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Revision of the family Carabodidae (Acari: Oribatida) XV. *Costacarabodes turrialbai* gen. nov., sp. nov. and *Tuberocepheus kompsosis* sp. nov from Costa Rica

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ABSTRACT

Costacarabodes turrialbai gen. nov., sp. nov. and *Tuberocepheus kompsosis* sp. nov. from Costa Rica are described using optical and scanning electron microscopy. *Costacarabodes turrialbai* gen. nov., sp. nov. is a new genus with particular characteristics: prodorsum with elevated interlamellar process divided by a deep depression; interlamellar, lamellar, and rostral setae very different in shape and size; eight pairs of notogastral setae; notogaster incompletely surrounded by circumgastric depression interrupting posterior notogastral zone; pedotectum I as normal extending lamina; pedotectum II reduced or absent; tutorium small, aligned dentitions present in inferior zone; epimeral zone with depressions; conspicuous longitudinal medial epimeral depression, demarcated by semicircular cuticular thickening; epimeral formulae 1-1-3-3; epimeral setae *3b, 3c* parallel to each other; articulation of genu-tibia III and IV each with dorsal socket.

T. kompsosis sp. nov. is differentiated from *T. longus* by pusticulate microsculture on ventral zone, humeral apophysis; lateral lamellar zone and epimeral zone; reticulate-foveate microsculpture on area of posterior prodorsal depression; punctate microsculpture on subcapitular zone; simple, setae with small dentitions: notogastral, rostral, interlamellar setae; simples basally inflated *a* sub-capitular setae; elevated interlamellar process with depressed central area, defining two triangular to polyhedral structures; polyhedral notogastral anterior depression well defined, with posterolateral cuticular ridges; three central notogastral promontories, of which two round to ovoid, and one semicircular; with lateral pairs of promontories (first pair large, oval; second pair medium sized, ovoid). Lateral prodorsum with anterior tutorial depression, well-developed posterior tutorial depression; anal plate with rounded depression anterior to sharp tip.

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Introduction

In our first paper on the revision of the Family Carabodidae (Fernandez et al. 2013a), we noted,

> When studying the family Carabodidae, one quickly arrives at the conclusion that the diagnostic features/characteristics at the generic level are very intricate, and in most instances difficult to interpret. This difficulty has been augmented by the loss of type specimens and/or difficulties in obtaining types. Many descriptions and even redescriptions were also incomplete.

In the interim, after more than 15 papers and more than six years of taxonomic study, the authors have studied 24 genera and 44 species (Fernandez et al. 2013a, 2013b, 2013c, 2013d, 2013e, 2014a, 2014b, 2014c, 2014d, 2015a, 2015b, 2016b, 2017a, 2017b, 2017c, 2017d, 2014e, 2016a).

Aided by the fact that we were able to access significant collections from different museums, as well as our own samples, we can attest to our initial opinion: the diversity of forms, characteristics, and particularities are impressive. Several geographic zones present a biodiversity of species with more peculiar characteristics than ever imagined, making the Carabodidae family an inexhaustible source of extraordinary material.

More recently, we embarked on the study of a large collection of material housed in the Natural History Museum of Geneva (NHMG). Amongst material from Costa Rica, we discovered two interesting species (objects of this study) and initiated a search for material resembling the new genus *Costacarabodes* gen. nov. We studied material from Costa Rica in the NHMG as well as our collections from Argentina, Paraguay, Brazil, Uruguay, Peru, Chili, Colombia, and Antilles, with the intention of finding groups closely related to this particular new genus. We focused our search on the presence of a set of characters not previously known to occur concurrently in the family, including the following. Conspicuous polyhedral prodorsal posterior depression; elevated interlamellar processes with depressed V-shaped central area; le setae situated dorsally on lamellae, close to rostral setae; lamellae developed dorsolaterally lacking sharp cuspis; notogastral anterior and posterior depressions present; elevated central notogastral zone with four pairs of setae; four pairs notogastral lateral setae; circumgastric notogastral depression interrupted on posterior zone; articulation of genu-tibia III, IV by means of dorsal socket.

