | (-)  |
| 38. Pedicel types               | (-)      | (±)   | (±)  | (+)       | (+)       | (+)           | (±)  | (±)     | (±)  |
| 39. Spinning apparatus          | (-)      | (±)   | (+)  | (+)       | (+)       | (+)           | (-)  | (-)     | (-)  |
| 40. Spinnerets                  | (-)      | (-)   | (+)  | (+)       | (+)       | (+)           | (-)  | (-)     | (-)  |
| 41. Spinneret position          |          |       | (-)  | (-)       | (+)       | (+)           |      |         |      |

Table 2 (continued).  
Таблица 2 (окончание).

|                            | Trig  | Urar  | Chim  | Meso    | Myga            | Aran                   | Ambl  | Thel      | Schi  |
|----------------------------|-------|-------|-------|---------|-----------------|------------------------|-------|-----------|-------|
| 42. Spinneret segmentation |       |       | (-)   | (-)     | (+)             | (+)                    |       |           |       |
| 43. ALS and PLS            |       |       | (-)   | (-)     | (±)             | (+)                    |       |           |       |
| 44. AMS                    |       |       | (-)   | (-) (±) | (+A)            | (+B) (+C)              |       |           |       |
| 45. PMS                    |       |       | (+A)  | (-) (±) | (+B)            | (+B)                   |       |           |       |
| 46. Epigastric apparatus   | (-)   | (-) ? | (+)   | (+)     | (+)             | (+)                    | (-)   | (-)       | (-)   |
| 47. Epiandrous spigots     |       |       | (-)   | (+A)    | (+A)            | (-R) (+A)<br>(+B) (+C) |       |           |       |
| 48. Pygidium               | (±)   | (-) ? | (-)   | (±)     | (+)             | (+)                    | (+)   | (-)       | (-)   |
| 49. Flagellum              | (+/-) | (-)   | (-)   | (+/-)   | (+/-)           | (+/-)                  | (+/-) | (-)       | (-)   |
| 50. Flagellar pubescence   |       | (-)   | (-)   |         |                 |                        |       | (-) (+/-) | (+/-) |
| 51. Leg cuticle            | (-)   | (-)   | (-)   | (-)     | (-)(+A)(+B)(+C) | (-)(+A)(+B)(+C)        | (-)   | (-) (+B)  | (-)   |
| 52. Scaly cuticle          | (-)   | (±)   | (±)   | (+)     | (-) (+)         | (-)                    | (+)   | (-)       | (-)   |
| 53. Cuticle glands         | (+)   | (+)   | (+)   | (+)     | (+)             | (+)                    | (+)   | (+)       | (+)   |
| 54. Slit-like pores        | (-)   | (-)   | (-)   | (-)     | (-)             | (-)                    | (+)   | (+)       | (+)   |
| 55. Cerotegument           | (+/-) | (+/-) | (+/-) | (-)     | (+/-)           | (+/-)                  | (-)   | (+/-)     | (+/-) |

Ambl — Amblypygi; Aran — Aranei: Araneomorphae; Chim — Chimerarachnidae; Meso — Aranei: Mesothelae; Myga — Aranei: Mygalomorphae; Schi — Schizomida; Thel — Thelyphonida; Trig — Trigonotarida; Urar — Uraraneida.

(-) — plesiomorphic (ancestral) state; (+) — apomorphic (derived) state, shared acquisition; (+/-) — apomorphic (derived) state, shared loss; (±) — intermediate (transitional) state, vestigial or *in statu nascendi*; (-R) — reversal to ancestral state; (+A) ... (+C) — various apomorphic states.

1. Carapace fovea (1.1.). (-) — absent; (+A) — deep, rounded or transverse, fovea [Filistatidae in basal araneomorphs]; (+B) — longitudinal 'thoracic groove'; (-R) — lost; (+C) — several shallow pits.

2. Set of eyes (1.2.). (-) — lateral minor lenses present; (+/-) — minor lenses lost [*Gelasinotarbus* in trigonotarids].

