

**The superfamily Plateremaeoidea (Acari: Oribatida) I.
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nov. from Argentina and its ontogenetic development,
and the new family Gaboneremaeidae**

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The superfamily Plateremaeoidea (Acari: Oribatida)

I. The family Plateremaeidae, *Plateremaeus cebilae* sp. nov. from Argentina and its ontogenetic development, and the new family Gaboneremaeidae

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Abstract: This is the first in a planned series of revisions of the superfamily Plateremaeoidea. A new species of Plateremaeidae, *Plateremaeus cebilae* sp. nov., is described from Argentina based on adults and immatures. This species is easily distinguishable from other congeners by: cerotegument covering body and legs; polyhedral structures of filaments on prodorsum, notogaster, epimeres, and ventral region; interlamellar setae covered by rose-flower-shaped cerotegument; sensillus uncinata; five pairs of notogastral setae situated posteriorly; pedotectal tooth well visible; epimeral neotrichy 8[7-9]-5[4-6]-6[5-6]-8[7-9]; genital plate ovoid, with nine pairs of small barbate setae in two rows; anal plate elongated-ovoid, with five pairs of setae; genito-anal bridge moderately developed. The ontogeny of this species is described. Gaboneremaeidae fam. nov. and *Gaboneremaeus* gen. nov. are established, with *G. patriciae* sp. nov. from Gabon as its type species. *Gaboneremaeus patriciae* sp. nov. is distinguished by: cerotegument of two types, covering body and legs; prodorsum with cuticular folds; bothridial ring sigmoid, complex; notogaster rounded, pleurophragma present; three pairs of posterior setae; posterior medial zone with small rounded pit; epimeral zone well delimited, with epimeric furrows, apodemes and cuticular thickening; parastigmatic enantiophysis and discidium present; epimeral hypertrichy 9[8-10]-6-9[8-10]-9[8-11]; nine pairs of barbate genital setae in two rows; anal plate with ten pairs of setae inserted in paraxial groove of each valve.

Keywords: Taxonomy - juveniles - leg setation - developmental stages.

INTRODUCTION

The Plateremaeoidea (a senior synonym of Gymnodamaeidae) is a very complex group. Many authors have worked on the different families that comprise the superfamily (see Hunt & Lee, 1995; Norton & Behan-Pelletier, 2009; Paschoal, 1989; Paschoal & Johnston, 1982a, b; Walter, 2009; Woas, 1992, 2002). These studies have highlighted the complexity, ambiguities and controversies of the included genera and species. Studies of the cerotegument layer were poor, or were performed without obtaining detailed information, although the cerotegument provides important character states.

There have also been some interesting publications on ontogenetic development: Bayartogtokh & Ermilov (2013); Bayartogtokh & Schatz (2009); Bulanova-Zakhvatkina (1967); Canestrini & Fanzago (1877); Eguaras *et al.* (1990); Ermilov & Anichkin (2011); Ermilov & Łochyńska (2010); Ermilov *et al.* (2010); Fernandez & Cleva (1999, 2010); Fernandez (1987, 1990); Fernandez *et al.* (2021); Grandjean (1931a, b, 1933a, b, 1934, 1949a, b, 1964); Lions (1970); Seniczak & Seniczak (2011, 2019); Seniczak *et al.* (2012); Seniczak *et al.* (2016); Seniczak *et al.* (2020); Walter (2009).

Initially we planned to produce a complete revision of the superfamily, but given the difficulty and extensiveness of

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the task, we divide this study into several parts, of which this is part 1. The present study is based on material from Argentina and from the Republic of Gabon.

MATERIAL AND METHODS

We studied the specimens with optical microscopy (classic and confocal) and with scanning electron microscope (SEM). The specimens were collected from forest litter using a standard Berlese-Tullgren Funnel. They were extracted alive and transferred to boxes with plaster-charcoal as substrate. Subsequently, a few specimens were separated for description, whereas others were reared to obtain immatures. These stocks were installed in controlled chambers with a temperature of 20°C and 60% relative humidity and were examined twice a day. Specimens were studied by means of light microscopy following the techniques described by Grandjean (1949a) (see Travé & Vachon, 1975) and Krantz & Walter (2009). The presence of a cerotegumental layer is a problem in optical microscopy as it hinders or prevents observations, and it needs to be removed. In our case the layer was very resistant and difficult to remove, possibly because specimens were fresh. We used different methods, mostly without satisfactory results. With *P. cebilae* sp. nov. we got very good results using the technique proposed by Grandjean (1949a), which consists of putting the animals in chloroform for one day. After that time the cerotegument loses its adherence to the cuticle and is easily removable with the help of an insect pin. Subsequently, the specimens were macerated in a warm 70% lactic acid solution for a week. With *G. patriciae* sp. nov. the situation was more difficult. We tried many different alternatives without success. We were able to dissolve the cerotegument by placing adults in 15% sodium hypochlorite for forty-five minutes. With immatures it was impossible to eliminate the cerotegument, which prevented us from conducting ontogenetic studies.

Drawings were made using a Zeiss Axioskop microscope equipped with a drawing tube and a photo camera. Adults and immatures were studied under a Carl Zeiss Sigma scanning electron microscope (SEM) at the Material Analysis Laboratory, Physical Institute "Enrique Gaviola" LAMARX, Faculty of Mathematics, Astronomy, Physics and Computation, Argentina National University, Cordoba. All specimens were fixed in 2.5% glutaraldehyde buffered in a cacodylate buffer (pH 7.4, 0.05 mol) at 4-5°C. Postfixation with 1% OsO₄ in cacodylate buffer (pH 7.4, 0.05 mol) for two hours; rinsing in cacodylate buffer solution (pH 7.4, 0.05 mol); next dehydration in a series of graded ethanols and drying in a critical point apparatus. All specimens were mounted on aluminium stubs with double-sided sticky tape and then gold-coated in a sputter apparatus (see Alberti & Fernandez, 1988, 1990; Fernandez *et al.*, 1991).

Measurements: Total length (from tip of rostrum to posterior edge of notogaster) and width (widest part of

notogaster) are in micrometers (µm). In some cases, the measurements are given in nanometers (nm). The numbers between parentheses are the maximum and minimum values. Leg chaetotaxy was studied with standard, polarized and phase contrast microscopes and with a SEM. The setal formula of the legs include the number of solenidia (in parentheses); the tarsal setal formula includes the famulus (ε).

Morphological terminology: Morphological terms and abbreviations used are those developed by Grandjean (see Travé & Vachon, 1975; Norton & Behan-Pelletier, 2009). As a number of specific morphological characters have not previously been described in detail, and no terminology or abbreviations exist, we have included the following in the text and in the figures for the sake of clarity: elevated central anal zone (*e.z*); concave anal depression (*c.d*); low anal zone (*l.z*); associated promontories (*a.p*); basal cerotegumental zone (*b.c.z*); basal layer (*b.l*); basic ball-shaped cerotegumental structures (*b.s*); cuticular fold (*c.f*); cuticular thickening (*c.t*); depressed zone (*d.z*); elevated irregular cells (*e.i.c*); flat irregular structure (*f.i.s*); flat granulous sheet (*f.g.s*); irregular convex structures (*i.c.s*); isolated promontories (*i.p*); lobe-like structures (*l.l.s*); notogastral margin (*ng.m*); parastigmatic enantiophysis (*p.e*); pedotectal tooth (*pd.to*); pleurophragma (*phr*); pre-genital sclerite (*p.g.s*); posterior digitiform depression (*p.d*); rose flower sheet (*r.f.s*); small irregular to polyhedral promontories (*s.i.p*); small ovoid promontories (*s.o.p*); starfish-shaped promontories (*s.s*); totally coated cerotegument (*t.c.c*); ventral projection (*v.p*).

Acronyms: MHNG - Muséum d'histoire naturelle de Genève, Switzerland; CNF - private collection of Nestor Fernandez.

TAXONOMY

Superfamily Plateremaeoidea

Family Plateremaeidae

Plateremaeus cebilae sp. nov.

Figs 1-64

Etymology: The specific epithet is a name in the genitive, taken from "La Cebila", the locality of origin of the type of material.

Holotype: MHNG; ♀; Argentina, Catamarca Province, La Cebila, litter of *Ceiba speciosa*, Yungas Forest; 21.1.2017; coll. S. Leiva & N. Fernandez.

Paratypes: MHNG; ten adult ♀ specimens; five of them collected with the holotype, five others from Argentina, Cordoba Province, phytogeographic district of Chaqueño Serrano, Bialeto Massé, from litter of *Prosopis ferox* situated on mountains slopes; 21.2.2018; coll. N. Fernandez & S. Leiva.

Other material: CNF; ten adult ♀ specimens studied with SEM.

Diagnosis: Adult females. Prodorsum polyhedral; notogaster round, ovoid, flat, slightly concave. Without scalps of preceding instars. Cerotegument complex, covering body and legs: filaments with polyhedral structure; *in* setae covered by characteristic cerotegumental layer, rose-flower-shaped; *ro* and *le* setae curved, similar in shape and length, directed towards center, close to each other. Bothridium, cup-shaped; bothridial ring smooth. Sensillus uncinated, arching upward and directed towards side or rear. Notogastral margin smooth; notogaster with five pairs of setae: h_1, p_1, p_2, p_3, lp . Pedotectal tooth well visible. Epimeral hypertrichy: 8[7-9]-5[4-6]-6[5-6]-8[7-9]. Genital plate ovoid; nine pairs of genital setae, four paraxial and five anti-axial. Anal plate elongated ovoid: five pairs of setae aligned, in paraxial position. Genital and anal plates separated by moderately broad bridge. Legs heterotridactylous. Setal formulae I (1-9-4-4-18-3) (1-2-2); II (1-6-4-5-15-3) (1-1-2); III (1-5-3-4-13-3) (1-1-0); IV (3-5-3-4-12-3) (0-1-0).

Description of adults: *Measurements:* Females. SEM, 653 µm (643-658) x 439 µm (432-445) (measurements taken from five specimens). Light microscopy, 663 µm (635-681) x 442 µm (398-461) (measurements taken from five specimens). Males. SEM, 568 µm (559-598) x 439 µm (435-456), measurements taken from three specimens. Light microscopy, 592 µm (563-598) x 436 µm (432-446), measurements taken from five specimens.

Shape: Prodorsum polyhedral; notogaster round-ovoid (Figs 11, 38).

Colour: Specimens without cerotegument, brown to light brown when observed in reflected light.

Cerotegument: Complex layer covering body, legs, and some setae (Figs 1, 5, 6, 10, 11, 17, 19, 25, 26, 29). Body and legs with three principal components: 1) Basal layer (*b.l*) (0.3-0.5 µm thick) covering the animal everywhere and following the cuticular irregularities (Figs 2, 4, 26). 2) Series of triangular to irregular elevated promontories, these either isolated (*i.p*) (Fig. 27) or linked (*a.p*) (Figs 2, 4). Linked promontories: delimiting polyhedral structures found on prodorsum, notogaster, epimeral region, ventral zone (Figs 2, 4, 26). Isolated promontories: found on *bo*, subcapitulum, epimeres, prodorsum, notogaster, legs (Figs 10, 11, 19, 29). 3) Amorphous sheet in the form of: a) a flat irregular structure (*f.i.s*) situated in anterior third of prodorsum and extending towards rostrum and trochanter IV; on rostrum present as a transversal cord (Fig. 8 indicated by ♦) (see Remarks); b) a rose-flower-shaped structure (*r.f.s*) found on setae *in* (Fig. 12), and c) elevated irregular cells (*e.i.c*) and lobe-like structures (*l.l.s*), these polyhedral (Fig. 3), 16-31 µm high, situated on subcapitulum, setae *h* and legs (Figs 5, 6, 17, 19, 23), in longitudinal section showing similarity with a bee hive cell (Fig. 3). Lobe-like structures (*l.l.s*) (Fig. 9), with *i.p*,

a.p on their surface, found near basal setal zone of setae *le*, *ro*.

1) Setae completely covered by cerotegument (*t.c.c*): $p_1, p_2, p_3, h_1, h_2, ad_1, ad_2, ad_3$ (Figs 15, 16, 20). 2) Setae with cerotegument present only in basal zone (*b.c.z*): Cerotegument present as intricate labyrinth of *a.p* (Figs 24, 25b, 32, 34, 35) with *i.p* on outer surface, in most cases cerotegument reaching setal insertion level: *ro*, *le*, *g* (paraxial setae), *an*, *ad*, *ag* (Figs 25b, 28, 31, 32, 34). In epimeral and sub-capitular seta *h* cerotegument located above basal area, leaving a zone free of cerotegument (Fig. 24, indicated by arrow). Removal of *b.c.z* area where the cerotegument was located leaves a smooth area without barbs (Fig. 42, indicated by arrow). 3) Leg setae and solenidia with cerotegumental layer in extended basal zone, but either *i.p* and/or *e.i.c* (Fig. 6).