Materials and methods

Specimens were studied by means of light microscopy (Olympus BHC compound microscope – Zeiss Axio Scope (Carl Zeiss Microscopy GmbH, Jena, Germany; equipped with a drawing tube) following the techniques described by Grandjean (1949) and Krantz and Walter (2009). Specimens studied under a scanning electron microscope (SEM), (FEI Quanta Feg 250, with 10 Kv and working distant (WD) variable), followed the techniques of Alberti and Fernandez (1990a) (Alberti and Fernandez 1990b, Alberti et al. 1991, 1997, 2007) and Fernandez et al. (1991). The same equipment was used as in previous studies (see Fernandez et al. 2017a).

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Drawings of optical observations were deemed necessary in order to provide semi-schematics, especially with reference to cuticular microsculpture and setal shapes. Studies with SEM increased the level of precision and detailed figures could be produced.

Measurements taken: total body length (tip of rostrum to posterior edge of notogaster), width (widest part of notogaster), in µm. Measurements of setae were taken on three specimens under SEM; lengths of setae are to be considered provisional as, though well preserved, these mites were in alcohol for over 35 years and damage to setal tips could not be easily ascertained.

Leg chaetotaxy were studied by the use of optical microscopy (standard, polarized, and phase contrast). Setal formulae of the legs include the number of solenidia (in parentheses); tarsal setal formulae include the famulus (ε).

Morphological terminology

Morphological terms and abbreviations used are those developed by Grandjean (1928–1974) (cf. Travé and Vachon 1975; Norton and Behan-Pelletier 2009; Fernandez et al.; 2013a; 2013b, 2013c.: adanal setae (*ad$_1$, ad$_2$, ad$_3$*); aggenital setae (*ag*); anal setae (*an$_1$, an$_2$*); anterior genital plate furrow (*a.g.f*); anterior tutorial depression (*a.tu.d*); apodemes (*apo 1; apo2; apo. sj; apo3*); bothridial ring (*bo.ri*); bothridial tooth (*bo.to*); bothridium (*bo*); circumgastric furrow (*s.c*); depressions (*dep*); discidium (*dis*); dorso-sejugal depression (*d.sj*); elevated interlamellar processes (*e.i.p*); epimeric setae (*1a, 1b, 1c, 2a, 3a, 3b, 3c, 4a, 4b, 4c*); femoral groove (*f.g*); genital setae (*ge*); humeral apophysis (*h. ap*); lamellae (*lam*); lamellar setae (*le*); latero-abdominal gland (*gla*); low lamellar furrow (*l.l.f*); naso superior cornea (CSO); notogastral anterior depression (*n.a.d*); notogastral margin (*b.ng*); notogastral posterior depression (*n.p.d*); notogastral setae (*ng*) (*da, dm, dp, la, la, lp, h$_1$, h$_2$, h$_3$, p$_1$, p$_2$, p$_3$*); pedotectum I (*Pd I*); pedotectum II (*Pd II*); posterior tutorial depression (*p.tu.d*); prodorsal posterior depression (*p.p.d*); promontories (*prm*); rostral setae (*ro*); sensillus (*si*); subcapitular setae (*a, h, m*); supra tutorial depression (*s.tu.d*); tutorium (*Tu*). For setal types we followed Evans (1992:73) and for ornamentation of cuticular surfaces we followed Murley (1951 in Evans *op.cit*: 9).

Material studied

NHMG : "Costa Rica, CR 0978 TU 18a, Turrialba forêt naturelle de CATIE alt. 560 m; racines d'épiphytes sur branche tombe 1 mois *avant* 24/IX/1978".

