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The cuticle of liphistiomorph spiders is coated with a cerotegument: the first record for the order (Arachnida: Aranei: Liphistiomorphae)

Кутикула лифистиоморфных пауков покрыта церотегументом: первое указание для отряда (Arachnida: Aranei: Liphistiomorphae)

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КЛЮЧЕВЫЕ СЛОВА: Arachnida, Araneae, Mesothelae, Amblypygi, морфология кутикулы, церотегумент.

ABSTRACT: The cerotegument, a secretory layer over the epicuticle, previously unknown in the order Aranei, is discovered in liphistiomorphan spiders from both extant families: Liphistiidae and Heptathelidae. The cuticle of the examined spiders turned out to be closely similar to that of Amblypygi in the presence of a cerotegument as well as in the general cuticular morphology. The cerotegument appears to be an additional putative synapomorphy of the Aranei + Amblypygi clade of the Tetrapulmonata arachnids. Its structure differs between the families Liphistiidae and Heptathelidae and seems to be family-specific, as it has previously been demonstrated for various amblypygid families.

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РЕЗЮМЕ: Церотегумент — секреторный слой со сложной трехмерной структурой, покрывающий эпикутикулу, неизвестный ранее у пауков — обнаружен в обоих современных семействах лифистиоморфов, Liphistiidae и Heptathelidae. По общей структуре кутикулы и наличию церотегумента лифистиоморфы четко отличны от всех прочих представителей отряда, и при этом весьма сходны с фринами (Amblypygi). Церотегумент может считаться еще одной синапоморфией клады Aranei + Amblypygi в составе тетрапульмонатных арахнид. Тонкая структура церотегумента в семействах Liphistiidae и Heptathelidae различается и кажется диагностичной, так же, как это уже было установлено для разных семейств фринов.

1. Introduction

The cerotegument is a thick secretory extracuticular coating with a complicated three-dimensional structure. It has evolved independently in several unrelated lineages of arthropods, which inhabit semi-aquatic and floodable habitats. The cuticle of such arthropods, e.g. mites [Pugh *et al*., 1987] and millipedes [Adis *et al*., 1988], is water-repellent, which facilitates so-called 'plastron respiration' in semi-aquatic conditions. This is due to Cassie's law in which an air film is formed between the cuticle and the water, which may act as a physical gill [Wolff *et al*., 2016].

Plastron respiration was quite unexpectedly discovered in whip-spiders (Amblypygi), large-sized arachnids from the Tetrapulmonata clade: "All previous examples of plastron respiration have involved animals with tracheal systems, but amblypygids respire through the use of two pairs of book lungs. This study provides the first example of plastron respiration not only in the order Amblypygi, but also, in any non-tracheate arthropod" [Hebets, Chapman, 2000: 13]. Wolff *et al*. [2016] have connected this ability of whip-spiders with their water-repellent cerotegument, formed by a colloidal extracuticular secretion self-assembling into hierarchical microstructures. The microstructure of the cerotegument turned out to be quite diverse in various families and genera of Amblypygi, thus supplementing diagnostic characters of these taxa [Wolff *et al*., 2017; Seiter *et al*., 2022]. Additionally, the thick three-dimensional cerotegument of whip-spiders was shown to serve as a substrate for growth of potentially symbiotic fungi [Gibbons *et al*., 2019].

Extracuticular coats have also been reported in other arachnid orders from the Tetrapulmonata clade

and the Palpigradi (as its probable sister group): "Solid epicuticular secretions are present in Amblypygi and Thelyphonida. […] Unlike Amblypygi, however, these secretion layers were generally amorphous or irregular in Thelyphonida [...] Therefore, the secretion crust of Thelyphonida is appropriately referred to as an epicuticular layer of an amorphous or granular structure, rather than a cerotegument. In contrast to Amblypygi and Thelyphonida, solid epicuticular secretions were absent in the exemplar species of Schizomida and Palpigradi" [Seiter *et al*., 2021: 1167]. To our knowledge, no such secretory coats have so far been reported in the fourth lineage of the Tetrapulmonata clade, the order Aranei.

In the course of our investigation of cuticular microstructures of segmented spiders (Eskov *et al*., 2024), we noticed structures, which seemed indistinguishable from cerotegument of whip-spiders. These were found in liphistiomorph spiders, representing both extant families: Liphistiidae and Heptathelidae. The present paper contains a review of these structures in the examined taxa, as well as a comparison between the cerotegument of Amblypygi and Liphistiomorphae.

2. Material and methods

SEM images of cuticle were taken from the four species of liphistiomorph spiders, represent both Liphistiidae and Heptathelidae and from whip-spiders (Charinidae), as well as from mygalomorph and araneomorph spiders, whip-scorpions and schizomids.