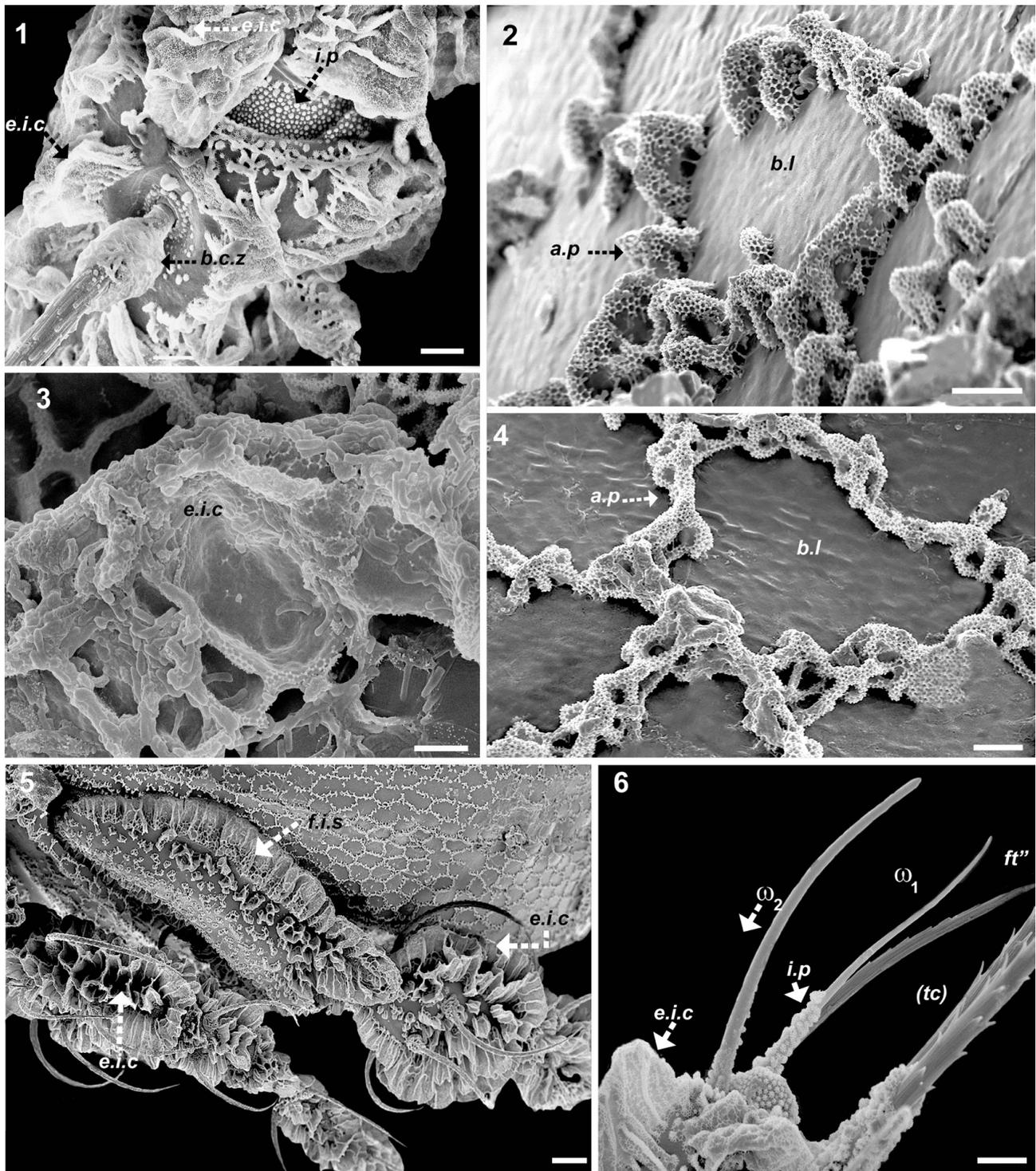
Integument: Smooth, with small stretch marks (Fig. 13). *Prodorsum:* 346 µm (332-375) in length. Polyhedral, with basal zone expanded laterally (in dorsal view) (Figs 11, 38); triangular (in lateral view) (Fig. 17); central zone slightly convex (Fig. 17). No costulae, crests or enantiophyses. Rostral margin slightly rounded (Fig. 38). Rostral setae (*ro*) situated ventrally, lamellar setae (*le*) dorsolaterally; both at same level and adjacent to each other; curved, directed towards center and similar in shape and length, 112 µm (106-122) (ten specimens measured); their tips adjacent or touching (Figs 11, 19, 40); setal surface with digitiform projections, these 4 µm (3-5) long, adhered to surface (Fig. 25a, b). Interlamellar setae (*in*) situated at level of *bo* (Fig. 11); rose-flower-shaped structure (*r.f.s*, determined by cerotegumental layer) 7 µm (5-9) long (Figs 11, 12, 14). Bothridium (*bo*) cup-shaped; bothridial opening directed upward; bothridial ring (*bo.ri*) smooth, complete, well defined (Figs 10, 11, 38). Sensillus (*Si*) 109 µm (107-114) long, uncinated, arching upward and directed towards side or rear; apical zone pointed, with short spines; pedicel with tiny spines (Figs 7, 10, 11, 18).

Notogaster: Without scalps of immatures stages; 825 µm (801-832) in length. In dorsal view ovoid, with notogastral margin (*ng.m*) smooth, well defined, elevated; internally to *ng.m* with a weak depression and in medial notogastral zone barely elevated (well visible in lateral view) (Figs 11, 17); dorsosejugal furrow (*d.sj*) narrow, convex, clearly delimited (Figs 11, 17, 38).

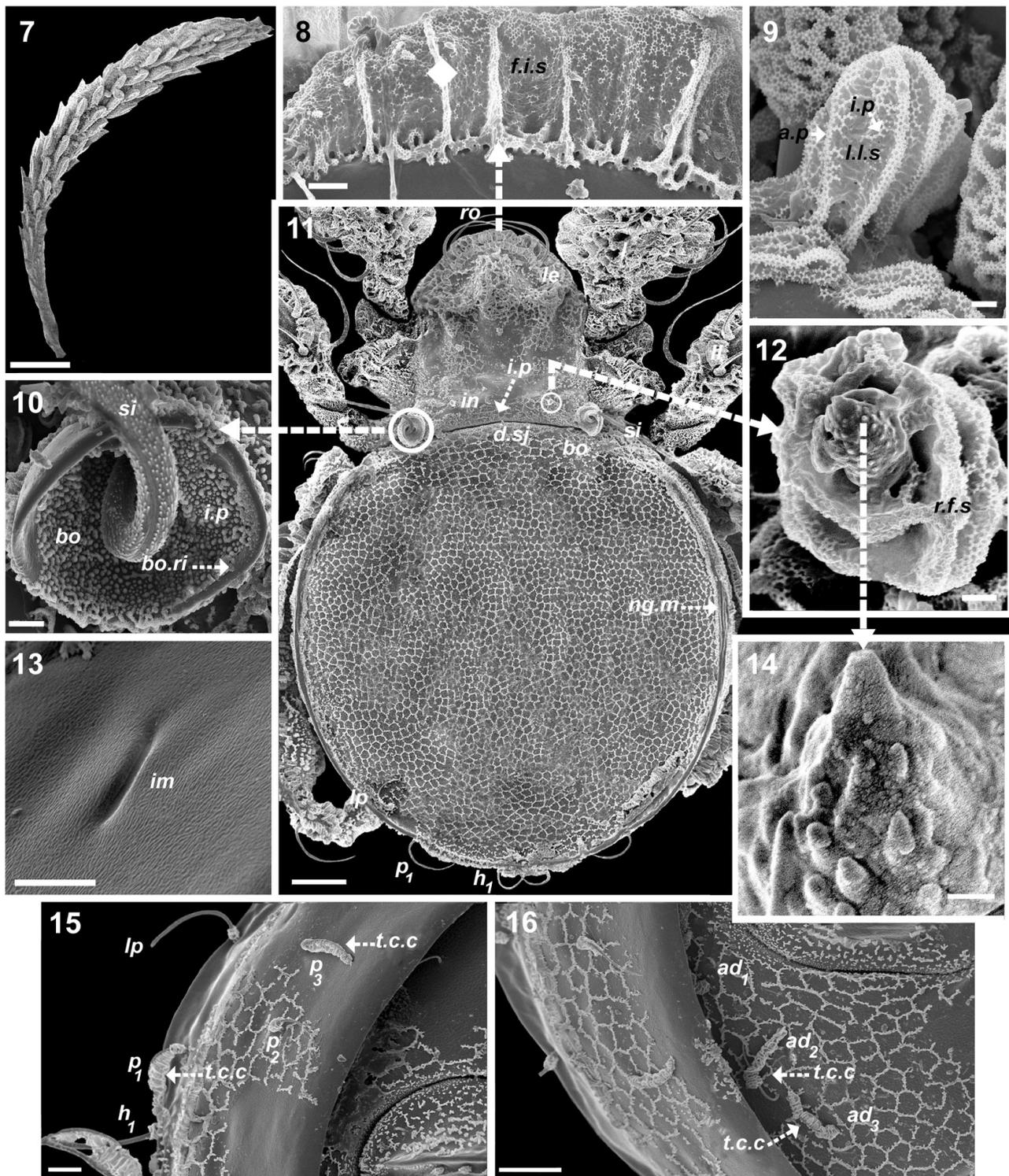
Notogastral setae lengths: h_1 48 µm (40-51); h_2 47 µm (43-54); p_1 33 µm (30-36); p_2 15 µm (13-22); p_3 25 µm (23-27). Setae completely coated by cerotegument (*t.c.c*) (Fig. 20). All setae simple, similar in shape, with small spines; p_1 directed towards rear and curved downward (Fig. 20); p_2 and p_3 similarly adherent to cuticle (Fig. 20); h_1, h_2 directed outward, curved (Fig. 11). Five pairs of lyrifissures, *ia*, *im*, *ih*, *ips*, *ip* (Figs 38, 41); *im* well discernible anterior of seta p_3 (Fig. 13).

Lateral region: *Si* uncinated, arching upward (Figs 17, 18); *ng.m* smooth, well defined; *pd.to* well visible.

Ventral region: Subcapitulum diarthric. Subcapitular



Figs 1-6. *Plateremaeus cebilae* sp. nov., adult female; SEM-micrographs of cerotegumental layer. (1) Detail of cerotegumental layer, femur-tibia of leg I. (2) Detail of promontories, ventral zone, view of inclined surface. (3) Anterior-prodorsal zone, dorsal view, transversal section. (4) General distribution of promontories, ventral zone, dorsal view. (5) Legs III-IV, lateral view. (6) Details of tarsus I, anti-axial view. For abbreviations see Material and Methods. Scale bars: 1 μm (2), 2 μm (3, 4), 4 μm (1), 5 μm (6), 20 μm (5).



Figs 7-16. *Plateremaeus cebilae* sp. nov., adult female, dorsal view; SEM-micrographs of cuticle with cerotegumental layer (7-12, 14-16) and without such layer (13). (7) Apical zone of sensillus. (8) Rostral zone. (9) Details of lobe-like structures (*l.l.s*) in rostral zone. (10) Bothridium, dorsal view. (11) Body in dorsal view. (12) Interlamellar setae. (13) Lyrifissure *im*. (14) Detail of apical zone of interlamellar seta. (15) Posterior zone of notogaster. (16) Detail of posterior notogastral zone and of posterior ventral zone. For abbreviations see Material and Methods. Scale bars: 300 nm (14), 1 μ m (9, 10, 12), 3 μ m (8), 10 μ m (7, 13, 16), 20 μ m (15), 100 μ m (11).

setae barbed; *a* 31 μm (28.5-43), slightly curved and directed towards front (Figs 19, 29, 40); *m* 46.8 μm (30.9-45.5) long; *h* 38 μm (33.7-46) long; setae *m*, *h* curved and directed towards body axis, their apical zones crisscrossing each other (Figs 19, 23, 40); cerotegumental layer of setae *a*, *m* not present (Fig. 19); setae *h* with cerotegument of type *b.c.z* reaching setal insertion (Fig. 21). Palp thin, elongate, *sul*, (*ul*), *acm* well discernible, digitiform; *acm* not associated with solenidion W. Setal formulae 0-2-1-3-9(1) (Fig. 39). Chelicerae almost colorless, with small light brown teeth; seta *cha* longer than *chb*, both barbed (Fig. 43).

Epimera slightly elevated; I, II only delimited by shallow furrows (*bo.2*; *bo.sj*) (Fig. 41) (see Discussion); lateral epimeral setae extending towards rear to paraxial level of genital openings; lateral genital openings developed as oblique, little elevated cuticular thickening (*c.t*) (Figs 29, 41, 44).

Epimeral chaetotaxy neotrichous: 8[7-9]-5[4-6]-6[5-6]-8[7-9] (in twenty specimens); in general setae progressively longer from paraxial to antiaxial. Lengths: Epimere 1: 1a 22 μm (20-26); 1a' 54 μm (44-60); 1a'' 68.5 μm (60-77); 1a''' 89 μm (82-95); 1a'''' 92 μm (90-96); 1b 18 μm (14-22); 1b' 19 μm (17-22); 1c 26 μm (23-30). Epimere 2: 2a 9.25 μm (9-9.5); 2a' 9.8 μm (9.9-9.7); 2b 13.5 μm (12.8-14.15); 2b' 6.7 μm (5.85-17.57); 2c 7.0 μm (6.8-7.04); 2c' 5.8 μm (5.6-6.2). Epimere 3: 3a 3.2 μm (3-3.4); 3a' 8.2 μm (7.7-9); 3b 10.4 μm (10.2-10.7); 3b' 14.4 μm (13.5-15); 3c 18 μm (16.7-19.2); 3c' 22.7 μm (21.8-23.5); 3c'' 20 μm (19-23). Epimere 4: 4a 2 μm (1.9-2.1); 4a' 2.16 μm (1.8-2.4); 4a'' 2.26 μm (1.9-2.5); 4b 2.30 μm (1.7-2.7); 4b' 3.86 μm (3.5-4.2); 4c 3.5 μm (3.2-4.37); 4c' 3 (2.9-3.2).

Epimeral setae with cerotegument *b.c.z* present, not reaching setal insertion (Figs 24, 35). Setae with small barbs, like those on genital antiaxial setae (Fig. 33) (see Remarks).

Pedotectal tooth (*pd.to*) well visible, situated laterally (Figs 29, 41) (see Remarks) and with tubercle ventrally *v.p* (Fig. 41).