Additional material was collected:

Argentina: Escobar, Prov. Buenos Aires, selva marginal; mantillo. 21/VII/1984 Coll. Fernandez, N.; Alpasinche, Prov. La Rioja, mantillo de *Prosopis nigra*, 9/12/2017; Ranchillos, Prov. Tucuman, mantillo, 6/IX/91. Coll. Fernandez, N. **Paraguay**: Obligado; Itapua, Troncos en decomposicion; 12/XI/2015, Coll. M. Schroetlin; Obligado; Obligado, Itapua, mantillo 9/6/2013. Coll. M. Schroetlin. **Brazil**: Cachoeira do Sul; Rio Grande do sul; 6/VII/2003. Mantillo con restos de troncos en descomposición. Coll. Fernandez, N. **Uruguay**: Paysandú; Dep. Paisandú. Mantillo, *Cortaderia* spp, margen Rio Uruguay. 16/1/1995. Coll. Fernandez, N. **Peru**. Tingo Maria, proximidad Parque Nacional Tingo Maria, mantillo, Yunga. 4/VI/1999. Coll. Fernandez, N. **Chili**: San Vicente de Taguataguam, Prov. Cachapoal liquen *Placolecanora* spp. 1/12/2001. Coll. Fernandez, N. **Colombia**: Ibagué, Dep. de Tolima, Mantillo con troncos en descomposición. 9/IX/1995. Coll. Fernandez, N. **Antilles**: Guadeloupe, margen riviere Carbet, branche tronc mort. 4/VIII/1986, Coll. Fernandez, N.

New taxa descriptions

Costacarabodes gen. nov.

Etymology

The generic prefix "Costa" is derived from Costa Rica, country of origin of the type material.

Diagnosis (adult female).

Body shape ovoid. Cuticular microsculpture very complex. Prodorsum: deep depression dividing elevated interlamellar process into two separate structures; lamellae without sharp tip; *le* setae situated dorsally; prodorsal posterior depression present; tutorium small, aligned dentitions present in inferior zone. Notogaster: anterior notogastral depression present; posterior notogastral depression present; eight pairs of notogastral setae: four pairs dorsal, four pairs lateral; circumdorsal depression interrupting posterior notogastral zone; pedotectum I with extended lamina; pedotectum II reduced or absent; discidium present; epimeral zone with clearly delimited depressions; with more or less semicircular cuticular thickenings; epimeral formulae 1-1-3-3; epimeral setae *3b, 3c* situated parallel to each other; ventral chaetotaxy: genital setae: 4; aggenital setae: 1; adanal setae: 3; A anal setae: 2; articulation genu-tibia III and IV by means of a dorsal socket.

Type species: *Costacarabodes turrialbai* gen. nov., sp. nov.

Costacarabodes turrialbai gen. nov., sp. nov. (Figures 1–46)

Etymology

The specific epithet "turrialbai" is derived from the Turrialba forest, collection area of the type material.

Diagnosis (adult female).

Cuticular microsculpture complex. Setae: genital, aggenital setae simple; notogastral, lamellar, rostral, adanal setae lanceolate-barbate; interlamellar setae lanceolate-barbate with central vein; epimeral setae setiform; subcapitular setae *a* spiniform, curved; subcapitular setae *h, m* serrate-barbate; anal setae spiniform with small barbs; *le* setae situated dorsally on lamellae, near *ro* setae. Lamellae well developed, without sharp cuspis; superior cornea of naso well visible; Notogastral posterior depression with ribbed microsculpture interrupting circumgastric depression; three pocket depressions between pedotectum I and tutorium; aggenital furrow followed by depressed zone; polyhedral depressed zone between genital and anal openings.

Material examined

Holotype: Female "Costa Rica, CR 0978 TU 18a, Turrialba forêt naturelle de CATIE alt. 560m; racines d'épiphytes sur branche tombe 1 mois avant 24/IX/1978 Leg. P. Werner", deposited in the Collection of the Muséum d'Histoire naturelles Geneva, Switzerland. Three other specimens (same locality as type material) Turrialba, Costa Rica., observed under SEM, were not deposited; all specimens preserved in 70% ethanol.