3. Pattern of major lens eyes (1.2.). (-) — both median and lateral eye groups: median pair + two lateral triads [*Gelasinotarbus* in trigonotarids]; (+A) — single median eye group [*Aculeatarbus* in trigonotarids, Filistatidae in basal araneomorphs]; (-R) — disintegration of single median eye group [few advanced atypoids and 'non-atypoids' in mygalomorphs]; (+B) — median eyes lost, two lateral eyes present or lost.

4. Median eye tubercle (1.2.). (-) — absent; (+A) — present [Filistatidae in basal araneomorphs]; (-R) — lost; (+B) — secondary tubercle [Dysderidae in advanced haplogynes].

5. Number of major lens eyes (1.2.). (-) — eight eyes; (+A) — six eyes on tubercle; (+B) — six sessile eyes; (+C) — six eyes on secondary tubercle [Dysderidae in advanced haplogynes]; (+D) — two eyes or eyeless.

6. Coxae (1.3.). (-) — movable, cylindrical, laterally directed; (+) — widened and consolidated, forming almost all ventral surface of prosoma.

7. Movable coxae IV (1.3.). (-) — unmodified; (+) — with peculiar invaginations.

8. Sternum (1.3.). (-) — broad, consolidated; (+) — extremely narrowed, tripartite.

9. Consolidated sternum width (1.3.). (-) — unmodified, wider than labium; (+) — narrowed to width of the labium, elevated in profile [extant Liphistiidae in mesothelae].

10. Sigilla (1.3.). (-) — absent; (+) — present [Filistatidae and Hypochilidae in basal araneomorphs]; (-R) — lost.

11. Coxosternal 'hair plates' (1.3.). (-) — absent; (+) — present.

12. Chelicera: fang (2.1.). {Cheliceral fang setose in non-tetrapulmonate arachnids, such as *Scorpiones*}. (-) — setose; (+/-) — naked.

13. Chelicera: type (2.1.). (-) — subchelate; (+) — 'jackknife'.

14. 'Jackknife' chelicera: direction of basal joints (2.1.). (-) — plagiognathous [Hypochilidae in basal araneomorphs]; (+A) — orthognathous; (+B) — labidognathous.

15. Venom glands (2.1.). (-) — absent; (±) — endo-cheliceral [Hypochilidae in basal araneomorphs]; (+) — placed into cephalothorax.

16. Pedipalps (2.2.). (-) — unmodified, leg-like, at least in females; (+) — raptorial.

17. Male palps (2.2.). (-) — unmodified, leg-like; (+) — complex, adapted for sperm transfer.

18. Sperm-transferring male palp (2.2.). (-) — bipartite cymbium and complex bulbus; (±) — partially bipartite cymbium and complex bulbus [Hypochilidae in basal araneomorphs]; (+A) — undivided cymbium and simplified pyriform bulbus; (+B) — undivided cymbium and complex bulbus.

19. Leg I (2.3.1.). (–) — unmodified; (±) — antenniform in statu nascendi [*Mesothelyphonus xiaoe* in basalmost thelyphonids]; (+) — antenniform.

20. Patellae (2.3.1.). (–) — unmodified, without CZY; (±) — CZY in statu nascendi; (+) — CZY.

21. Leg setation (2.3.2.). (–) — diverse, at least two types of tactile hairs; (+) — simplified, single type of tactile hairs.

22. Macrosetae (2.3.2.). (–) — absent; (+A) — flattened, longitudinally striated; (+B) — conical, spirally striated; (+C) — conical, longitudinally striated.

23. Chemosensory setae (2.3.2.). (–) — absent; (+) — present.

24. Tarsal claws (2.3.3.1.). {Smooth in all non-tetrapulmonates}. (–) — smooth; (±) — combed in statu nascendi; (+) — combed.

25. Serrate accessory claw setae (SAS) (2.3.3.2.). (–) — absent; (±) — SAS in statu nascendi [Filistatidae and Hypochilidae in basal araneomorphs]; (+) — present; (–R) — lost.