Genital plate ovoid, 105 ± 2 μm long, 83 ± 1 μm wide, situated in elevated zone. Nine pairs of genital setae; four pairs paraxial, and five antiaxial. Paraxial seta 13.2 μm (12.7-13.7) long, aligned, without cerotegumental layer; two specimens with g_1 duplicate (Fig. 37). Barbs of medium size. Antiaxial setae 14 μm (13.4-14.5) long, *b.c.z* with cerotegumental layer (Fig. 34), all barbs with apical hole (Figs 33, 36) (see Remarks). Genital and anal opening separated by moderately broad, 15.5 ± 3 μm long bridge (Figs 29, 41).

Anal plate elongated ovoid, 120 ± 2 μm long, 96 ± 3 μm wide. Five pairs of anal setae with cerotegumental layer *b.c.z* (Fig. 32), their barbs different from those of genital setae (see Remarks).

Aggenital setae 7 ± 1 μm long, posterolateral of genital opening (Figs 29, 41), with similar characteristics as epimeral setae; *b.c.z* cerotegumental layer not reaching setal insertion.

Adanal setae 29 μm (31-25) long, posterolateral of anal opening, in an oblique line directed away from body axis (Figs 16, 29); *ad*₁ setae closest to anal opening. Adanal setae with small barbs and with complete cerotegumental layer (*t.c.c*). Lyrifissure *iad* not discernible.

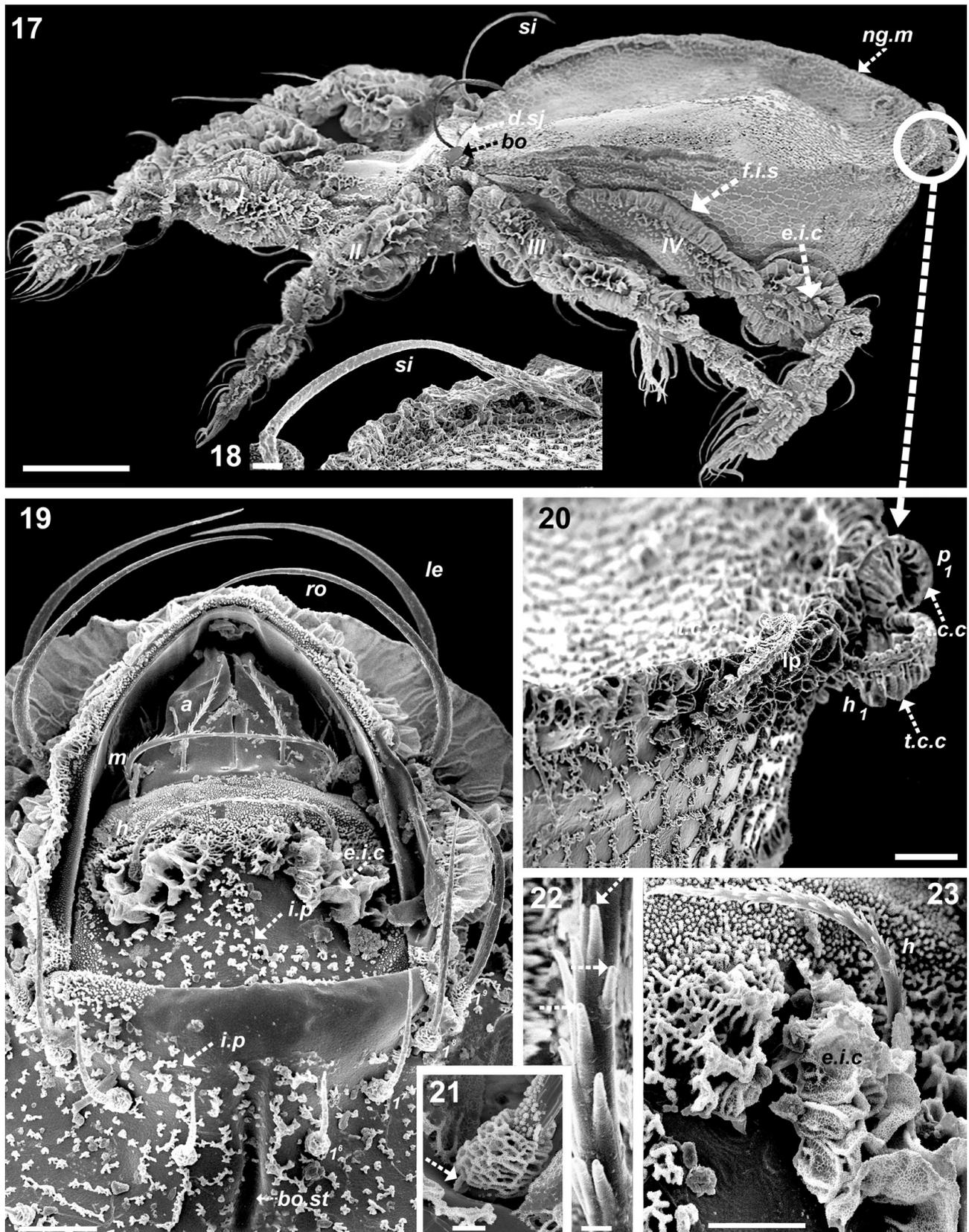
Legs (Figs 45-49): Setal formulae I (1-9-4-4-18-3) (1-2-2); II (1-6-4-5-15-3) (1-1-2); III (1-5-3-4-13-3) (1-1-0); IV (3-5-3-4-12-3) (0-1-0) (Figs 45-48). Famulus (*E*) situated internally, on small cuticular protuberance (Fig. 45). Tibial solenidia j_1 , j_2 presents. Tibia I with different cuticular surface textures; with longitudinal striae and with longitudinal slits (Fig. 49a, b). Genua, tibiae, tarsi I-IV with sockets (retropecta), these more developed ventrally than dorsally (Figs 45-48).

Remarks: The cerotegumental layer found in the superior zone of trochanter IV is different to that of other legs. In this case the trochanter is big and flat near the notogastral border and the flattened cerotegument (*f.i.s*) allows for movement (Figs 5, 17). One specimen has a seta present on *pd.to* (Fig. 41). On epimeral setae the barbs are small and adhere to the cuticular surface over much of their length, like those found on genital antiaxial setae (Figs 32, 34); there are only small differences in size between the barbs of the genital setae and those of the epimeral setae. The barbs of the genital paraxial setae are longer and more widely spaced (Figs 36, 37). On anal setae the barbs are longer and more directed towards the apex (Fig. 32). An interesting observation is the presence of a single pore on the apex of all barbs (Figs 33, 36, indicated by arrows). The position of the pore is like that of the TP type terminal pore of sensilla (Alberti & Coons, 1999), but it is situated on the tip of barbs.

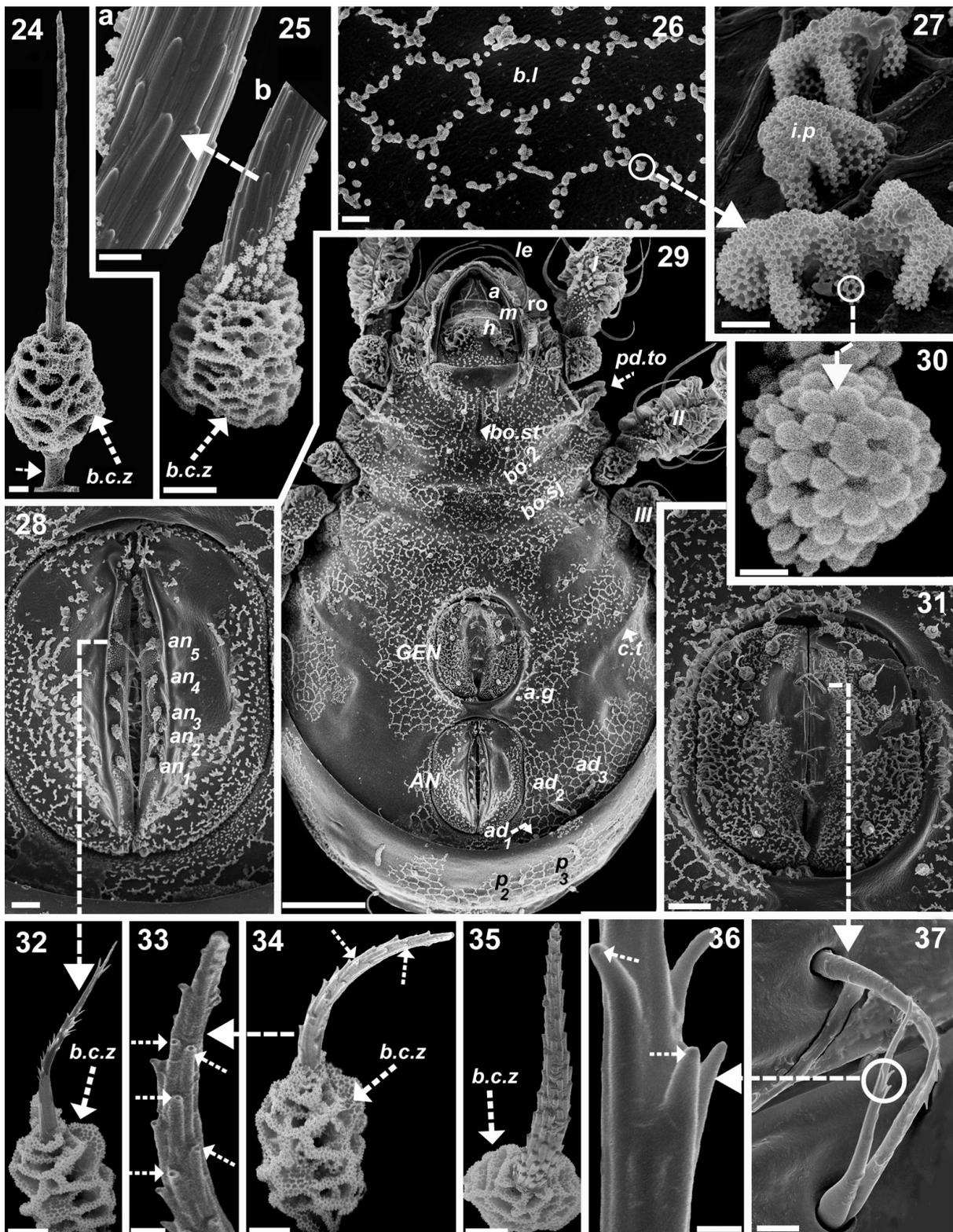
Description of immature instars (Figs 50-55): *Measurements:* Length of larva 370 μm (350-390), of protonymph 476 μm (460-493), of deutonymph 510 μm (496-512), of tritonymph 580 μm (576-584) (three specimens of each instar examined). All nymphs flat and carrying the scalps of preceding instars.

Colour (observed in reflected light): Larva dull whitish; nymphs with light brown prodorsum, its gastronomic region even lighter.

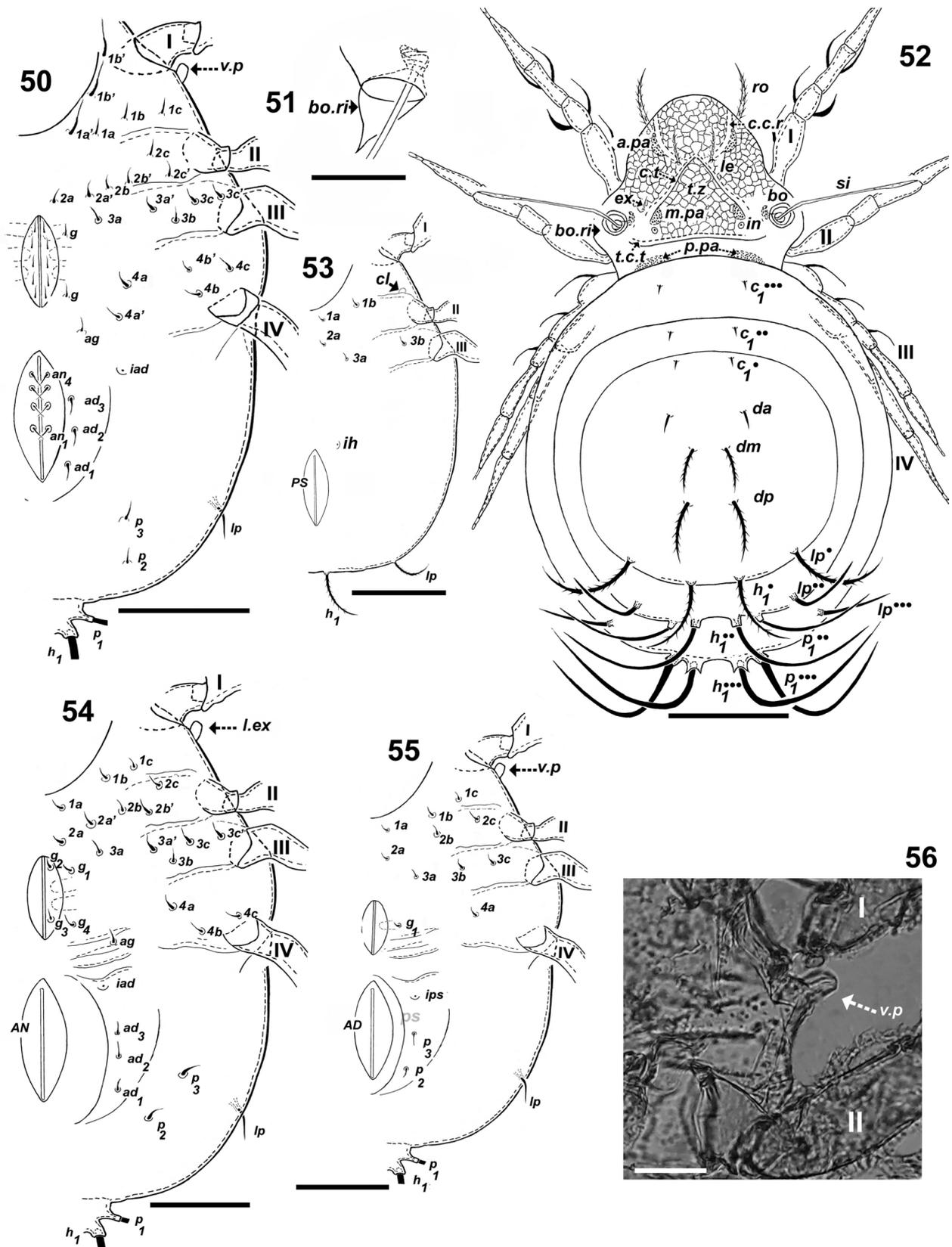
Cerotegument: Complex layer covering body (Fig. 57) and legs, similar to that of adults, with elevated isolated promontories (*i.p*), associated promontories (*a.p*), flat irregular structures (*f.i.s*), rose-flower-shaped structures (*r.f.s*), elevated irregular cells (*e.i.c*), and lobe-like structures (*l.l.s*). Prodorsal zone with anteriorly extending rostrum *f.i.s* (Fig. 59); *i.p* (Fig. 60) on prodorsum, bothridium and notogaster; *a.p* (Fig. 57) being the most common structure on notogaster; *l.l.s* in marginal prodorsal zone; *e.i.c* marginal, in notogastral zone (Fig. 63); *r.f.s* on *in* setae (Fig. 60). Setae *ro*, *le*, *ex* without cerotegumental layer. Gastronomic larval setae *c*₁, *da*, *dm*, *dp*, *lp*, *h*₁ (Figs 52, 57) totally cover by cerotegument; larval *c*₁, *da*, *dm*, *dp* and nymphal *c*₁ very difficult to see