It should be noted that liphistiids and heptathelids are considered sometimes as families, sometimes as subfamilies of the unite family Liphistiidae [see Xu *et al*., 2015]. In any case, they are regarded as two monophyletic sister taxa. Thus, their formal ranking is insufficient for our study, and we prefer more old, familiar naming.

The studied specimens belong to the following institutions: AMNH — American Museum of Natural History, New York, USA; MMUE — The Manchester Museum, University of Manchester, UK; ZMMU — Zoological Museum of the Moscow State University, Moscow, Russia.

Aranei: Liphistiomorphae

Family Liphistiidae Thorell, 1869
Liphistius desultor Schiødte, 1849
♀ (MMUE A-136): *Malaysia*, Penang, July 1977 (E.W. Classey leg.).
Liphistius panching Platnick et Sedgwick, 1984
♀ (AMNH): *Malaysia*, Gua Panching, 31.07.1982 (W. Sedgwick leg.).

Family Heptathelidae Kishida, 1923
Heptathela sp.
♀ (ZMMU): *Japan*, Kyushu Isl., env. of Beppu, forest litter, 7.07.1973 (A.G. Ponomarenko leg.).
Vinathela sp.
♀ (ZMMU): *Vietnam*, central Vietnam, 12°35′39.2″N, 108°44′18.3″E, 26.01.2024 (Khang Nguyn leg.).

Aranei: Mygalomorphae

Family Macrothelidae Simon, 1892
Macrothele sp.
♀ (ZMMU): *Vietnam*, Cat Tien NP, 11.458922°N 107.364657°E, 25.01.2024 (D. Osipov leg.).

Aranei: Araneomorphae

Family Araneidae Clerck, 1757
Melychiopharis sp.
♀ (ZMMU): *Peru*, Junin Prov., Calabaza, 11°30′33″S, 74°50′35″W, 2500 m, cloud forest, in epiphytes, 19.09.2017 (K. Eskov leg.).

Amblypygi

Family Charinidae Guintero, 1986
Charinus sp.
Inadult (ZMMU): *Peru*, Junin Region, Pichiquia, 11°23′ 07″S, 74°06′05″W, 500 m, valley forest, under bark of logs, 26.09.2017 (K. Eskov leg.).

Uropygi

Family Thelyphonidae Lucas, 1835
Thelyphonus (?) sp.
♀ (ZMMU): *Vietnam*, 5 km N of Ankhe, under stones, 21.10.1979 (V.K. Yanushev leg.).

Schizomida

Family Hubbardiidae Cook, 1899
Trythyreus (?) sp.
♀ (ZMMU): *Peru*, Junin Region, 16 km NW from Satipo, Rio Venado, 1120 m, 14.09.2017, slope forest, in litter (K. Eskov leg.).

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

Abbreviations of leg joints: fe — femur, pt — patella, ti — tibia, mt — metatarsus, ta — tarsus.

Nomenclature of the cerotegument details is given after Wolff *et al*. [2017].

3. Results

Lehtinen [1996: 403] stated that the liphistiomorph cuticle is unique among spiders: "The leg skin structure has been preliminarily studied in various mygalomorph and in both liphistiomorph families. The leg skin structure of Liphistiomorpha […] could be classified as scaly, but it is unique among Araneae. […] The heptathelid 'scales' are separate, rounded triangular extensions of the skin, well separated by continuous, nearly smooth skin. It is difficult to derive this type from the basic scaly type of Amblypygi, nor do any of the mygalomorph groups seems to share this autapomorphy of the recent Liphistiomorpha".

We agree with Lehtinen's general conclusion about the uniqueness of the liphistiomorph cuticle, but some of his arguments should be corrected. He adequately described "the heptathelid 'scales'", and they certainly have nothing in common with the true 'scale/imbricate' type of cuticle.