Description

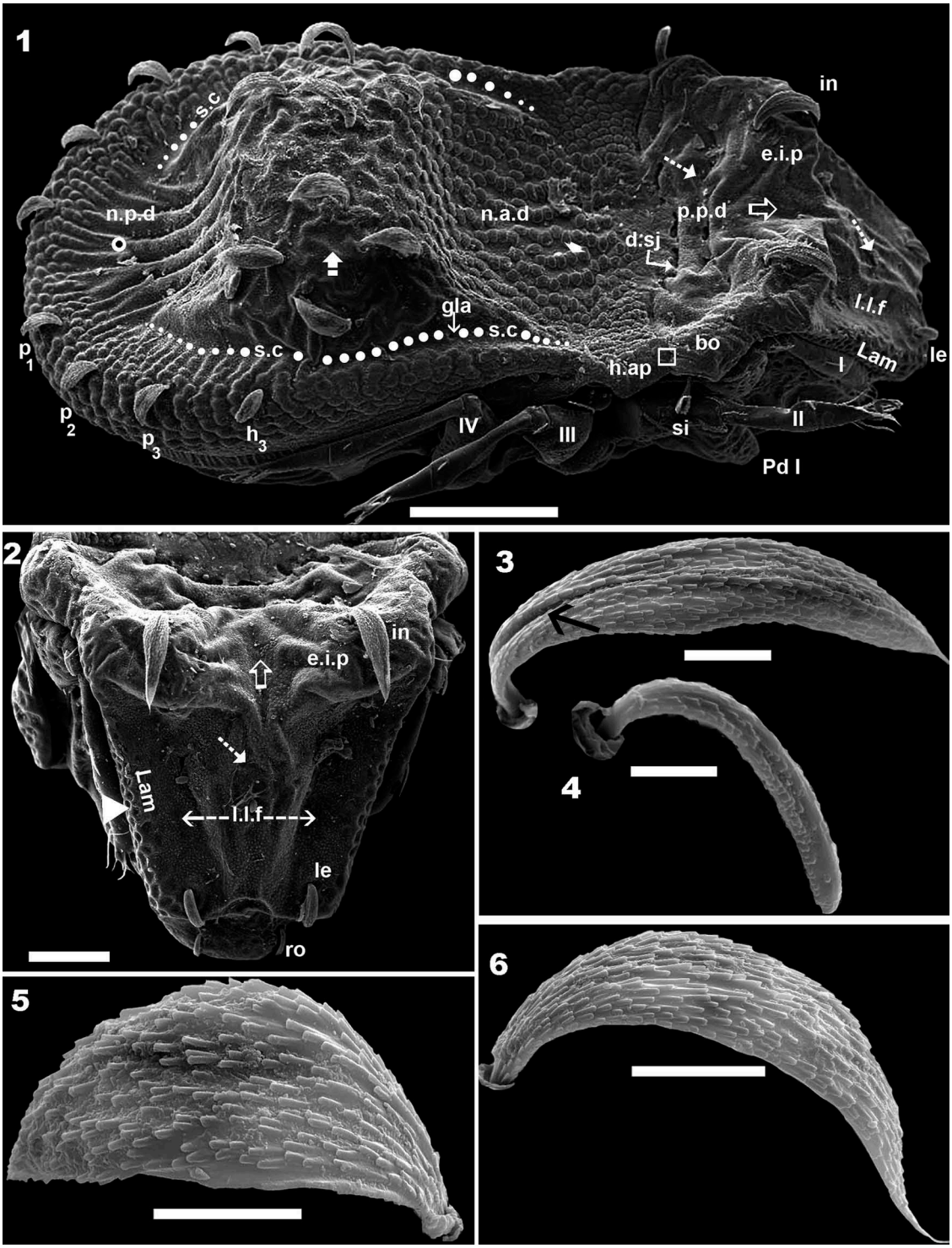
Measurements. SEM: 601 (596–631) × 180 (176–187) (n: 3). Light microscopy: 612 × 183 (n: 1); all specimens female.