26. Pseudopulvillae (2.3.3.3.). (–) — absent; (+) — present; (–R) — lost [extant Liphistiidae in mesotheles].

27. Tarsal processus (2.3.3.4.). {Present in some non-tetrapulmonates: Scorpiones and Opiliones–Laniatores}. (–) — present; (±) — vestigial; (+) — lost.

28. Trichobothrial pattern (2.3.4.). (–) — simple: 1 or 2 per leg, on single joint — ti or mt, never on ta; (+A) — completely lost; (+B) — complex: several on ti, mt and ta; (+C) — complex: several on ti, 1 on pt.

29. Bothrial principal structure (2.3.5.). {In all non-tetrapulmonate orders bothria simple, cup-shaped}. (–) — simple, cup-shaped; (+) — complex, with ‘diaphragm’ overlapping alveolus; (–R) — secondarily simplified to cup-shaped, ‘diaphragm’-less.

30. ‘Diaphragmed’ bothria (2.3.5.). (–) — simple, ‘diaphragm’ more or less flattened; (+) — complex, ‘diaphragm’ transformed into ‘distal bothrial plate’.

31. Proportion of slit groups and aggregated lyriform organs, LOs (2.3.6.). {Non-tetrapulmonates, such as Scorpiones, have groups of single slits instead of LO}. (–) — mainly slit groups, less than two LOs per leg; (+) — numerous LOs per leg.

32. Lateral LOs on non-metatarsal joints (2.3.6.). (–) — absent; (+) — present.

33. VSO with transversely oriented slits on the metatarsi (2.3.6.). (–) — absent; (+) — present.

34. At least two LOs with particularly oriented slits on the patella (2.3.6.). (–) — absent; (+) — present.

35. Tarsal organs, TOs (2.3.7.). (–) — absent; (+A) — present on tarsi I–IV; (+B) — present only on tarsus of I, antenniform leg.

36. Non-amblypigid TO types (2.3.7.). (–) — lobulated TO; (+A) — pit TO [all ‘Hypochiloidea’ and some Haplogynae families in basal araneomorphs]; (+B) — capsulate TO.

37. Opisthosoma, general appearance (3.1.). {Segmented opisthosoma in all arachnid orders except Aranei and Acari}. (–) — flattened, completely segmented; (±) — subglobular, vestigially segmented; (+) — subglobular, segmentation lost.

38. Prosoma-opisthosoma juncture (3.2.). (–) — non-pedicellar; (±) — ‘ricinuleid type’ of pedicel; (+) — ‘aranean type’ of pedicel.

39. Spinning apparatus (3.3.). (–) — absent; (±) — spigots dispersed on opisthosomal sternites; (+) — spigots localized on spinnerets.

40. Spinnerets (3.3.) (–) — absent; (+) — present.

41. Spinneret position (3.3.). (–) — on middle portion of opisthosoma; (+) — on terminal portion of opisthosoma.

42. Spinneret segmentation (3.3.). (–) — multiarticulated; (+) — few-segmented.

43. Spinnerets: ALS and PLS (3.3.). (–) — spigots arranged along entire length of long multi-articulated lateral spinnerets; (±) — spigots distributed over entire length of few-segmented lateral spinnerets; (+) — spigots localized on apical segments of spinnerets.

44. Spinnerets: AMS (3.3.). (–) — functional, with 1–2 spigots [*Liphistius* in mesotheles]; (±) — vestigial, spigot-less [*Heptathela* in mesotheles]; (+A) — completely lost; (+B) — transformed to cribellum; (+C) — transformed to colulus.

45. Spinnerets: PMS (3.3.). (–) — functional, with single spigot [*Liphistius* in mesotheles]; (±) — vestigial, spigot-less, fused into colulus-like structure [*Heptathela* in mesotheles]; (+A) — completely lost; (+B) — functional, with numerous spigots.

46. Epigastric apparatus (3.4.). (–) — absent; (+) — present.

47. Epiandrous spigots (3.4.). (–) — single row of few flask-shaped spigots; (+A) — numerous dispersed tubular spigots [some Filistatidae in basal araneomorphs]; (–R) — reversion to single row of few flask-shaped spigots [some Filistatidae and Synspermiata in basal araneomorphs]; (+B) — tubular spigots in a single row or two patches; (+C) — completely lost.