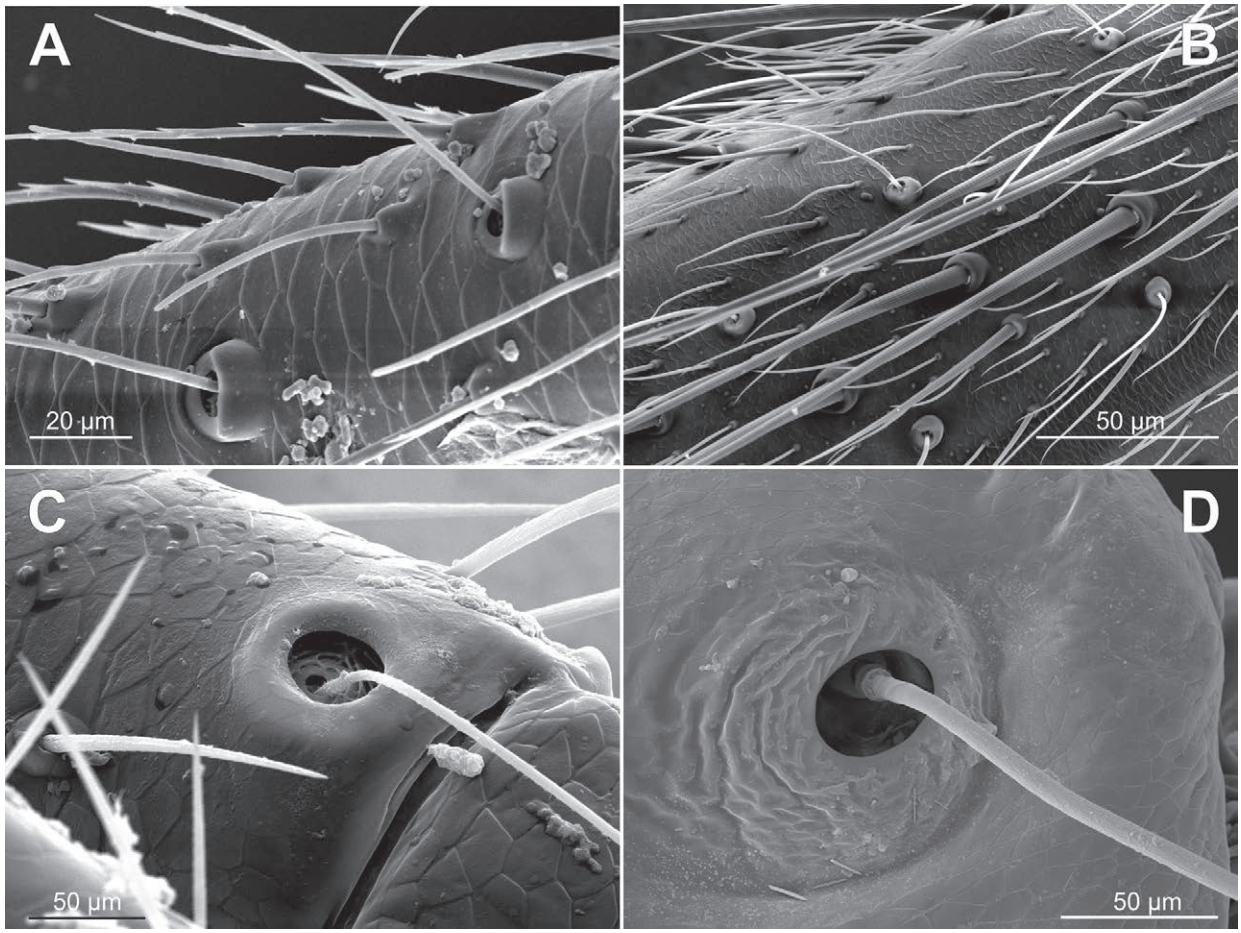

Fig. 1. Scale/imbricate leg cuticle in various arachnids. A — *Melychiopharis* sp. (Aranei: Araneomorphae), mt 3 dorsally; B — *Macrothele* sp. (Aranei: Mygalomorphae), ti 3 dorsally; C — *Trythyreus* (?) sp. (Schizomida), dorsodistal end of ti 2; D — *Thelyphonus* (?) sp. (Uropygi), dorsodistal end of ti 4.

Рис. 1. Чешуйчатая/черепитчатая кутикула различных арахнид. A — *Melychiopharis* sp. (Aranei: Araneomorphae), метатарзус 3 дорзально; B — *Macrothele* sp. (Aranei: Mygalomorphae), голень 3 дорзально; C — *Trythyreus* (?) sp. (Schizomida), дорзодистальная оконечность голени 2; D — *Thelyphonus* (?) sp. (Uropygi), дорзодистальная оконечность голени 4.

The typical scale cuticle consists of flat polygonal plates, overlapping distally. It is widespread among spiders, both araneomorphs (Fig. 1A) and mygalomorphs (Fig. 1B), as well in other arachnid orders, e.g. in Schizomida (Fig. 1C) and Uropygi (Fig. 1D). So, it could even be supposed that this is the basal cuticular type, at least in the Tetrapulmonata. The liphistiomorph 'scales', protruding "rounded triangular extensions of the skin", well separated from each other, look entirely different (Fig. 2A–B). On the other hand, they seem relevant rather to the petal-like outgrowths of the Amblypygi leg cuticle (Fig. 2E–F). The latter also has nothing in common with the "basic scaly type". We propose the name 'pseudoscale' for this cuticular type.

Another, and more significant, similarity between the liphistiomorph cuticle and that of whip-spider is the extracuticular cerotegument, unreported previously in the order Aranei and not found by us in any other spider lineage. The water-repellent cerotegument of whip-spiders is formed by a colloidal extracuticular secretion self-assembling into hierarchical microstructures. This secretion is produced by the cuticular "major glands" with characteristic "openings with valve-like brim" [Wolff *et al*., 2017: fig. 7B, F]. The same structures were found also in the liphistiomorphs (Fig. 4A, C).