Shape. Elongate oval (e.g. Figure 1).

Colour. Specimens without cerotegument (*ce*) light to dark brown, slightly shiny when observed in reflected light.

Cerotegument. Consistently thick layer (0.8–1.5) covering body and legs, with cuticular irregularities (Figure 37 indicated by arrow). Rugous on ventral epimeral zone (Figures 23, 29). Thick layer also covering legs, with the addition of rugous patches (Figures 43, 46. indicated by ⇧).

Integument. Microsculpture complicated, varying according to body region. Creased (Figures 1, 2 indicated by dashed arrow): prodorsal posterior depression zone (*p.p.d*) between dorsosejugal



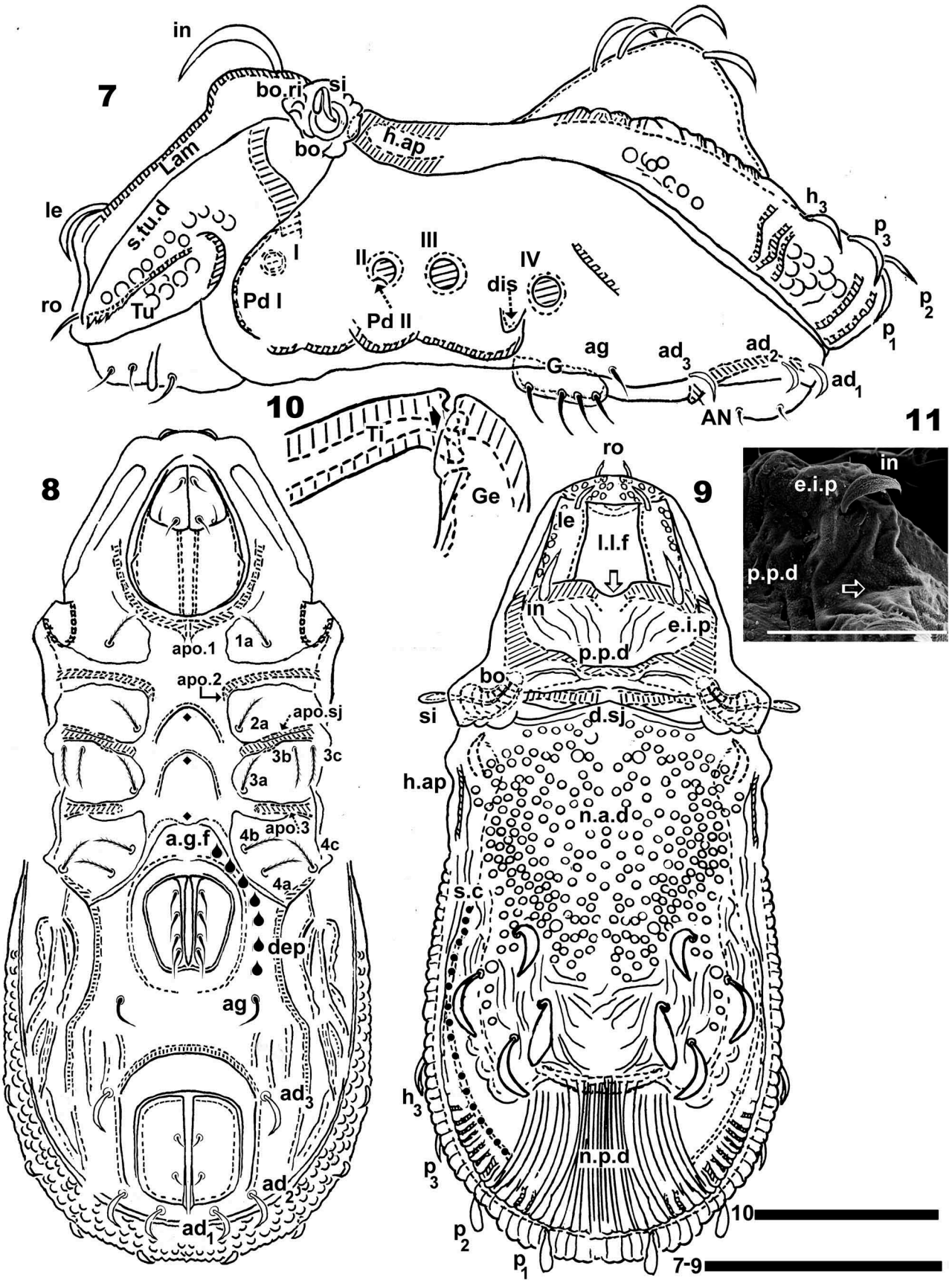
Figures 1–6. ***Costacarabodes turrialbai* gen. nov., sp. nov**. Adult female, SEM observations. **1**. dorsolateral view; **2**. frontal view; **3**. interlamellar setae; **4**. rostral setae; **5**. notogastral setae, lateral. **6**. lamellar setae. (See text for explanation of symbols.) Scale bars: 1 = 100 µm; 2 = 50 µm; 6 = 15 µm 3, 5 = 10 µm; 4 = 5 µm.