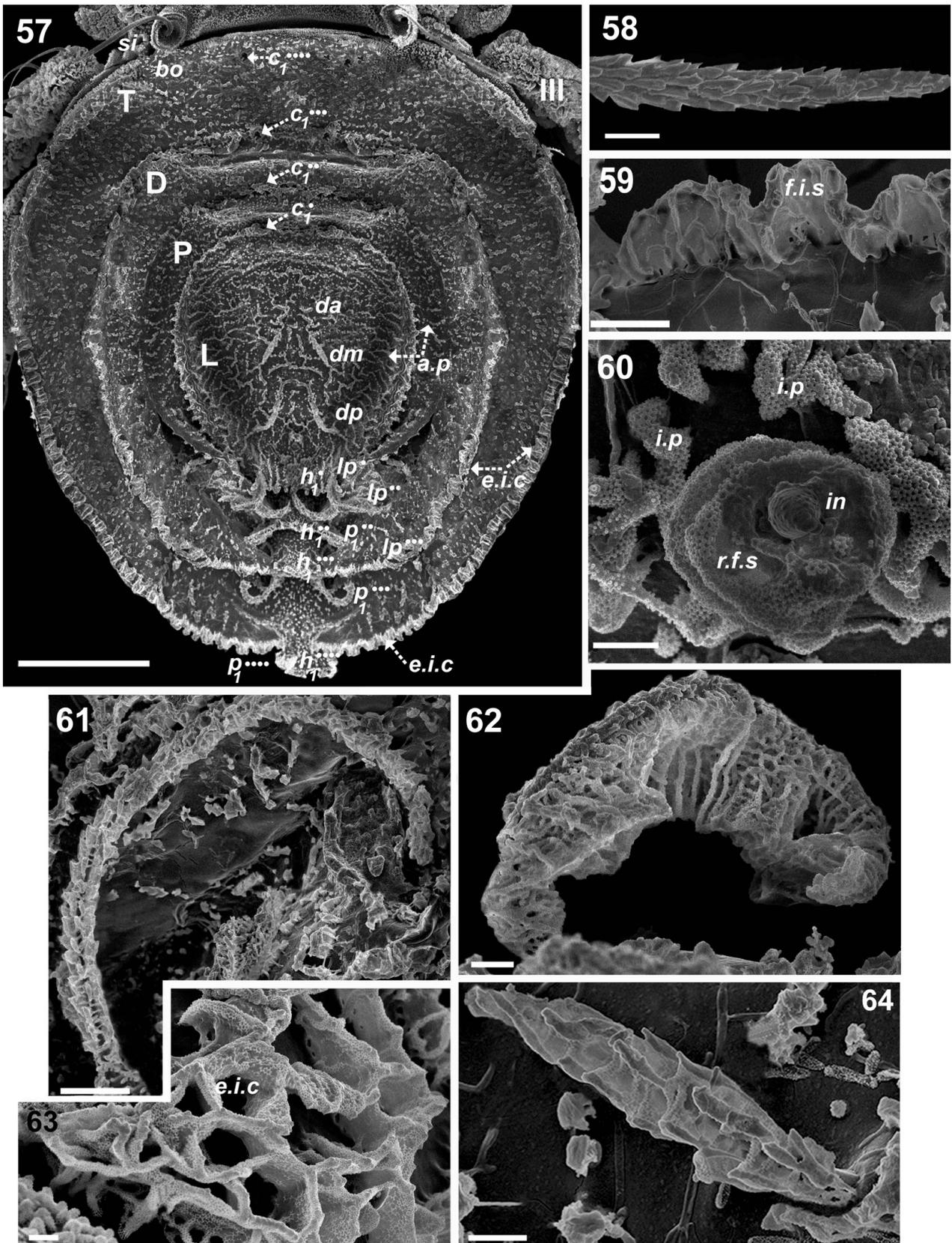
Figs 17-23. *Plateremaeus cebilae* sp. nov., adult female, lateral view; SEM-micrographs of cuticle with cerotegumental layer. (17) Body in lateral view. (18) Sensillus. (19) Subcapitulum. (20) Posterior notogastral zone. (21) Subcapitular seta *h* in basal zone. (22) Subcapitular seta *h* showing barbs with apical pore. (23) Subcapitular seta *h* and cerotegument in detail. For abbreviations see Material and Methods. Scale bars: 300 nm (22), 1 μ m (21), 10 μ m (18, 23), 20 μ m (1, 20), 100 μ m (17).



Figs 24-37. *Plateremaes cebilae* sp. nov., adult female; SEM-micrographs of cuticle with cerotegumental layer. (24) Epimeral seta. (25) Rostral seta in detail. (26) General view of ventral cerotegumental layer. (27) Detail of ventral cerotegumental layer. (28) Anal plate. (29) Body in ventral view. (30) Cerotegumental layer showing polyhedral structure (*p.s.*). (31) Genital plate. (32) Anal seta. (33) Detail of genital anti-axial seta with barbs in its apical zone showing pores (indicated by arrows). (34) Genital anti-axial seta. (35) Epimeral seta. (36) Paraxial genital seta with detail of barbs and pores (indicated by arrows). (37) Total of paraxial genital setae. For abbreviations see Material and Methods. Scale bars: 200 nm (30), 500 nm (33), 1 μ m (24, 25, 27, 35), 2 μ m (26, 32, 34, 37), 10 μ m (28, 31), 100 μ m (29, 36).



Figs 50-56. *Plateremaeus cebilae* sp. nov., immature stages; line drawings not showing cerotegumental layer (50-55); photo taken of object under a compound microscope (56). (50) Tritonymph, ventral view. (51) Bothridium of tritonymph, dorso-lateral view. (52) Deutonymph with scalps of larva and protonymph, dorsal view. (53) Larva, ventral view. (54) Deutonymph, ventral view. (55) Protonymph, ventral view. (56) Ventral projection between leg I and II of protonymph. For abbreviations see Material and Methods. Scale bars: 2 μ m (56), 80 μ m (53, 55), 90 μ m (51), 100 μ m (50), 130 μ m (54), 150 μ m (52).



Figs 57-64. *Plateremaeus cebilae* sp. nov., tritonymph; SEM-micrographs of cuticle with cerotegumental layer. (57) General view of notogaster with attached scalps. (58) Sensillus. (59) Rostral zone. (60) Seta *in*. (61) Seta *h₁*. (62) Seta *c₁*. (63) Elevated irregular cells (*e.i.c*). (64) Seta *dm*. For abbreviations see Material and Methods. Scale bars: 2 μ m (60, 63), 3 μ m (64), 4 μ m (62), 20 μ m (61), 30 μ m (58, 59), 100 μ m (57).

in dorsal view because of small size and cerotegumental layer of body (Figs 62, 64). Nymphal setae h_p , lp , p_1 more easily observable because of larger size; these with barbs and without complete cover by cerotegument (Fig. 61).

Prodorsal region: Polyhedral in shape (in dorsal view), similar in all instars; central zone slightly convex. Rostral margin rounded (Fig. 52). Larvae and nymphs with similar prodorsal structures, but these less defined in larvae. Middle prodorsal zone with cuticular thickening (*c.t*) outlining triangular zone (*t.z*), extending to level of seta *le* and transversal cuticular thickening (*t.c.t*) (Fig. 52); apical zone of *t.z* with curved smooth cuticular ribbon (*c.c.r*) directed towards prodorsal apical zone.

Setae (all without cerotegument): *ro* 53-61 μm long, curved, barbed (Fig. 52); *le* 25-31 μm , erect, barbed (Fig. 52); *in* 3-5 μm ; *ex* 7-9 μm , with small barbs, anterolateral *bo*, and lateral *c.t* at level of *m.pa* (Fig. 52). Three pair of porose areas (*pa*) poorly visible in larvae and well visible in nymphs: 1) *a.pa* (anterior) situated lateral to *c.c.r*; 2) *m.pa* (medial) situated anterior of seta *in* and in *t.z*; 3) *p.pa* (posterior) situated posterior of seta *in* and near dorsosejugal furrow (Fig. 52); *bo* cup-shaped; bothridial opening directed upwards; *bo.ri* rounded, with triangular posterolateral expansion in some immature instars (Figs 51, 52) (see Remarks). *Si* 96-103 μm in length, uncinated, arching upward and directed towards side (Figs 52, 57); pedicel with tiny spines; apical zone pointed, with small barbs (Fig. 58).

Gastronotum: In larva plicate, with six pairs of barbed setae: c_1 , *da*, *dm*, *dp*, *lp*, h_1 ; cupule *ih* situated anterolaterally of segment *PS* (Figs 52, 53).

Nymphs without d-series of setae; c_1 small, barbed (Fig. 52); setae lp , p_1 , h_1 curved and barbed, present in all nymphal instars; *lp* situated laterally, p_1 , h_1 on "croupion" (Grandjean, 1964); p_1 situated in paraxial, h_1 in antiaxial position. Dorsal part of gastronotum flat, with scalps of previous instars.

Ventral region: Unsclerotized surface plicate. Nymphs with rectangular ventral projection (*v.p*) (Fig. 56) situated posterior of acetabulum I (Figs 50, 54-56).

Larvae and deutonymphs with paraproctal valves and glabrous paraproctal atrichosy (AT_3); tritonymphs with four pairs of paraxial setae. Segment Ad of deutonymphs and tritonymphs with normal chaetotaxy.

All *p* setae similar in all instars from protonymph onward; h_2 , h_3 absent. One pair of aggenital setae on protonymph and all following instars. Tritonymph with four pairs of anal setae. Setal formulae: anal (03333) (0333) (045); gastronotal (6-6-5); genital (1-4-7-9); aggenital (0-1-1-1-1).

Larvae with Claparède organs small and covered by cochleariform seta *lc*.

Starting from deutonymph, neotrichy in epimeral region with two additional setae on second and third epimeres, tritonymph with three additional setae on first and second epimeres and with two setae on third and fourth epimeres. Adult with first epimere carrying two additional setae,

third with one additional seta, and fourth with three additional setae (Figs 50, 52, 54, 55). Epimeral formulae (3-1-2) (3-3-3-1) (3-5-5-3) (6-6-5-5) (8[7-9]-5[4-6]-6[5-6]-8[7-9]).

Legs: Immatures with weakly developed sockets on genu, tibia, and tarsus. Tibial apophysis very small in larvae.

Setal formulae: Leg I: larva (0-2-2-4-16-1) (1-1-1); protonymph (0-4-3-4-16-1) (1-1-2); deutonymph (1-4-3-4-16-1) (1-2-2); tritonymph (1-5-4-4-18-1) (1-2-2); adult (1-9-4-4-18-3) (1-2-2). Leg II: larva (0-2-3-3-13-1) (1-1-1); protonymph (0-4-3-4-15-1) (1-1-1); deutonymph (1-4-4-5-15-1) (1-1-2); tritonymph (1-5-4-5-15-1) (1-1-2); adult (1-6-4-5-15-3) (1-1-2). Leg III: larva (0-2-3-3-13-1) (1-1-1); protonymph (0-2-3-4-13-1) (1-1-1); deutonymph (1-3-3-4-13-1) (1-1-2); tritonymph (1-3-3-4-13-1) (1-1-0); adult (1-5-3-4-14-3) (1-1-0). Leg IV: protonymph (0-0-0-0-7-1) (0-0-0); deutonymph (1-2-2-2-10-1) (0-1-0); tritonymph (2-3-3-4-12-1) (0-1-0); adult (3-5-3-4-12-3) (0-1-0).

Remarks: Grandjean (1964: 379), in his description of *Pheroliodes wehncke* (Willman, 1930), and subsequent authors (Fernandez, 1990; Eguaras *et al.*, 1990) considered setae p_1 and h_1 to be situated on the "croupion".