The main components of the whip-spider cerotegument are the hydrophobic globules, sometimes with connecting fibres (Fig. 3B, C; Wolff *et al*., 2017: fig. 1E). The surface of the globules, as well as the presence or absence of the connecting fibres, differs in various families/genera of Amblypygi and is stated as diagnostic [Wolff *et al*., 2017: fig. 6]. It should be noted that, at least in Charinidae, two types of fibres can be distinguished: thicker, directly connected globules, and thinner, forming a solid felt-like coat of a cuticle. The former type of fibre is present in the cerotegument of the carapace, but is absent in the cerotegument of the pseudoscale leg cuticle (cf. Figs 3B–C and 3D–F).

The general appearance of the liphistiomorph cerotegument is quite different. Instead of the large regular globules more or less evenly distributed over the surface, as in whip-spiders (Fig. 3C, D), there are numerous small globules (or sub-globular structures) forming linear aggregations along the edges of the protruded extensions

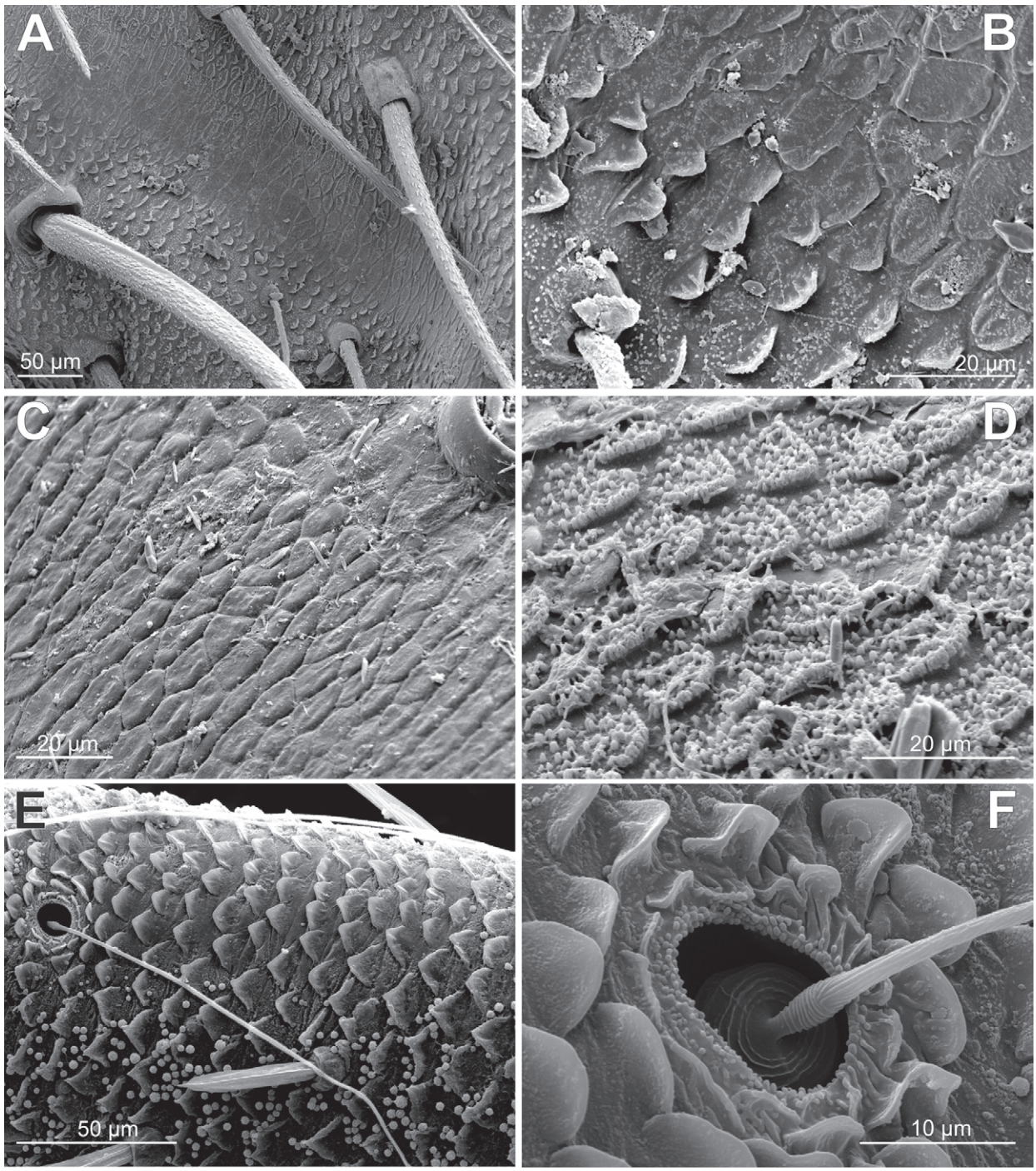

Fig. 2. Pseudoscale leg cuticle in Liphistiomorphae (A–D) and Amblypygi (E–F). A — *Heptathela* sp., ti 3 dorsally, area devoid of cerotegument; B — the same, enlarged; C — *Liphistius panching*, pt 3 dorsally, area devoid of cerotegument; D — *L. panching*, ti 3 dorsally, area with cerotegument; E — *Charinus* sp., ti 3 dorsally; F — the same, enlarged.