*Integumental m*icrosculpture: Creased, indicated by dashed arrow ⇡; Wrinkled, hardly raised, with very shallow folds, indicated by ⇧; Aligned, ribbed, indicated by ◯; Undulate indicated by □; Elevated, more or less circular shapes, with scalloped edges indicated by y ◡; *e.i.p* V-shaped, central area, indicated by ⇨; *s.c* trajectory indicated by solid dot on ● ; *in* setae furrow indicated by ↓.

depression *(d.sj*) and elevated interlamellar process (*e.i.p*); all surfaces of *e.i.p;* between low lamellar furrows (*l.l.f*).

Wrinkled, hardly raised, with very shallow folds (Figures 1, 12, 13 indicated by ⇧): elevated notogastral zone where four pairs of central notogastral setae situated. Elevated, more or less circular shapes, with scalloped edges (Figure 14 indicated by solid arrow): notogastral anterior depression (*n.a.d*) between *d.sj* and first notogastral seta (Figures 1, 12, 13, indicated by solid arrow); on the lateral zones of *n.a.d* and near humeral apophysis (*h.ap*) irregularly distributed (Figures 1, 13), but on rest of *n.a.d* longitudinally aligned (Figures 1, 20, 22). Aligned, ribbed (Figures 1, 13, 21 indicated by ◯): notogastral posterior depression (*n.p.d*) extending to near posterior notogastral zone (Figure 13).