Genital valves of the protonymph carry one pair of setae; three additional pairs are present in the deutonymph (one pair medially and two pairs laterally) [as in *L. mirabilis* (Csiszár in Csiszár & Jeleva, 1962), see Seniczak *et al.*, 2020]; tritonymph with three additional pairs, one pair medially and two pairs laterally.

The notation of epimeral setae is complicated from the tritonymph onward, mainly in the adult. For that reason, we have not indicated the notation of the stage. The epimeral neotrichy shows some variation in adults in samples of 50 specimens from each sampling site (La Cebila and Biale Massé), but no pattern was found. In the case of nymphs, we have only studied four protonymphs, ten deutonymphs and one tritonymph. We did not find any substantial variation, possibly due to the small number of specimens studied.

The *bo.ri* has a posterior triangular expansion in the larvae, which is less visible in protonymphs and not observable in deuto- and tritonymphs (Figs 51, 52).

Gaboneremaeidae fam. nov.

Etymology: The first part of the name refers to Gabon, the country of origin of the type of material.

Type genus: *Gaboneremaeus* gen. nov.

Diagnosis: Pedotecta I-II absent; pedotectal tooth and ventral projection present. Prodorsum: enantiophysis A and transverse furrow absent; cuticular fold present. Notogaster ovoid, flat to slightly concave; scalps absent; notogastral margin elevated; pleurophragma present; three pairs of setae positioned posteriorly. Coxisternal region neotrichous, well delimited from ano-genital

region; parastigmatic enantiophysis, pregenital sclerite and discidium present; anal setal neutrichous. Legs not filiform, femora with expansion pointing downward; sockets present on genua, tibiae and tarsi, these more developed ventrally than dorsally. Femur I with six setae, femur IV with three, trochanter IV with two. Total length 880-911 μm .

Gaboneremaeus gen. nov.

Diagnosis: Adult female: Prodorsum with elevated and depressed zones, delimited by cuticular thickening; bothridium cup-shaped, its external margin with slit and ear-shaped expansion; sensillus filiform, with small barbs; *in* setae situated on longitudinal thickening; middle posterior and central zone of notogaster with finger-like depression. Epimera well defined; epimeral furrows, apodemes and elevated cuticular thickenings present; nine genital setae; ten anal setae; aggenital setae large, situated anterior and lateral to anal plate; anal and genital apertures distant from each other; famulus elongate.

Type species: *Gaboneremaeus patriciae* sp. nov.

Gaboneremaeus patriciae sp. nov.

Figs 65-109

Etymology: The specific epithet, a name in the genitive, is an homage to Professor Nilda Patricia Soria for her friendly collaboration and assistance in various technical projects.

Holotype: MHNG; ♀; Republic of Gabon, Makokou, north-eastern Ogoové-Ivindo Province, 0°34'0"N, 12°52'0"E, 500 m altitude, dense evergreen humid forest; I.1974; coll. Y. Coineau.

Paratypes: MHNG; 2 ♀; same date and locality as for holotype.

Other material: CNF; 10 specimens; same data as for holotype.

Diagnosis: Adult female: Relatively large; body and legs covered with thick cerotegument composed of rounded structures and polyhedral granules, with architecture particular to different body zones; *Si* long, filiform, directed upward and backward; *in* setae small, covered by granular cerotegument, situated on cuticular thickening. Bothridium complex, cup-shaped, its external margin with slit and ear-shaped expansion. Notogaster round and flat; pleurophragma present; middle posterior and central zones with small pits; three pairs of posteriorly notogastral setae; pedotectal tooth acute. Epimeral neutrichy: 9[8-10]-6-9[8-10]-9[8-11]; parastigmatic enantiophysis, pregenital sclerite and discidium present; genital plate rectangular-polyhedral, with nine setae in two rows; aggenital setae

strong, 35-40 μm in length and situated posterior to genital plate; anal plate elongated ovoid-rectangular, its smooth surface with complex structure and with ten pairs of setae; genito-anal bridge normal. Legs heterotridactylous. Setal formula I (1-6-2-4-18-3) (1-2-2); II (2-5-2-5-17-3) (1-1-2); III (3-4-2-4-15-3) (1-1-0); IV (2-3-3-4-12-3) (0-1-0). All femora similar in shape, with acute anterior zone; famulus elongated.

Description of adults: *Measurements:* Females. SEM 891 μm (882-911) x 565 μm (522-570) (measurements of five specimens). Light microscopy 998 μm (893-1002) x 570 μm (562-587) (measurements of five specimens). No differences in measurements between males and females.

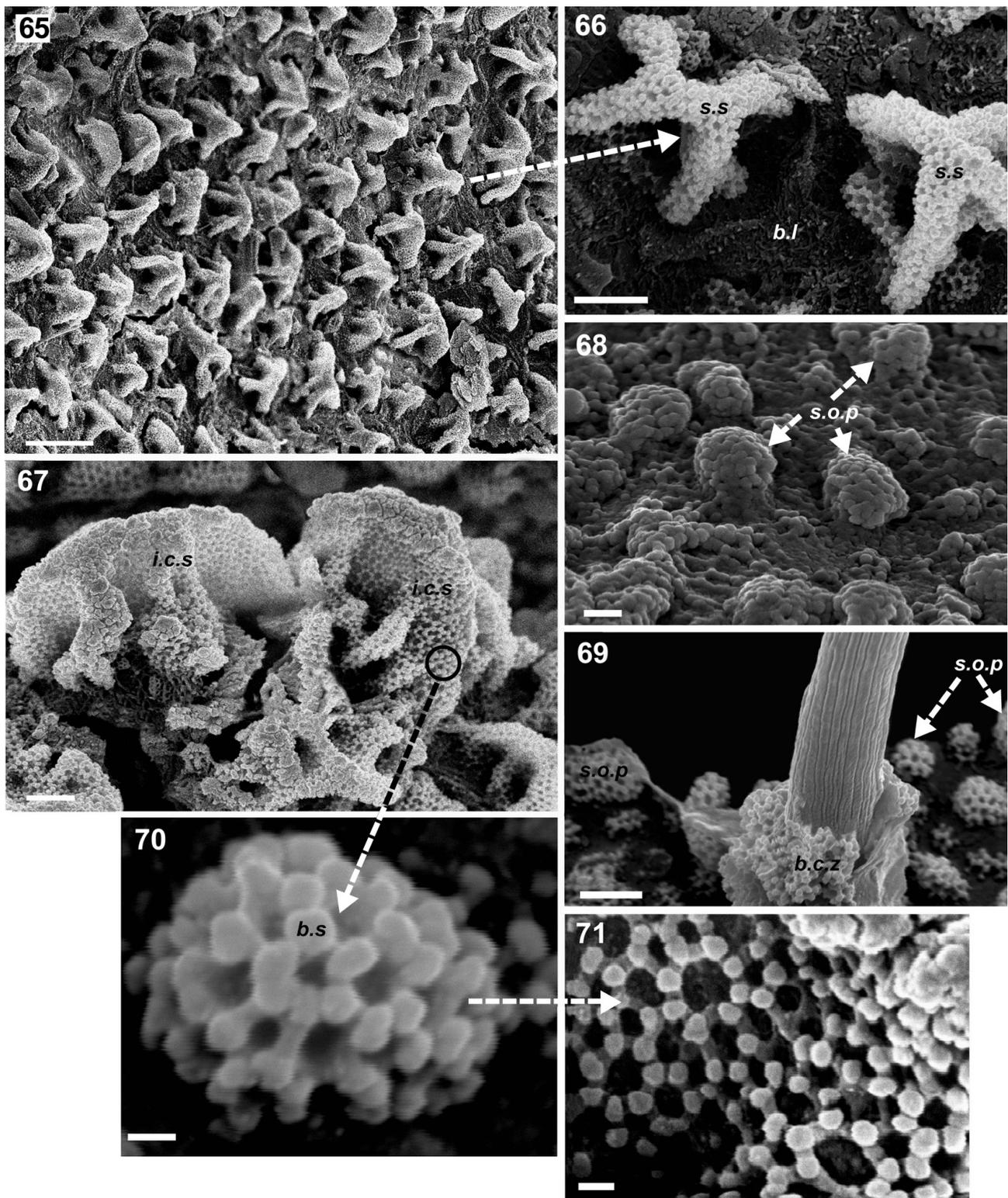
Shape in dorsal view: Prodorsum polyhedral; notogaster round-ovoid (Fig. 72).

Colour: Specimens without cerotegument, brown to light brown when observed in reflected light.

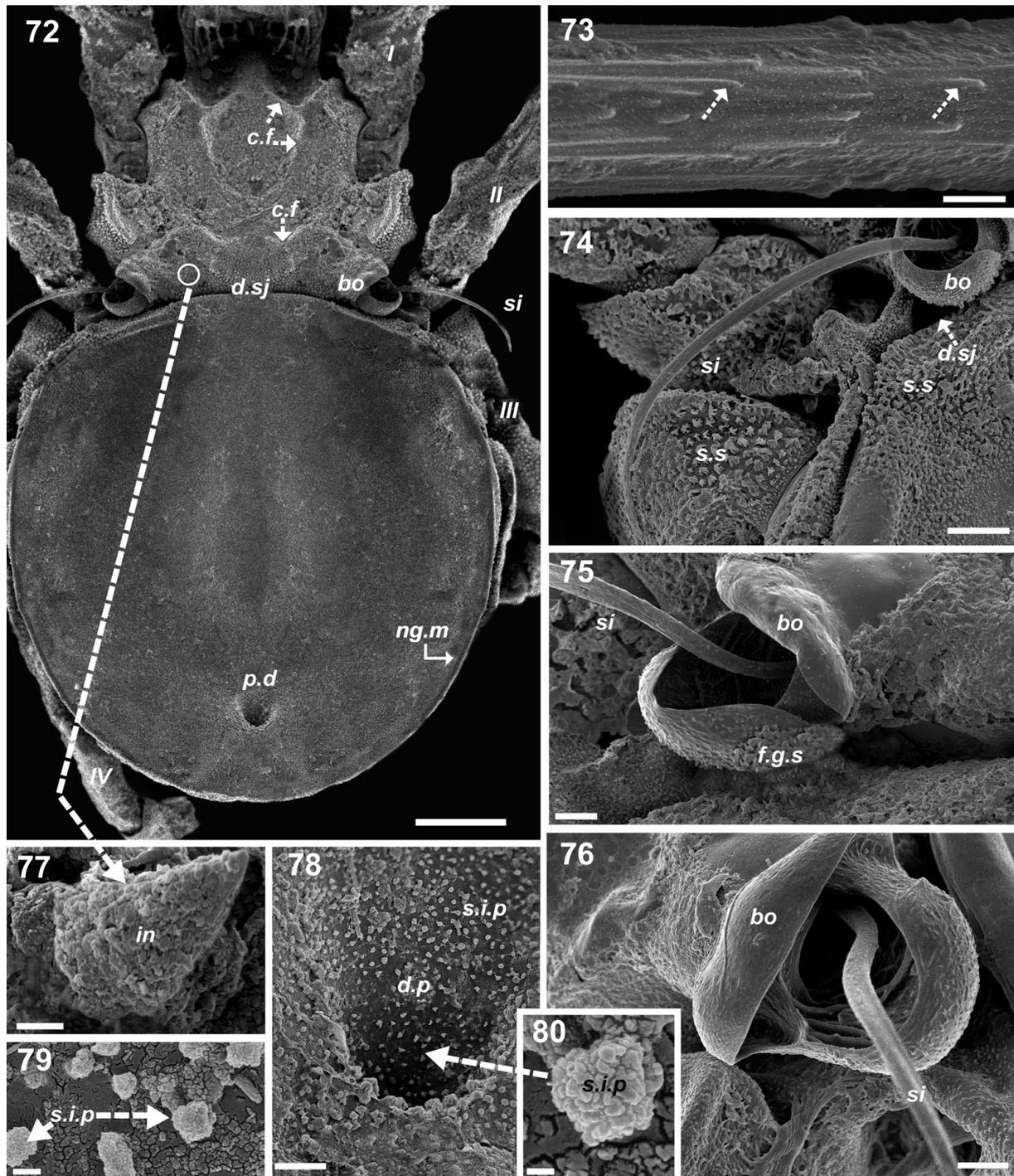
Cerotegument: Complex layer covering body, legs and some setae, very difficult to remove (see Discussion). Cerotegument composed of 1) Basal layer (*b.l*) (0.5-0.7 μm in thickness) covering animal everywhere and following cuticular irregularities; with irregular surface, weakly rugous (Fig. 66). 2) Flat granulous sheet (*f.g.s*), i.e. a thin layer with polyhedral to irregular granularity (Fig. 87), thickness between 30-250 nm, partially also covering prodorsum, cuticular fold (*c.f*), *bo*, notogaster, ventral region and subcapitulum (Figs 72, 75, 77, 82, 83, 85, 86, 93, 100, 101). 3) Elevated structures: a) starfish-shaped structures (*s.s*) (Fig. 66) with four to nine arms (Figs 65, 83), mainly found near rostrum, on ventral body surface and on external margin of anal plate and legs (Figs 65, 74, 83) (see Remarks); b) irregular convex structures (*i.c.s*) (Fig. 67) situated on external anal plate margin and around anal opening (Figs 82, 83); c) small ovoid promontories (*s.o.p*) (Fig. 68) mainly found near *d.sj* (Fig. 108), epimeral setal insertion (Fig. 69) and near internal fold of anal plate (Fig. 85); d) basal cerotegument zone (*b.c.z*) situated at bases of epimeric setae in first row (Fig. 69). These four types are made of variable numbers (4-8) of ball-shaped structures (*b.s*) (Fig. 70) forming circular to polyhedral groups (Figs 70, 71). Additionally, there are e) small irregular to polyhedral promontories (*s.i.p*) (Figs 79, 80) situated on the notogaster surface near *ng.m*, around the posterior notogastral depression (*d.p*) (Fig. 78).