Рис. 2. Псевдочешуйчатая кутикула ног Liphistiomorphae (A–D) и Amblypygi (E–F). A — *Heptathela* sp., голень 3 дорзально, участок лишенный церотегумента; B — то же, увеличено; C — *Liphistius panching*, колено 3 дорзально, участок лишенный церотегумента; D — *L. panching*, голень 3 дорзально, участок с церотегументом; E — *Charinus* sp., голень 3 дорзально; F — то же, увеличено.

of the pseudoscale leg cuticle (Figs 2D; 4B–C). When viewed from above, this creates the illusion of a ‘scale’ pattern (Figs 4A, D; 5A, D). Connecting fibres of various shapes are always present (Figs 4B; 5B).

The cerotegiments of Liphistiidae and Heptathelidae differ from each other. The globules in both studied species of *Liphistius* Schiødte, 1849 are transformed to subconical structures (Fig. 5C, F), whereas in both studied heptathelid genera, *Heptathela* Kishida, 1923 and *Vinathela* Ono, 2000, they remain spherical (Fig. 4C, F), although reduced in dimensions relative to the amblypygid ones more than twice (Fig. 2D, E). The fibres

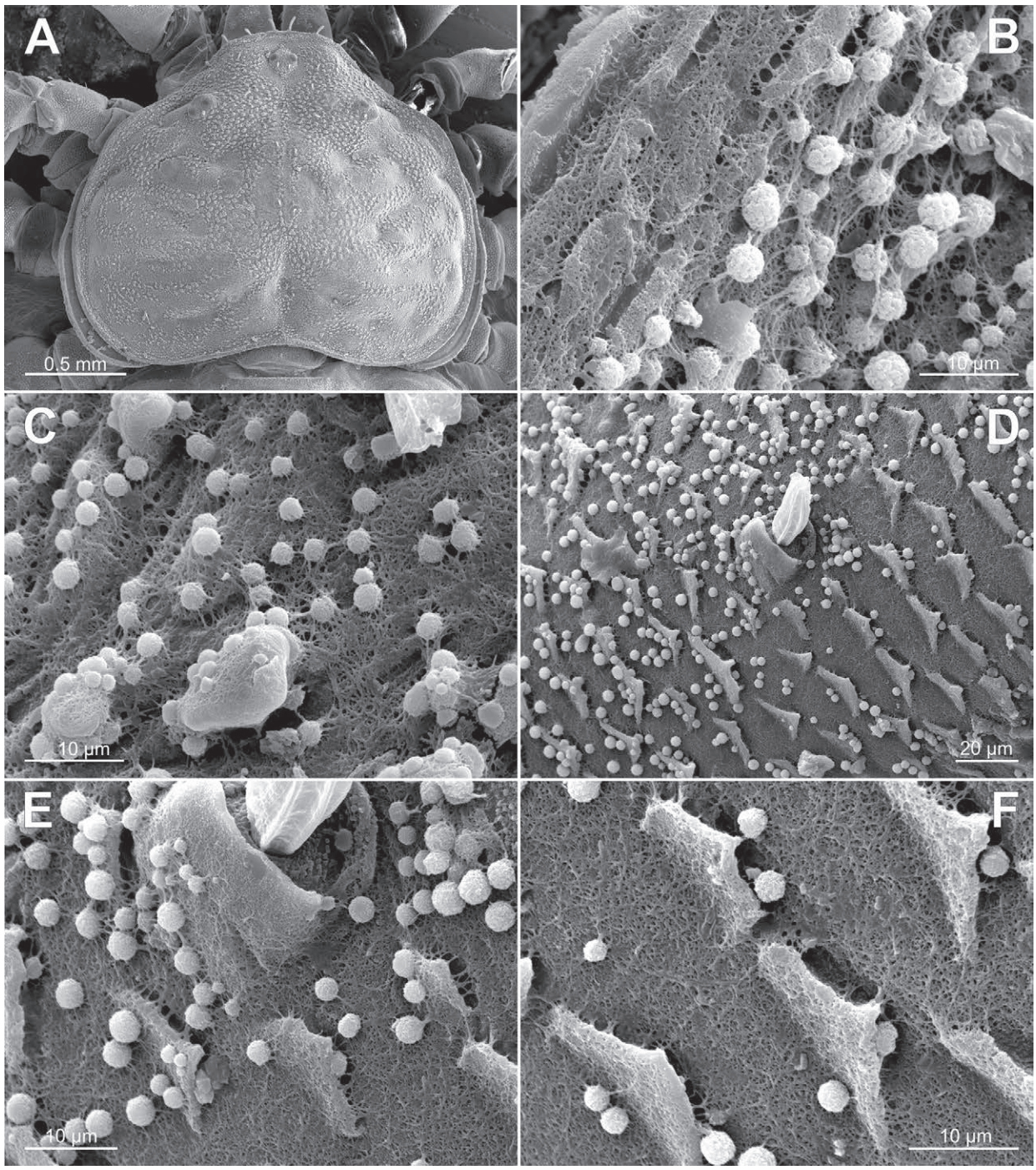

Fig. 3. Cerotegument of Amblypygi (*Charinus* sp.). A — carapace, general appearance; B — edge of carapace, enlarged; C — middle part of carapace, enlarged; D — fe 3 dorsally; E — the same, enlarged; F — the same, enlarged.

Рис. 3. Церотегумент Amblypygi (*Charinus* sp.). A — карапакс, общий вид; B — край карапакса, увеличено; C — средняя часть карапакса, увеличено; D — бедро 3 дорзально; E — то же, увеличено; F — то же, увеличено.

in heptathelids form a dense irregular grid (Fig. 4B–C), whereas in liphistiids there are relatively sparse direct connections between the 'globules' (Fig. 5B–C).

Thus, the fine structure of the cerotegument in liphistiomorph spiders seems diagnostic, at least on family level, as it has been demonstrated for various families and genera of Amblypygi [Wolff *et al*., 2017; Seiter *et al*., 2022].

Discussion

Our targeted search for a cerotegument in other archaic spider lineages (mygalomorphs, 'hypochiloids' and synspermiates above all) have yielded no results. We have found some interesting unreported epicuticular structures (e.g. the remarkable frost-like coat of wax crystals in the basal filistatid genera *Filistata* Latreille, 1810 and *Zai-*