48. Pygidium (3.5.). {Multisegmented (four-segmented) pygidium in non-tetrapulmonate Palpigradi}. (–) — multisegmented (four- to three-segmented); (±) — two-segmented; (+) — single-segmented.

49. Flagellum (3.5.). {Flagellum-bearing pygidium in non-tetrapulmonate Palpigradi}. (–) — flagellum present; (+) — flagellum lost.

50. Flagellar pubescence (3.6.). {Regular, whorled flagellar pubescence in non-tetrapulmonate Palpigradi}. (–) — whorled pubescence [*Mesothelyphonus xiaoe* in basalmost thelyphonids]; (+) — whorls lost, irregular pubescence.

51. Leg cuticle (4.). {Scaly cuticle is ancestral, occurring in all tetrapulmonate orders, as well as in some non-tetrapulmonates}. (–) — scaly; (+A) — smooth; (+B) — fingerprint; (+C) — rugose.

52. Scaly cuticle modifications (4.). (–) — typical scaly; (±) — slightly modified scaly, with thickened and raised distal margins on every scale; (+) — strongly modified scaly, ‘pseudoscale’ [Pseudonemesiini in mygalomorphs].

53. Cuticle gland openings (4.). {Cuticle slit-like pores still unrecorded in non-tetrapulmonates}. (–) — absent; (+) — present.