Integument: Smooth, with small stretch marks.

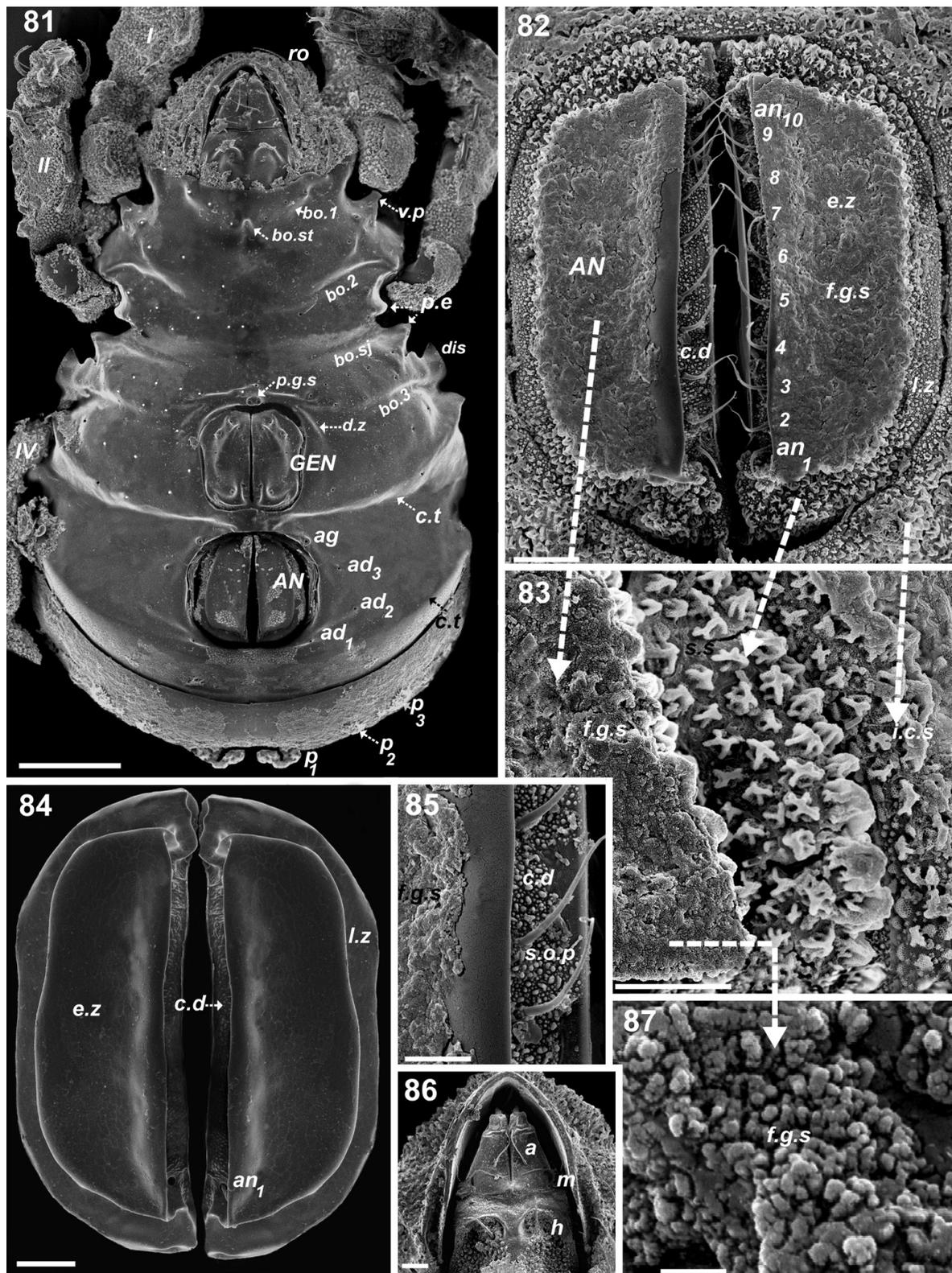
Prodorsum: 292 μm (289-296) in length, 330 μm (296-342) in width. Polyhedral (in dorsal view) (Figs 72, 90), triangular (in lateral view) (Fig. 94). Cuticular folds *c.f* present, delimiting elevated to depressed zones (Figs 90, 96, 99); rostral margin ovoid-rounded (Figs 89, 90, 96). Setae *ro* 120 μm long (116-124), situated ventrally (Fig. 100); *le* setae 145 μm (139-151) long, situated dorso-laterally (Figs 90, 100), both at same level, curved, similar in shape, directed towards the center;



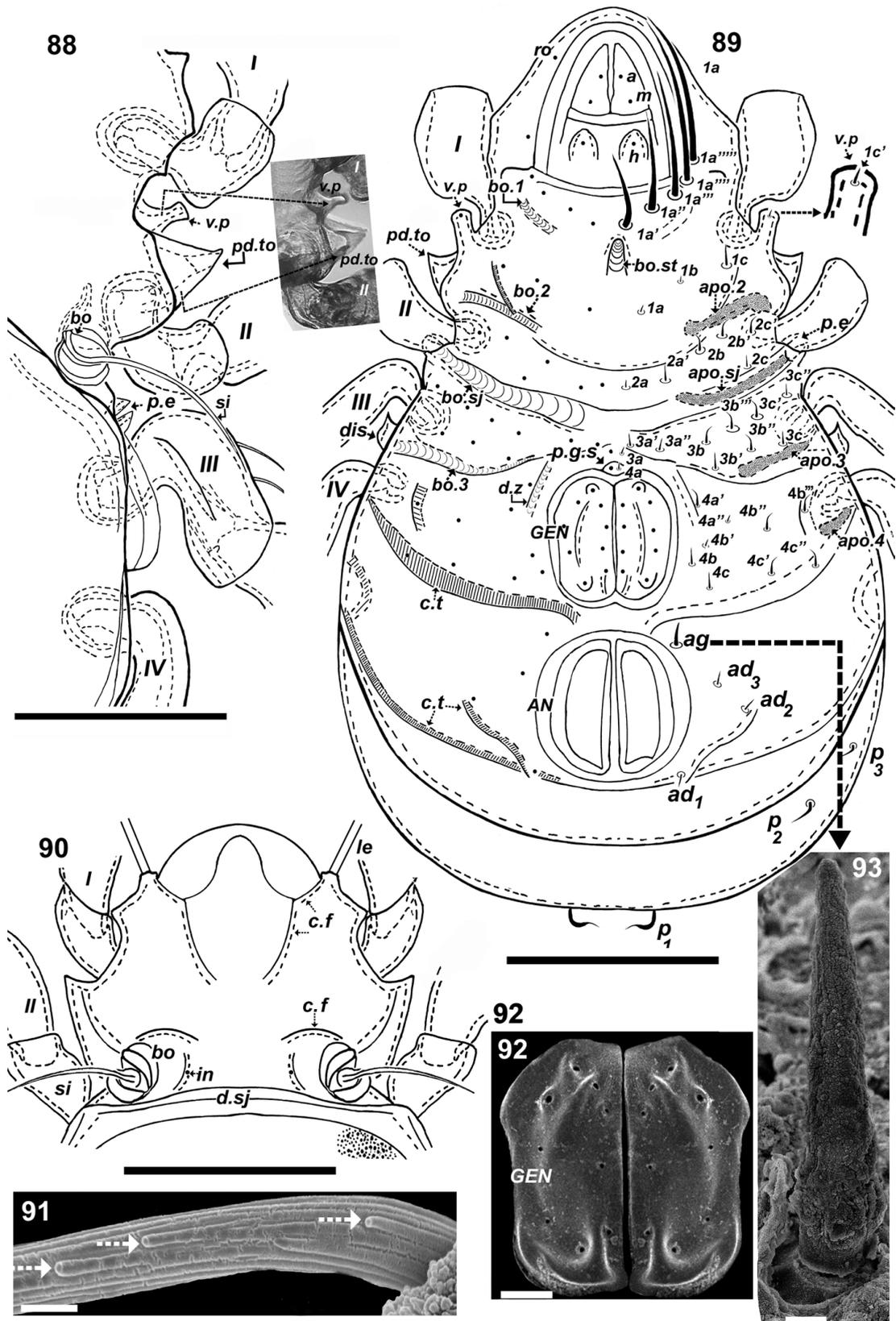
Figs 65-71. *Gaboneremaeus patriciae* sp. nov., adult female; SEM-micrographs of different kinds of cerotegumental layers. (65) Starfish-shaped structures (*s.s*) in general view. (66) Isolates of *s.s* in detail. (67) Elevated irregular cells in general view. (68) Small ovoid promontories (*s.o.p*). (69) Epimeral seta with basal cerotegumental zone. (70) Basic unit of cerotegument. (71) Basic unit with different numbers of ovoid-circular structures. For abbreviations see Material and Methods. Scale bars: 100 nm (70, 71), 400 nm (68), 1 μ m (66, 67, 69), 10 μ m (65).



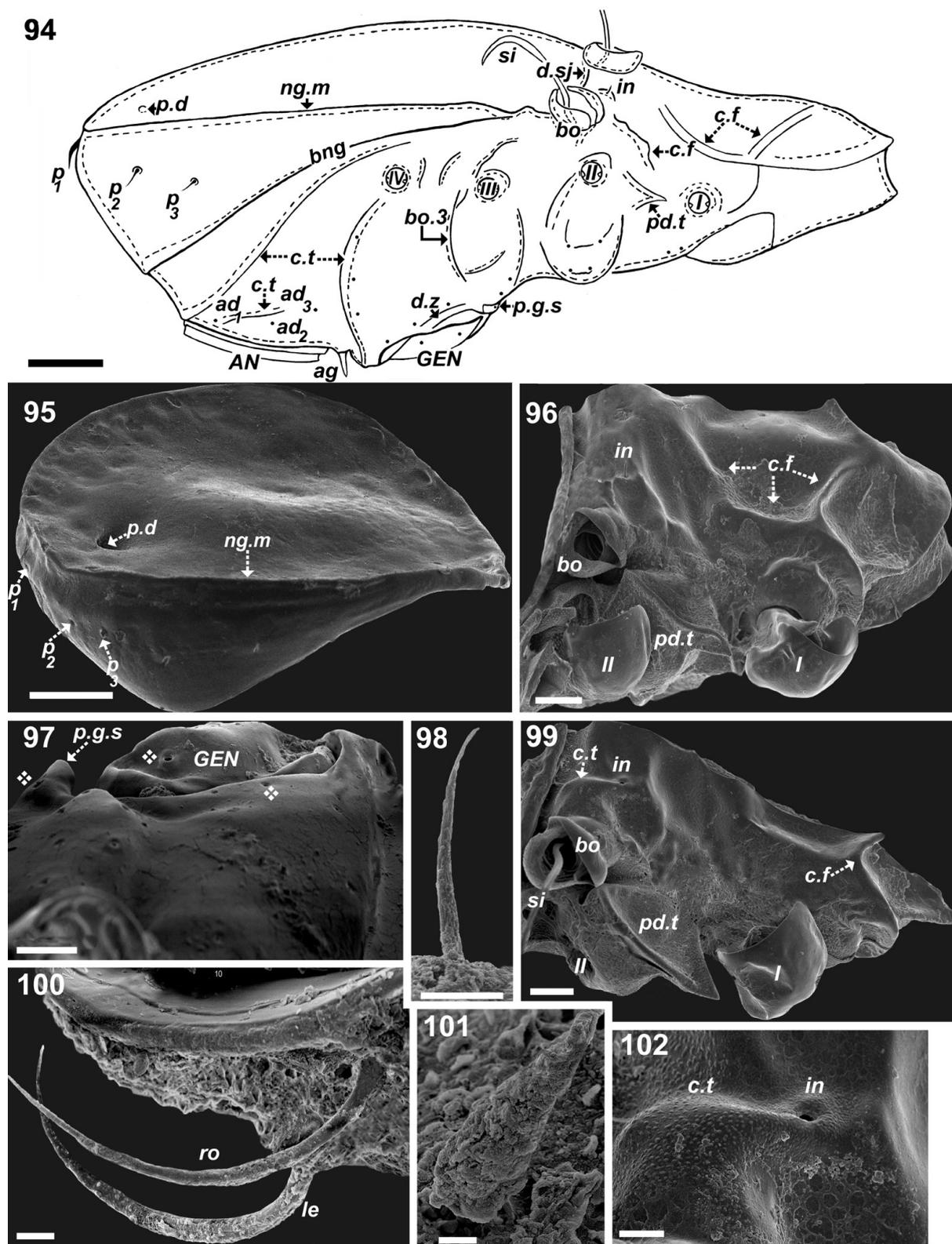
Figs 72-80. *Gaboneremaeus patriciae* sp. nov.; SEM micrographs of adult female. (72) Body in dorsal view, with cerotegumental layer partially removed. (73) Detail of sensillus. (74) Sensillus in lateral view. (75) Bothridium in lateral view. (76) Bothridium in frontal view. (77) Seta *in*. (78) Posterior notogastral depression. (79) Detail of cerotegumental layer *d.p.* (80) Small irregular to polyhedral promontory (*s.i.p.*). For abbreviations see Material and Methods. Scale bars: 300 nm (80), 1 μ m (77), 2 μ m (73, 79), 10 μ m (75, 76, 78), 20 μ m (74), 100 μ m (72).