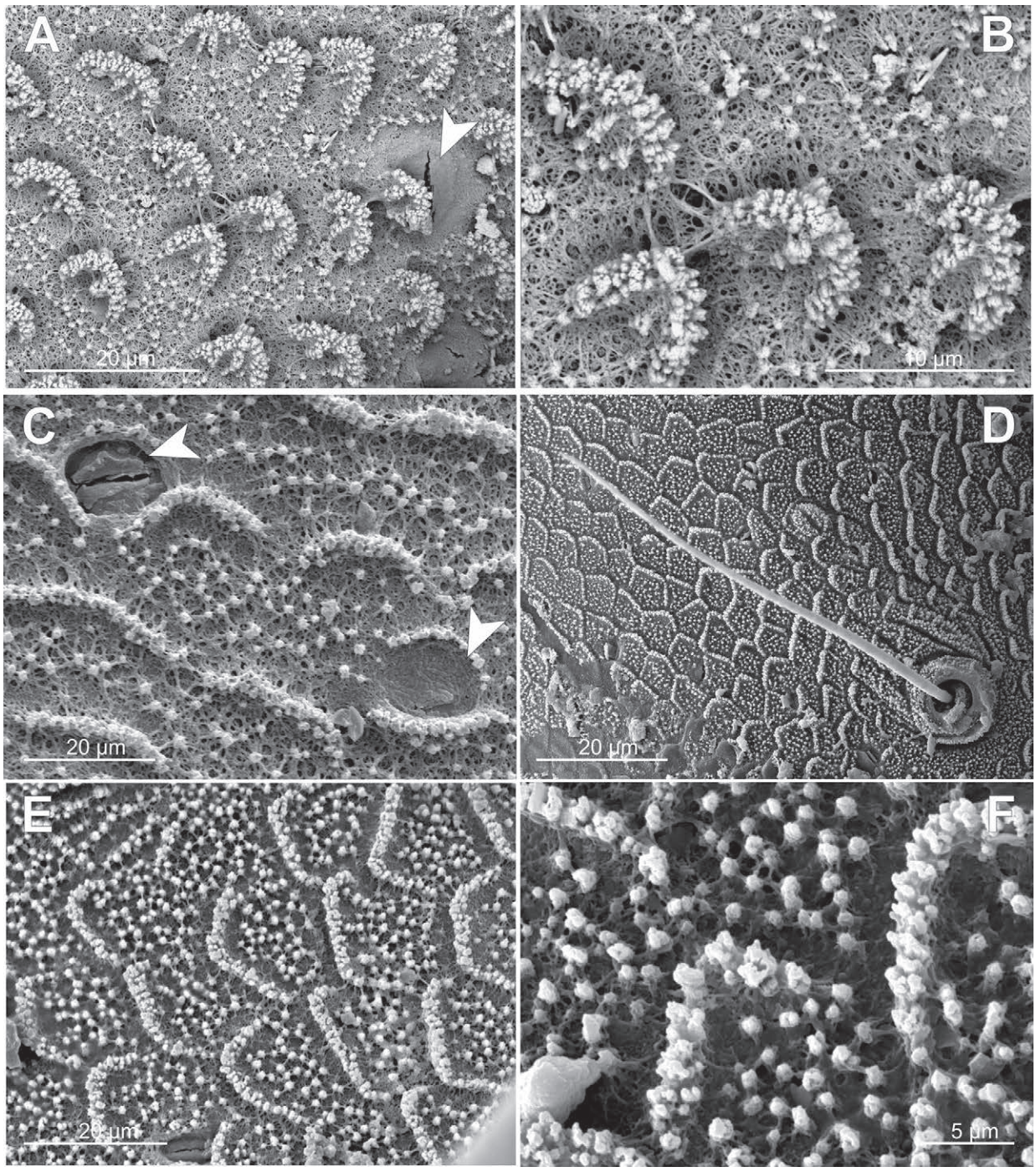

Fig. 4. Cerotegument of Heptathelidae, *Heptathela* sp. (A–C) and *Vinathela* sp. (D–F). A — ti 3 dorsally; B — the same, enlarged; C — fe 3 ventrally; D — fe 3 ventrally; E — the same, enlarged; F — the same, enlarged. Arrows — "major gland openings with valve-like brim" (by Wolff *et al*. [2017]).

Рис. 4. Церотегумент Heptathelidae, *Heptathela* sp. (A–C) and *Vinathela* sp. (D–F). A — голень 3 дорзально; B — то же, увеличено; C — бедро 3 вентрально; D — бедро 3 вентрально; E — то же, увеличено; F — то же, увеличено. Стрелки — "отверстия больших кутикулярных желез с клапанопообразным краем" (по Wolff *et al*., [2017]).

tunia Lehtinen, 1967), but none of them contains either the potentially water-repellent globules, or the connecting fibres. Thus, the cerotegument of Liphistiomorphae seems to be a unique feature among representatives of the order.

The Liphistiomorphae and the Amblypygi are the only pulmonate arachnids that possess a cerotegument. But is it their synapomorphy or a result of a parallel independent evolution, as it is in some other, certainly unrelated, arthropod lineages? In our opinion, the combination of the cerotegument with the unique 'pseudoscale' type of the leg cuticle in both taxa testifies in favour of the unity of origin the both cuticular structures. Thus, the