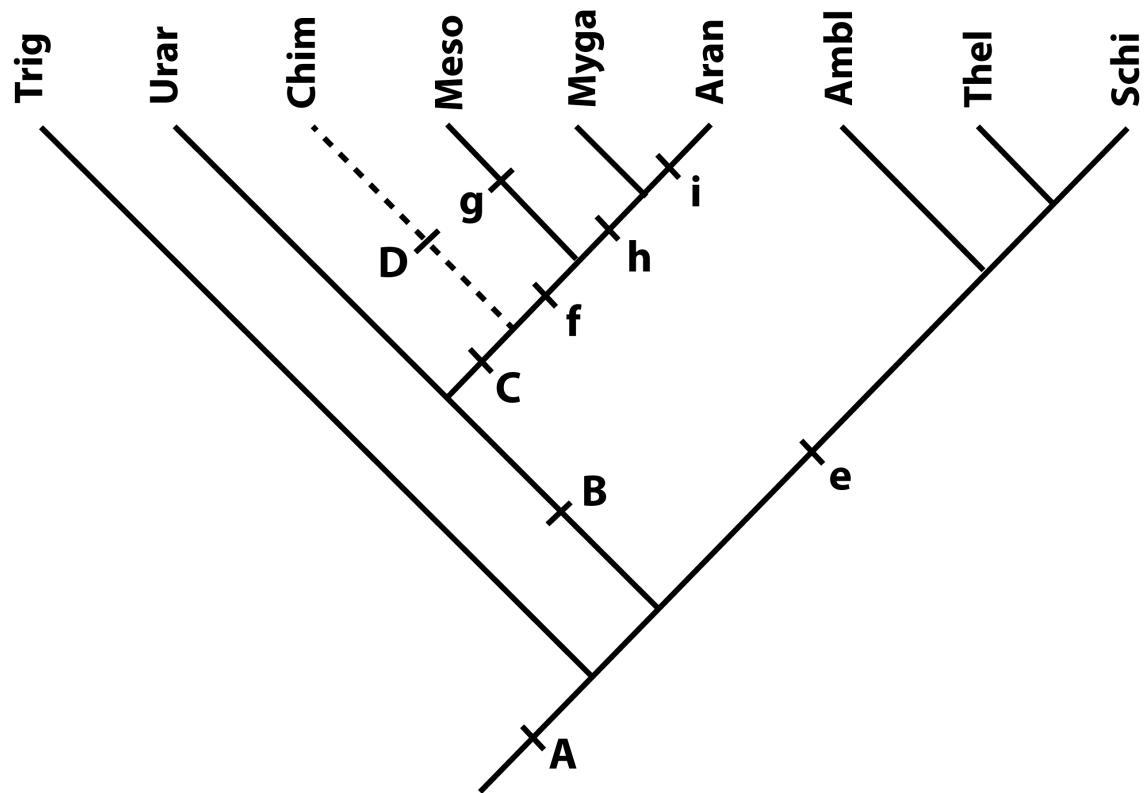


Fig. 24. Apomorphic and plesiomorphic states of 55 chimerarachnid characters, mapped onto the modified Selden *et al.*'s [1991: fig. 3] cladogram of Tetrapulmonata. Abbreviated taxa names and numbering of characters as in Table 2. See also Supplements.

Рис. 24. Апоморфные и плезиоморфные состояния 55 признаков химерарахрид, нанесенные на модифицированную кладограмму Tetrapulmonata Selden *et al.*'s [1991: fig. 3]. Сокращенные названия таксонов и нумерация признаков как в таблице 2. См. также приложения в конце статьи.

**54.** Cuticle slit-like pores types (4). (–) — simple 'tiny slit-like pores'; (+) — more complex 'slit-like gland openings'.

**55.** Cerotegument coated cuticle (4). {Cerotegument presents in non-tetrapulmonate Palpigradi}. (–) — present; (+) — lost.

Apomorphic and plesiomorphic states of these 55 chimerarachnid characters are mapped onto the modified Selden *et al.*'s [1991: text-fig. 3] cladogram of Tetrapulmonata (Fig. 24).

## Conclusions

The 55 available morphological characters of chimerarachnids, listed and numbered in Table 2 and mapped onto the cladogram of Tetrapulmonata (Fig. 24), lead to the following conclusions.

Chimerarachnids completely lack synapomorphies with the Pedipalpi clade. The few apomorphic characters shared between chimerarachnids and individual pedipalpian, such as the absence of minor eye lenses (2), absence of the tarsal process (27), and absence of cerotegument (55), all represent 'apomorphies due to loss' and are most easily explained by parallel evolution.

All apomorphic states of the chimerarachnid characters are restricted to the opposite, non-pedipalpi, lineage of Tetrapulmonata. They form a sequence of synapomorphies of the 'urarachnid + chimerarachnid + 'true spiders' lineage' (11 characters, e.g., jackknife chelicerae (13) and spinning apparatus (39)); synapomorphies of the 'chimerarachnid + 'true spiders' lineage' (10 characters, e.g., sperm-transferring male palps (17) and spinnerets (40)); and autapomorphies of the 'chimerarachnid lineage' (3 characters, e.g., complete loss of PMS (45)).

On the other hand, chimerarachnids demonstrate plesiomorphies relative to 'true spider' lineages: to the order Aranei (7 characters, e.g., absence of venom glands (15) and a completely segmented opisthosoma (37)); to the suborder Mesothelae (2 characters, e.g., a suboval, non-modified sternum (9)); and to the suborder Opisthothelae (7 characters, e.g., absence of sigilla (10) and spigots along the entire length of multiarticulated ALS and PLS (43)).

Chimerarachnids share with Aranei two sets of apomorphies, in one way or another connected with two major evolutionary acquisitions of 'true spiders': the mechanism of indirect sperm transfer by the modified male palp (e.g., epiandrous spigots necessary for spinning a sperm web (46)) and the use of silk (e.g., combed

tarsal claws (24)). In addition to these, there are several microstructural synapomorphies of the ‘chimerarachnid + araneid lineage’ that appear to be unrelated to these behavioral adaptations (e.g., coxosternal hair plates (11) and patellae with CZY (20)).

Symplesiomorphies of chimerarachnids with phylogenetically distant lineages are of particular interest. Thus, the simplest trichobothrial pattern (28) and a non-transformed bothrial diaphragm (30), shared with *Uropygi s.l.* on the one hand and with Trigonotarbita on the other, appear to represent the ancestral condition for Tetrapulmonata. Furthermore, a pygidium of more than two segments (48) and a retained flagellum (49), shared with *Uropygi s.l.* on the one hand and with Palpigradi on the other, appear to have been inherited from pre-tetrapulmonate stages of arachnid evolution.