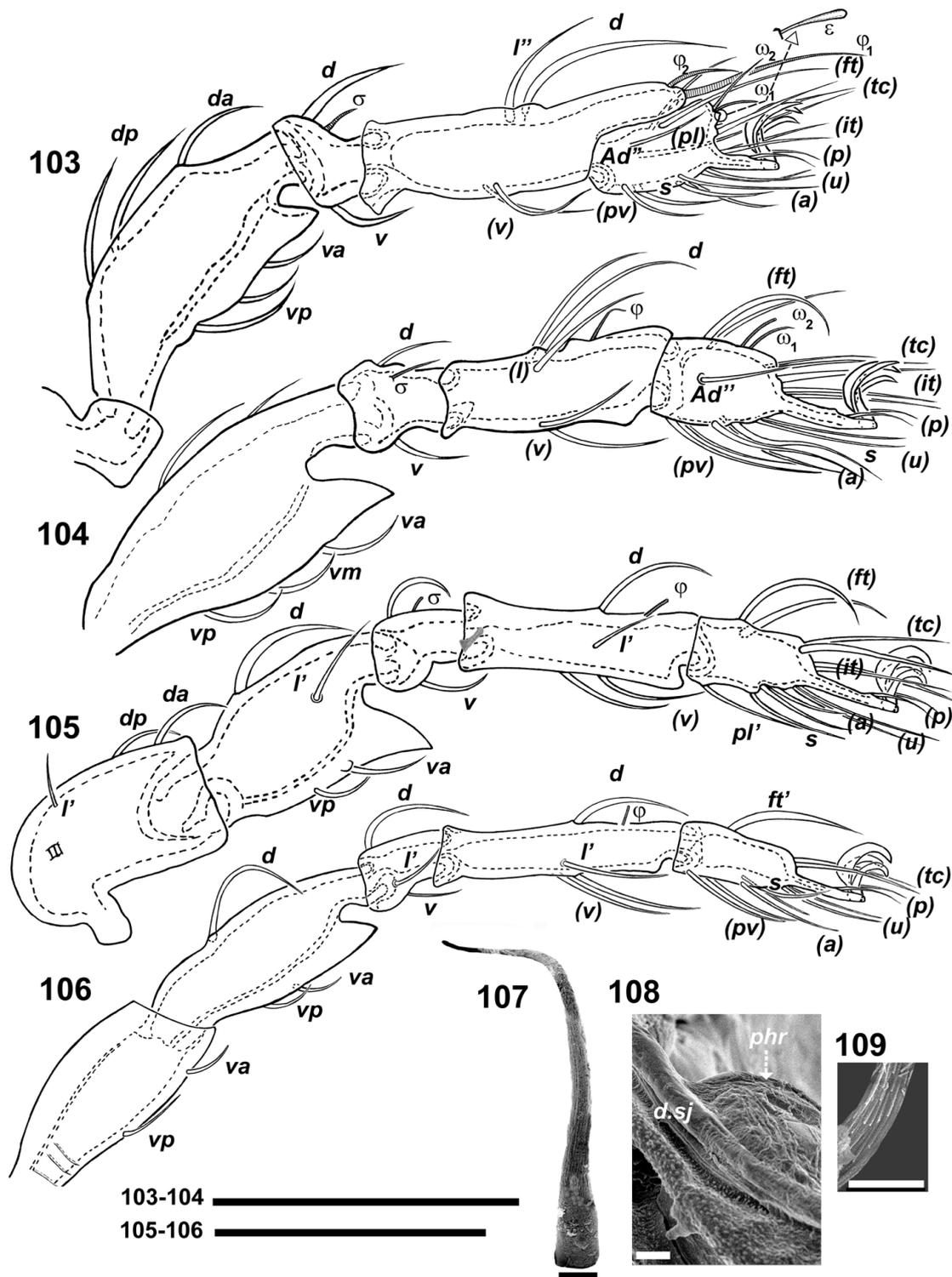
Figs 81-87. *Gaboneremaeus patriciae* sp. nov., adult female; SEM micrographs of cuticle with cerotegumental layer removed (81, 84); SEM micrographs of cerotegumental layer (82, 83, 85-87). (81) Body, ventral view. (82) Anal plate. (83) Detail of cerotegumental layer on genital plate. (84) Anal plates, ventral view. (85) Margin of anal plate, ventro-lateral view. (86) Subcapitulum. (87) Detail of cerotegumental layer developed as flat granulose sheet (*f.g.s*). For abbreviations see Material and Methods. Scale bars: 400 nm (87), 10 μ m (83, 85), 20 μ m (82, 84, 86), 140 μ m (81).



Figs 88-93. *Gaboneremaeus patriciae* sp. nov., adult female; line drawings (88-90) and SEM-micrographs (91-93). (88) Slightly inclined dorsal view of marginal body zone showing dorsal and ventral structures. (89) Ventral view of body. (90) Parts of prodorsum and notogaster, dorsal view. (91) Detail of genital seta. (92) Genital plates. (93) Aggenital seta. For abbreviations see Material and Methods. Scale bars: 5 μ m (93), 10 μ m (91), 25 μ m (92), 130 μ m (88), 200 μ m (89), 220 μ m (90).



Figs 94-102. *Gaboneremaeus patriciae* sp. nov., adult female; line drawing (94); SEM-micrographs showing cuticula with cerotegumental layer removed (95-99,102) and with cerotegument intact (100, 101). (94) Body in lateral view. (95) Notogaster in lateral view; prodorsum laterally inclined. (96) Prodorsum. (97) Genital plate, lateral view; some setal insertions indicated by v. (98) Epimeral seta without cerotegument. (99) Prodorsum in ventro-lateral view. (100) Laterally inclined prodorsum with cerotegumental layer. (101) Epimeral setae with cerotegument. (102) Insertion zone of *in* seta, lateral view. For abbreviations see Material and Methods. Scale bars: 3 μ m (101), 10 μ m (98, 100, 102), 20 μ m (97), 30 μ m (99), 40 μ m (96), 75 μ m (94), 100 μ m (95).



Figs 103-109. *Gaboneremaeus patriciae* sp. nov., adult female; line drawings (103-106) and SEM-micrographs (107-109). (103) Leg I, lateral view. (104) Leg II, lateral view. (105) Leg III, lateral view (106) Leg IV, lateral view. (107) Genital seta. (108) Pleurophragma, interior view. (109) Detail of barbs on genital seta. For abbreviations see Material and Methods. Scale bars: 2 μ m (107), 5 μ m (109), 10 μ m (108), 30 μ m (103, 104), 46 μ m (105, 106).

in setae 4 µm long (4.3-3.9), lateral to *bo* (Figs 72, 90, 94), situated on cuticular thickening (*c.t*) (Figs 99, 102), pyramidal in shape (Fig. 77) (*f.g.s.*, covered), without cerotegument, spiniform (Fig. 96); two *c.f* lobes anterior to *in* setae (Fig. 90). Bothridium complex, covered with *f.g.s.*, cup-shaped, its external margin with slit and ear-shaped expansion (Figs 75, 76, 96, 99); bothridial opening directed upward (Fig. 72). Setae *si* 145 µm long (136-154), filiform, directed towards rear (Figs 72, 74, 94), its pedicel long, curved, with small barbs (Figs 73, 74, 94). Pedotectal tooth well visible, 114 µm (105-123) in length (Figs 88, 89, 96, 99), triangular, with pointed apex (see Remarks).

Notogaster: 603 µm (589-635) in length, 505 µm (503-509) in width, ovoid, concave; notogastral margin (*ng.m*) well defined, smooth, elevated, from inner zone to margin depressed and at *bo* level elevated (Fig. 72). Middle posterior zone with small narrow pit (*p. d*); *d.sj* convex, clearly delimited (Fig. 72); pleurophragmata (*phr*) clearly visible (Fig. 108). Three pairs of setae: *p*₁ 43 µm long (39-50), *p*₂ 35 µm long (31-37), *p*₃ 29 µm long (31-34) (Fig. 89), all totally covered by cerotegumental layer (Fig. 81).

Lateral region: Elongate in shape (Fig. 94). Prodorsum laterally with alternatively elevated and depressed areas delimited by *c.f* (Figs 94, 96, 99). Setae *si* filiform, curved backward (Figs 74, 94). Pedotectal tooth (*pd. to*) well visible, situated between acetabula I and II, complex in shape, triangular, with sharply pointed tip. Superior notogastral zone with two parallel grooves (Figs 94, 96, 99). Notogaster triangular in lateral view (Figs 94, 95); *ng.m*, *p.d* and setae *p*₁, *p*₂, *p*₃ well visible; *bng* curved (Figs 95, 96). Epimeral zone with clearly delimited *c.t* and *d.z.*; insertion of epimeral setae and pre-genital sclerite (*p.g.s*) clearly discernible (Fig. 94); with parastigmatic enantiophysis (*p.e*) (Fig. 88).

Ventral region: Subcapitulum diarthric (Figs 81, 86). Subcapitular setae smooth; setae *a* 3 µm long (2.9-3.2), slightly curved, sigmoid and directed forward (Fig. 86); setae *m* 3.3 µm long (3-3.5), curved and directed toward body axis, apically all setae at same height but not crossing each other; setae *h* 3 µm long (2-8-3.3), straight or slightly curved, inserted in an ovoid depressed area, with a cerotegumental layer (Fig. 86).

Epimeral chaetotaxy (Figs 81, 89) neotrichous: 9[8-10]-6-9[8-10]-9[8-11] (in eleven specimens); setae in general becoming progressively longer from paraxial to antiaxial. All epimeres well defined by presence of epimeral furrows, apodemes and elevated cuticular thickenings, well demarcated against ano-genital region.

Epimere 1 big, polyhedral, with nine pairs of setae: 1a 19.2 µm long (18-21); 1a' 62.5 µm long (58-65); 1a'' 76 µm long (71-85); 1a''' 96.1 µm long (93-121); 1a'''' 133.8 µm long (129-140); 1a''''' 153.4 µm long (148-162); 1b 21 µm long (17-24); 1c 28.1 µm long (26-31); 1c' 13.6 µm long (7-15); shallow irregular *bo.1* situated a little below insertion level of 1a' to 1a'''' setae;

posterior setae 1a' in transversal groove (*bo.st*); ventral rectangular expansion (*v.p*) (Fig. 89) in lateral position, rectangular in shape, directed forward, situated anterior to *pd.to* and epimeric setae 1c'' (Fig. 89); *bo2* bifurcate (Figs 81, 89); *apo.2* (Fig. 89) situated at *bo.2* level, not reaching midline. Epimere 2 narrow and elongated, with six pairs of setae: 2a 9 µm long (7-11); 2a' 17.5 µm long (15-19); 2b 26.4 µm long (22-29); 2b' 27.5 µm long (25-29); 2c 23.2 µm long (20-24); 2c' 21.8 µm long (20-23); *bo.sj* large, deep, traversing midline (Figs 81, 89); parastigmatic enantiophysis (*p.e*) present laterally (Figs 81, 88, 89); *apo.sj* more or less of same length as *apo.2* (Figs 81, 88). Epimere 3 triangular, well defined, with ten pairs of setae: 3a 10.4 µm long (8-12); 3a' 11 µm long (8-13); 3a'' 15.6 µm long (13-17); 3b: 15.5 µm long (13-19); 3b' 21.3 µm long (18-24); 3b'' 26.4 µm long (24-28); 3b''' 31 µm long (29-34); 3c 31.4 µm long (28-33); 3c' 28.5 µm long (26-29); 3c'' 11.4 µm long (12-14); *bo.3* curved, ending near genital opening and depressed zone (*d.z*) (Figs 81, 89); *apo 3* small (Fig. 89). Epimere 4 big, polyhedral, with ten pairs of setae: 4a 10.5 µm long (8-12); 4a' 22.3 µm long (19-25); 4a'' 22 µm long (18-24); 4b 23.1 µm long (19-25); 4b' 24.2 µm long (22-25); 4b'' 36 µm long (35-39); 4b''' 37.4 µm long (35-41); 4c 32.1 µm long (28-39); 4c' 33.6 µm long (30-35); 4c'' 38.3 µm long (36-41); epimeres polyhedral, posteriorly delimited by elevated cuticular thickening (*c.t*) (Figs 81, 89); setae 4a on small pre-genital sclerite (*p.g.s*) (Figs 81, 89, 97); lateral genital plate with oblique depressed zone (*d.z*); *apo 4* small (Fig. 89).

Genital plate rectangular-polyhedral (Figs 81, 89, 92), 122 µm long (120-124); 117 µm wide (115-119). Nine pairs of setae, 31 µm long (29-34) (Fig. 107), carrying small barbs (Fig. 109); four of them situated paraxially, aligned, on ovoid elevated zone; five of them in antiaxial zone, curved (Figs 89, 92).

Anal plate elongated ovoid-rectangular (Fig. 84); 159 µm (156-169) long, 122 µm (119-124) wide. Ten pairs of setae (neotrichy) (Figs 82, 85), 23 µm (21-24) in length; surface with longitudinal striae and with some digitiform barbs carrying apical pores (Fig. 91); basal cerotegumental zone present (*b.c.z*) (Fig. 69). Plate structure complex: central zone elevated (*e.z*), surrounded by another low zone (*l.z*) with setae of similar shape (Fig. 82); *e.z*, *l.z*, *c.d* zones with different cerotegumental layers (*f.g.s*, *s.s*, *s.o.p*) (Figs 82, 83, 85, 87) (see description of cerotegument). Distance between genital-anal openings (i.e. anogenital bridge) 33 µm long (31-35) (Figs 81, 89). Agenital setae strong, 35 µm long (34-40) (Fig. 93), situated anterolateral of anal plate (Figs 81, 89), covered by *f.g.s.* cerotegumental layer. Adanal setae: *ad*₁ posterolateral of anal opening, on *c.t* (Fig. 94); *ad*₂, *ad*₃ lateral of anal opening (Figs 81, 89, 94). Lyrifissure *iad* not discernible.