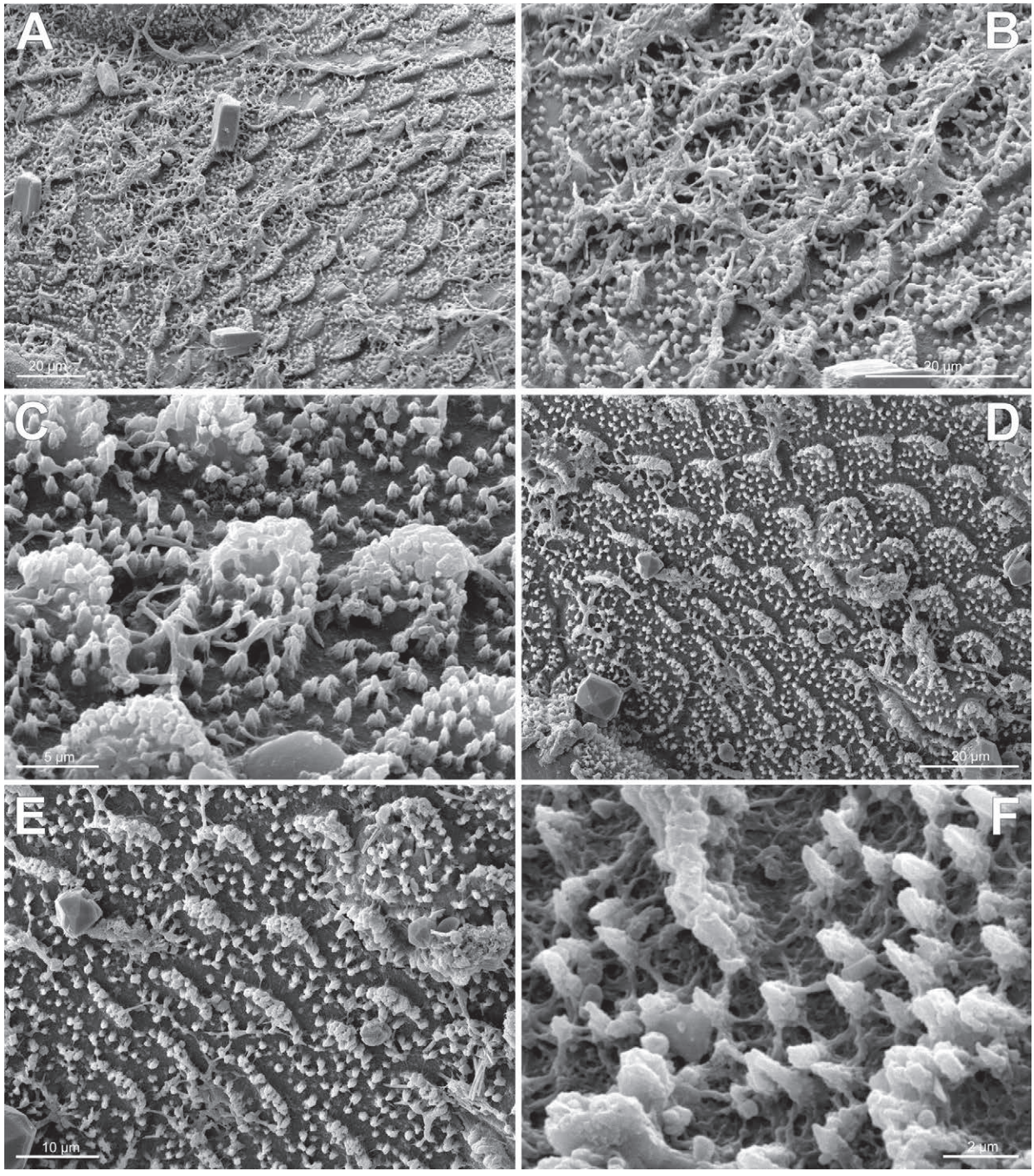

Fig. 5. Cerotegument of Liphistiidae, *Liphistius panching* (A–C) and *Liphistius desultor* (D–F). A — ti 3 dorsally; B — the same, enlarged; C — mt 3 dorsally; D — ti 3 dorsally; E — the same, enlarged; F — ta 3 dorsally.

Рис. 5. Церотегумент Liphistiidae, *Liphistius panching* (A–C) и *Liphistius desultor* (D–F). A — голень 3 дорзально; B — то же, увеличено; C — метатарзус 3 дорзально; D — голень 3 дорзально; E — то же, увеличено; F — тарзус 3 дорзально.

cerotegument is one more putative synampomorphy of the clade Aranei + Amblypygi within the wider arachnid clade Tetrapulmonata. At the same time, the loss of the cerotegument by all the non-liphistiomorph spiders is one more synapomorphy of the suborder Opisthothelae.

The function of the liphistiomorph cerogument is unclear. The water-repellent ceratogument of whip-spiders promotes the survival of these animals due to the 'plastron respiration' during flooding of their habitats [Hebets, Chapman, 2000; Wolff *et al*., 2016]. However, in the liphistiomorph case such an explanation does not seem convincing. First, the water-repellent properties of the liphistiomorph ceratogument are certainly less pronounced than those of the whip-spider one (or even

absent altogether), because of decreased globule size in the heptathelids and the disappearance of the globules in liphistiids (see above). Second, liphistiomorphs are the 'trap-door spiders': they live in burrows sealed with a thin circular woven door, which is disguised with soil and moss [Murphy, Murphy, 2000]. The risk of flooding for these animals is therefore minimal; Platnick & Sedgwick [1984: 4] explicitly say that flooding is not usually a problem for liphistiomorph spiders.

One hypothesis may be proposed. The segmented spiders have flourished in the Carboniferous and inhabited the so-called 'coal forests'. If those extinct Carboniferous animals did not belong to the 'trap-door spiders' a cerotegument may have been quite useful in these semi-aquatic and floodable habitats. In this scenario it would be retained in extant liphistomorphs as a vestigial structure, and the cerotegument of the genus *Liphistius*, completely lacked the globular structures, seems a final point of such an evolutionary trend.

Conclusions

1. A cerotegument is recorded in the order Aranei for the first time.

2. It seems to be present only in the suborder Liphistiomorphae, in both families, Liphistiidae and Heptathelidae.

3. The cerotegument and the particular 'pseudoscale' type of the leg cuticle are the additional synapomorphies of the clade Aranei + Amblypygi in Tetrapulmonata arachnids.

4. The fine structure of a cerotegument in Liphistiomorphae turned out to be diagnostic for the families, as it has been demonstrated previously for the various families and genera of Amblypygi.

5. The function of the liphistiomorph cerotegument is unclear. Probably it was useful for the ancient segmented spiders which flourished in the semi-aquatic and floodable habitats of the Carboniferous 'coal forests', and in extant liphistiomorphs it persists as a vestigial structure, having lost its former physiological function.

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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