Perhaps the most important conclusion is that no synapomorphies linking chimerarachnids and uraraneids within the ‘non-pedipalpi lineage’ of Tetrapulmonata have been found. Moreover, no synapomorphies have been found for the two known uraraneids, *Attercopus* and *Permarachne*, that would support Uraraneida as a monophyletic clade. This contradicts the conclusions of Huang *et al.* [2018], who insisted on the monophyly of Uraraneida (including *Chimerarachne*) without, however, listing the specific synapomorphies of the proposed clade.

In our opinion, *Chimerarachne* can be classified as an ‘uraraneid’ only if ‘Uraraneida’ is considered a grade at the base of the ‘non-pedipalpi lineage’ of tetrapulmonates. In the same way, the four-lunged ‘hypochiloids’ are considered currently not a superfamily, but a grade at the base of Araneomorphae [Platnick, 1977: fig. 31].

On the other hand, our results are fully consistent with the phylogeny proposed by Wang *et al.* [2018: 621]: “Our preferred tree (Fig. 5) is based on the Bayesian results <...> which yield a phylogeny of the form (Uraraneida (*Chimerarachne* (Mesothelae + Opisthothelae))) with strong support”. As regards the resulting classification, the union of ‘tailed spiders’ with ‘true spiders’ within a single order Aranei, as proposed by Wunderlich [2019], is in any case more convincing than the inclusion of *Chimerarachne* within the ‘order Uraraneida’, as proposed by Huang *et al.* [2018]. However, establishment of such an ‘expanded Aranei’ [*sensu* Wunderlich, 2019] leads, in our opinion, to an unjustified expansion of the order’s limits and a loss of clarity in the diagnosis of the order.

We support the caution of Wang *et al.* [2018: 621], who avoided making a formal decision regarding the controversial *Chimerarachne*: “We reiterate that there must have been a continuum of character reduction and character acquisition on the lineage towards the modern spiders and we leave open the question of whether Araneae *sensu stricto* should be defined by loss of the telson or by the appearance of the spinnerets and/or male palpal organ”.

Such “a continuum of character reduction and character acquisition” gives, oddly enough, a precise answer to the seemingly rhetorical question posed by Wang *et al.* [2018: 620]: “Is *C. yingi* a spider?” *Chimerarachne* should be considered a spider in exactly the same sense that the monotreme platypus is a mammal.

Previously, a basal split of monophyletic Mammalia into two monophyletic lineages, Theria (Marsupialia + Placentalia) and Prototheria (including Monotremata), was assumed; nowadays, however, ‘Prototheria’ is considered a grade (level of organization) within the mammalian lineage of cynodont mammal-like reptiles [Sereni, 2006: figs. 10.1, 10.2].

The key mammalian characters (e.g., tritubercular postcanine teeth) arose in parallel in various lineages of cynodonts (and, more broadly, in all theriodont lineages of therapsid reptiles); Tatarinov [1977] termed this process the ‘mammalization of theriodonts’. Only Theria acquired the ‘complete mammalian syndrome’ of all seven such key characters, whereas the retained theriodont lineages possessed only part of this set [Tatarinov, 1977: fig. 3].

This general evolutionary pattern, confirmed by paleontological evidence, appears to be quite universal. Alongside the above-mentioned ‘mammalization of theriodonts’ [Lopatin, 2019], there are the well-known ‘arthropodization of arthropods’ [Shubin *et al.*, 1997], the ‘angiospermization of gymnosperms’ [Krassilov, 1997], ‘brachycerization of dipterans’ [Lukashevich, Mostovski, 2023], and others.

Thus, we are faced here with the ‘araneization of tetrapulmonates’: ‘true spiders’ (Aranei) correspond to ‘true mammals’ or ‘live-bearing mammals’ (Theria), whereas *Attercopus*, *Permarachne*, and *Chimerarachne* correspond to various lineages of ‘Prototheria’ (including the extant platypus). By analogy, we may collectively refer to them as ‘protoaraneans’.