Legs: Heterotridactylous. Setal formula: I (1-6-2-4-19-3) (including famulus) (1-2-2); II (2-5-2-5-17-3) (1-1-2); III (3-4-2-4-14-3) (1-1-0); IV (2-3-3-4-12-3) (0-1-0) (Figs 103-106). Famulus elongated (Fig. 103, drawn separately

and indicated by arrow). All leg femora with ventrally pointed expansions.

Remarks: The elevated cerotegumental structures, starfish-shaped structures (*s.s*) and flat granulous sheets (*f.g.s*), covering the surfaces of prodorsum, notogaster, ventral region and legs, facilitate the attachment of soil particles. Obtaining specimens with a clean cerotegument was difficult. Removing the cerotegumental layer is complex, but necessary to allow detailed observations (see Discussion). When it was possible to remove the cerotegument, most of the setae were also removed and only their insertion sites can be seen (Figs 81, 92, 95, 97). It is necessary to see the pedotectal tooth in different positions to appreciate its shape and position related to other structures (Figs 88, 89, 94, 96, 99). A view of the dorsal lateral zone, with a tilt to the ventral side (Fig. 88), simultaneously allows to see the posterior pedotectal tooth and the ventral projection, while the ventral view (Fig. 89) allows the same observation from another angle. The lateral view (Figs 94, 96, 99) allows to observe the pedotectal tooth from a different angle.

DISCUSSION

Cerotegumental layer and character states: The cerotegument provides important taxonomic characters. Despite its importance in Plateremaeoidea and other Brachypylina, the cerotegumental layer was ignored in many taxa descriptions. Some studies only show SEM-micrographs without providing any further information. Observations with SEM imply keeping the cerotegumental layer (or the secreted layer) in perfect condition (Alberti & Fernandez, 1989; Alberti & Coons, 1999; Evans, 1992; Norton & Behan-Pelletier, 2009). In most cases it is essential to clean the surface and remove adhering particles or dirt without producing an alteration of the cerotegument. Likewise, it is necessary to obtain useful observations with high magnification. By contrast, observations with an optical microscope necessitate the complete elimination of the cerotegumental layer, which is sometimes difficult to do, as in the case of Plateremaeoidea (see Grandjean, 1949a, b; Walter, 2009). Thus, it is necessary to take into consideration that observations of the cerotegument “in situ” hinder or prevent description of the full range of character states. For example, for other Brachypylina (Eremaozetidae) Colloff (2012) and Fernandez *et al.* (2021, 2022) provided examples of this last aspect, pointing out that several species have been described with their cerotegument not removed, and that inconsistent information was given. In Plateremaeidae only *Lopheremaeus mirabilis* was studied with SEM, but unfortunately most of the photos do not provide enough details (see Seniczak *et al.*, 2020). Only the illustration of two legs of an adult (Seniczak *et al.*, 2020: fig. 7C, D) allow an understanding of the cerotegumental layer, which is not very similar to that

of *Plateremaeus cebilae* sp. nov. but apparently more like the starfish-shaped structures of *Gaboneremaeus patriciae* sp. nov. Hunt (1996), in his work about Pherolioididae of Australia, showed that *Pheroliodes springthorpei* Hunt, 1996, *P. barringtonensis* Hunt, 1996, *P. concavus* Hunt, 1996, *P. lindsayae* Hunt, 1996, *P. lordhowensis* Hunt, 1996 and *P. transversus* Hunt, 1996 possess starfish-shaped cerotegumental structures like those observed in *Gaboneremaeus patriciae* sp. nov., while the legs of *Pheroliodes monteithi* Hunt, 1996 (Hunt, 1996: fig. 13c) have elevated irregular cells (*e.i.c*) like those of *Plateremaeus cebilae* sp. nov.

Observations by Walter on *Joshuella agrosticula* Paschoal, 1983 (see Walter, 2009: fig. 25) and *Roy-nortonella gildersleeveae* (Hammer, 1952) (see Walter, 2009: figs 33, 35, 39) show a mostly hexagonal cerotegument (sometimes pentagonal or heptagonal) composed of spherical units as present in *Plateremaeus cebilae* sp. nov.

In addition to the cerotegument, setae *in* are a very useful character as well: in *Pedrocortesella montis* Fernandez, 1990 it resembles a small cauliflower (Fernandez, 1990: fig. 3F); in *Malgacheliodes guillaumeti* Fernandez & Cleva, 2010 it is surrounded by small vertical columns, leaving the apical part free (Fernandez & Cleva, 2010: figs 3E, F); in *Pedrocortesella tristius* Eguaras, Martinez & Fernandez, 1990 the apical zone has the shape of a sailor’s beret, and the rest of the body is more or less cylindrical, with longitudinal and transverse cerotegumentary ribs (Eguaras *et al.*, 1990: fig. 7A); in *Plateremaeus cebilae* sp. nov. it has the shape of a rose flower; in *Gaboneremaeus patriciae* sp. nov. it has a pyramidal shape (Fig. 77) and it is covered by a flat granulous sheet.

The family Plateremaeidae: This family was proposed by Trägårdh (1931). Berlese (1908) established the genus *Plateremaeus*, with *Damaeus ornatissimus* Berlese, 1888 as the type species. Paschoal (1988) and Woas (1992, 2002) gave reviews. Other authors (Csiszár & Jeleva, 1962; Grandjean, 1965; Arillo & Subias, 2006; Seniczak *et al.*, 2020) made contributions to our knowledge of the family. Paschoal (1988) studied all genera of the family Plateremaeidae, redescribed *Plateremaeus ornatissimus* (Berlese, 1888) and established three new genera: *Paralopheremaeus* Paschoal, 1988, *Calipteremaeus* Paschoal, 1988 and *Lopheremaeus* Paschoal, 1988. Woas (1992) defined the subfamily Plateremaeinae and explained that it corresponds to the Plateremaeidae of Paschoal (1988). Paschoal (1988) and Woas (1992, 2002) considered Plateremaeidae to include five genera: *Plateremaeus*, *Allodamaeus* Banks, 1947, *Paralopheremaeus*, *Calipteremaeus* and *Lopheremaeus*. Arillo & Subias (2006) described the genus *Balogheremaeus*, with *B. chimaera* as its type species. Subias (2007) included them in the family Plateremaeidae. This genus and species are poorly

described and illustrated. They need a proper and comprehensive revision. We consider them here as questionable taxa.

In their key to families, Norton & Behan-Pelletier (2009) wrote: “Prodorsum without enantiophysis A, transverse furrow present or absent. Notogaster without circummarginal furrow; notogaster not extending anteromedially to level of bothridium. Genua, tibiae, and tarsi I-IV with or without retrotecta. Femur I with minimum of 8 setae, femur IV with minimum of 5 setae, trochanter IV with 3 setae. Bothridial setae filiform. Coxisternal region neutrichous. Length: 600-800 μ m.” Seniczak *et al.* (2020) studied *Lopheremaeus mirabilis* with the principal aim to describe and illustrate its ontogeny. They noted (on page 2157) that “The presence of epimeral hypertrichy and crests on some leg segments support the membership of *L. mirabilis* in Plateremaeidae”.

The genus *Plateremaeus* Berlese, 1908 is considered by Subias (2004) to comprise: *P. ornatissimus* (Berlese, 1888); *P. anteriosetosus* Woas, 1992; *P. berleseii* Balogh & Mahunka, 1978; *P. complanatus* (Warburton, 1912); *P. costulatus* Balogh & Mahunka, 1978; *P. latus* Balogh, 1988; *P. novemsetosus* Balogh & Balogh, 1983; we here add *P. cebilae* sp. nov. from Argentina. To give an idea of the enormous complexity of Plateremaeoidea, Norton & Behan-Pelletier (2009) indicated in reference to the Plateremaeidae “the prodorsum without enantiophysis”, but in *P. ornatissimus* (Berlese, 1888) shown by Paschoal (1988: fig. 1) and by Mahunka & Mahunka-Papp (1995: fig. 19), and in *P. costulatus* Balogh & Mahunka (1978: fig. 5A) apparently exists an enantiophysis on the prodorsum, which is not mentioned in the corresponding texts.

Walter (2009: 23) noted “The taxonomy of the North American Gymnodamaeidae is currently intractable, because (1) the adults are covered in a thick, ornamented cerotegument that provides useful characters, but that obscures the cuticle; (2) many descriptions appear to be based on newly moulted or cleared specimens and are incomplete or contain misinterpretations; and (3) there is considerable disagreement in the literature about valid genera and generic limits, leading some authors to sink some or all of the North American genera into *Gymnodamaeus* s.l. Several nomenclatorial problems have added to the confusion”. Bayartogtokh & Schatz (2009: 48) in their discussion explain: “Concerning the species diversity of *Gymnodamaeus*, Paschoal (1982) assigned 13 species to this genus, including nine species described by him, but considered five previously known species as *species inquirendae*. However, most of his newly described species, such as *G. gregarius*, *G. knowltoni*, *G. notoapodematus*, *G. saltuensis*, *G. taedaceus*, *G. umbraticus*, *G. victoriae*, should be regarded as *species inquirendae*, since there are no illustrations, and the available descriptions are not suitable for reconstruction of the species characters”.

The situation pointed out by Walter (2009) and Bayartogtokh & Schatz (2009) is like the one observed by us in Paschoal’s (1988) revision of the family Plateremaeidae.

To solve the existing problems, it is necessary to conduct detailed redescriptions using modern methods.

Immatures: Until the publication of Seniczak *et al.* (2020) only the ontogeny of *Lopheremaeus mirabilis* was known for Plateremaeidae. We add here the complete ontogeny of *Plateremaeus cebilae* sp. nov. To study immatures, we established breeding colonies. Initially we worked with twenty specimens (ten males and ten females, which are easy to distinguish by size). We inspected them twice daily, and generally on the second day copious quantities of spermatophores have been observed, but we did not see eggs, prelarvae, larvae or protonymphs.

The deutonymphs and tritonymphs were found as they were walking on or between the tiny pieces of decomposing wood of *Ceiba speciosa*, on which they fed. The adults dig tunnels inside clusters of wood. We think that it is possible that larvae and protonymphs can be found inside those galleries, but we have not opened these clusters of wood to access them. We set up six breeding colonies of fifty animals each. In this way we were able to obtain larvae and protonymphs which were always together with the adults and did not leave the tunnels. It is unclear whether adults lay eggs or prelarvae, because we never found any.

The comparison between *Plateremaeus cebilae* sp. nov. and *Lopheremaeus mirabilis* provides interesting information. The structure of the prodorsum of larvae to tritonymphs of *P. cebilae* sp. nov. is different from that of *L. mirabilis* which has: three pairs of porose areas *a.pa*, *m.pa*, *p.pa*; a cuticular thickening (*ct*) delimiting a triangular surface (*t.z*), and *le* setae situated near *t.z* in the apical zone of the prodorsum. The bothridial ring (*bo.ri*) is developed as a triangular posterolateral expansion that is visible in the larva, proto- and deutonymph, but that is not evident in the tritonymph.

There are also differences in gastronotal setae between *L. mirabilis* and *P. cebilae* sp. nov.: larvae of *L. mirabilis* with *c*₁, *c*₂, *da*, *dm*, *dp*, *h*₁, *h*₂, *lp*; larvae of *P. cebilae* without *c*₂ and *h*₂. In nymphs of both species *d* series setae are absent.

Neotrichy is evident on the epimeres of both species, with differences on all but epimere I. The number of genital setae is different in the tritonymph and adult of *P. cebilae* sp. nov. Finally, a very interesting interspecific variation exists in the aggenital formulae, with *L. mirabilis* having four setae as adults, while *P. cebilae* sp. nov. has only one (Table 1).

Taxonomic position of Gaboneremaeidae fam. nov. in the superfamily Plateremaeoidea: We considered the Gaboneremaeidae as a new family of the superfamily

Table 1. Comparison of seta formulae of *Plateremaeus cebilae* sp. nov. and *Lopheremaeus mirabilis* (Csiszár in Csiszár & Jeleva, 1962).

setae	<i>L. mirabilis</i>	<i>P. cebilae</i> sp. nov.
gastronotal	(8-8-6)	(6-6-5)
epimeral	(3-1-2) (3-2-3-1) (3-2-6-2) (7-5-7-4) (8-7-12-4)	(3-1-2) (3-3-3-1) (3-5-5-3) (6-6-5-5) (8[7-9]-5[4-6]-6[5-6]-8[7-9])
genital	(1-4-5-7)	(1-4-7-9)
aggenital	(0-0-1-1-4)	(0-1-1-1-1)
anal	(03333) (0333) (0[4-5]-[4-5])	(03333) (0333) (045)

Plateremaeoidea based on the definition of Norton & Behan-Pelletier (2009: 454): “With subnormal apodemato-acetabular system, lacking trachea I; with or without porose sac opening into acetabulum. Well-developed cerotegument covering body and setae. Prodorsum usually with deep transverse furrow. Prodorsal lamellae and costulae absent. Parastigmatic enantiophysis, dorsophragmata, and pleurophragmata absent. Notogaster flattish in lateral aspect; usually concave inside distinct margin; 4, 5, or 6 of pairs notogastral setae. Genal notch absent. Subcapitulum diarthric; palpal eupathidium acm separate from solenidion. Tibia I with long apophysis distally, bearing solenidia ϕ_1 and ϕ_2 ; femora III-IV with retroecta; tibiae with or without retroecta. Tarsus II with 1-2 solenidia. Leg segments with or without internalized porose organs.”

For the reasons stated above, we propose that the following modification are made to the definition of the superfamily: “Parastigmatic enantiophysis, dorsophragmata, discidium, and pleurophragmata present or absent.” With respect to the notogastral setae, we here modify the definition: “3, 4, 5, or 6 pairs of notogastral setae” and we add: “pregenital sclerite present or absent; anal setae neutrichous or not.

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