It should be noted that the cladistic methodology currently dominant in phylogenetics is poorly suited to dealing with such cases of parallel evolution. Wang *et al.* [2018: 620–621] encountered the fact that the shape of the final cladogram was critically dependent on the chosen calculation method: “Different analysis techniques yield different internal topologies”. It is therefore not surprising that they were forced to avoid answering their own question: “Is *Chimerarachne* a spider?” — since, within the framework of cladistic methodology, this is essentially an unsolvable problem.

#### Compliance with ethical standards

CONFLICT OF INTEREST: The authors declare that they have no conflict of interest.

**Ethical approval:** No ethical issues were raised during our research.

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## Supplements (to Fig. 24)

### Supplement I. Chimerarachnid apomorphies shared with the following lineages (A–C):

**A — Tetrapulmonata lineage (3):** 29 — diaphragmed bothria (reversal in Ambl); 53 — cuticle slit-like pores; 55 — cerotegument lost (retained in Meso and Ambl).

**B — Urar + Chim + Aranei lineage (11):** 12 — naked cheliceral fang; 13 — jackknife chelicera; 22 — macrosetae; 24 — combed tarsal claws; 31 — numerous LOs per leg; 32 — non-metatarsal lateral LOs; 33 — metatarsal VSO; 34 — 2+ LOs on patella; 35 — tarsal organs; 39 — a spinning apparatus; 52 — modified scaly cuticle.

**C — Chim + Aranei lineage (10):** 2 — minor eye lenses lost (parallel in Ambl and Schi); 3 — single median eye group (reversal in higher Myga and Aran); 4 — eye tubercle (lost in Aran); 11 — coxosternal hair plates; 17 — sperm-transferring male palps; 20 — patellae with CZY; 26 — pseudopulvillus (lost in Opisthothelae); 27 — tarsal processus lost (parallel in Schi and partial Thel); 40 — spinnerets; 46 — epigastric apparatus.

### Supplement II. Chimerarachnid autapomorphies.

**D (3):** 5 — eye number reduced to six (parallel in some Aran); 25 — SAS in statu nascendi (parallel in some Aran); 45 — complete loss of PMS.

### Supplement III. Chimerarachnid plesiomorphies, opposed to synapomorphies of the following lineages (e–i):

**e — Pedipalpi (6):** 6 — unmodified, movable coxae; 8 — unmodified, non-tripartite sternum; 16 — unmodified, non-raptorial palps; 19 — unmodified, non-antenniform leg I; 21 — diverse, non-simplified leg setation; 54 — simple slit-like cuticular pores.

**f — Aranei (7):** 1 — fovea absent; 14 — plagiognathous chelicera; 15 — venom glands absent; 23 — chemosensitive setae absent; 37 — opisthosoma completely segmented; 38 — non-‘aranean’ type of pedicel; 47 — single row of few flask-shaped epiandrous spigots (reversal in some haplogynae Aran).

**g — Mesothelae (2):** 7 — coxae IV unmodified; 9 — sternum suboval, wider than labium, non-elevated in profile.

**h — Opisthothelae (7):** 10 — sigilla absent; 18 — male palp with complex bulbus and bipartite cymbium; 41 — spinnerets on the middle portion of opisthosoma; 42 — long, multiarticulated spinnerets; 43 — spigots along the entire length of ALS and PLS; 44 — AMS with 1–2 spigots; 51 — only scaly leg cuticle.

**i — Araneomorphae (1):** 36 — lobulated TO.

### Supplement IV. Chimerarachnid symplesiomorphies independently retained in various lineages (not mapped on cladogram)

**Symplesiomorphies shared with Trig, Thel and Schi (2):** 28 — simplest trichobothrial pattern, 1–2 trichobothria per leg; 30 — bothrial diaphragm not transformed into ‘distal bothrial plate’.

**Symplesiomorphies shared with Urar, Thel and Schi (2):** 48 — 3+ segmented pygidium; 49 — flagellum retained.

**Symplesiomorphies shared with Urar (1):** 50 — whorled pubescence of flagellum.