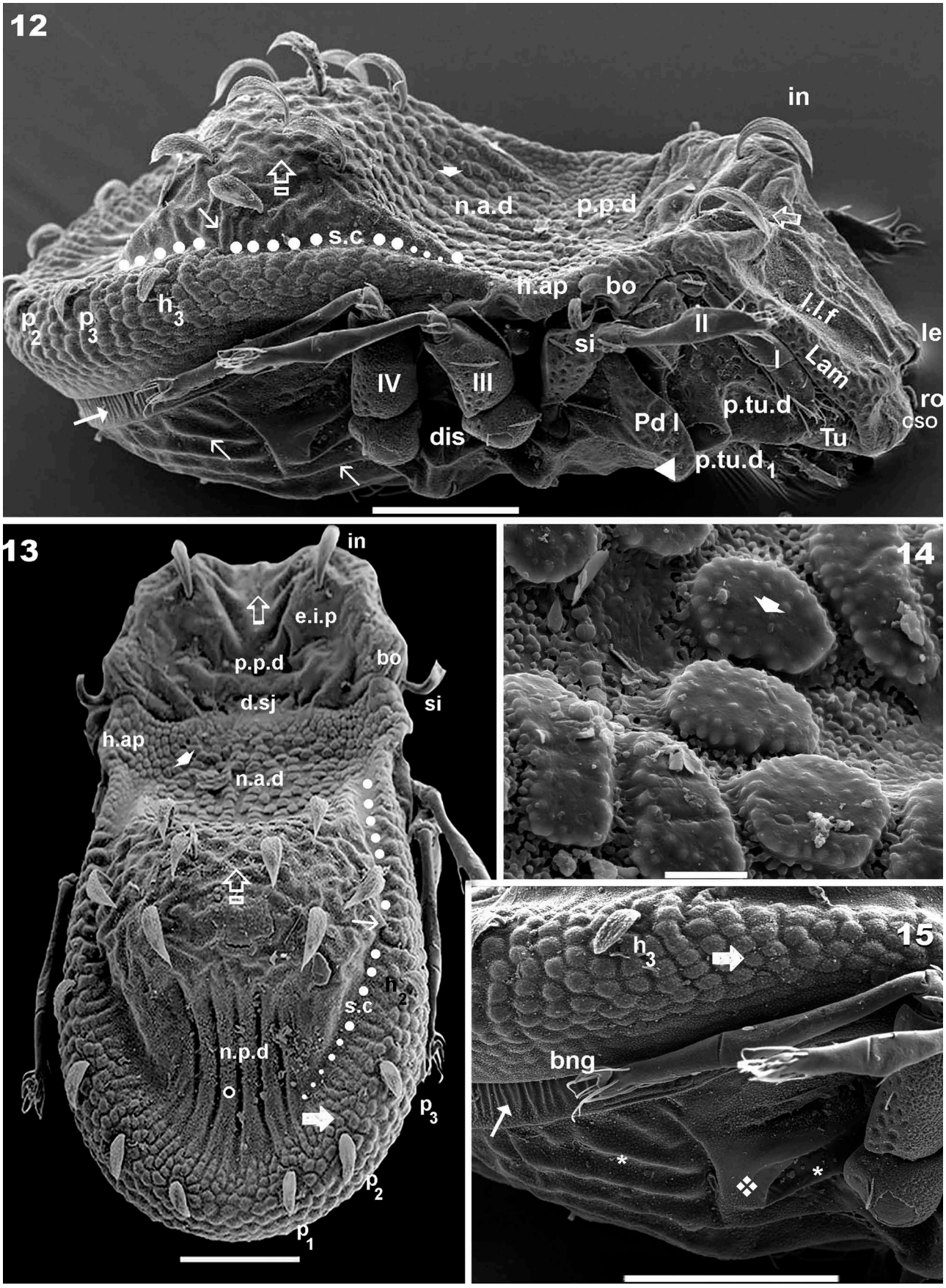
Irregularly ribbed (Figures 15, 37 indicated by asterisk) extending from ventral shield (Figure 23) laterally to genital and anal openings; in lateral view irregular ribbed zone divided into two zones by smooth polyhedral surface (Figure 15 indicated by ❖). Colliculate (Figures 1, 13, 15, 34 indicated by ⇨); notogaster surrounded by colliculate microsculpture, extending on either side from posterior zone of *h.ap* (Figures 1, 13) to notogastral margin (*b.ng)*; circumgastric furrows (*s.c*) delimits this microsculpture, except on posterior ribbed zone (Figure 13).



Figures 7–11. ***Costacarabodes turrialbai* gen. nov. sp. nov**. Adult female. **7**. lateral view; **8**. ventral view; **9**. dorsal view. 10. genu-tibial articulation, leg III; **11**. dorsal view, detail *e.i.p*. Scale bars: 7–9 = 220 µm; 11 = 100 µm; 10 = 35 µm.

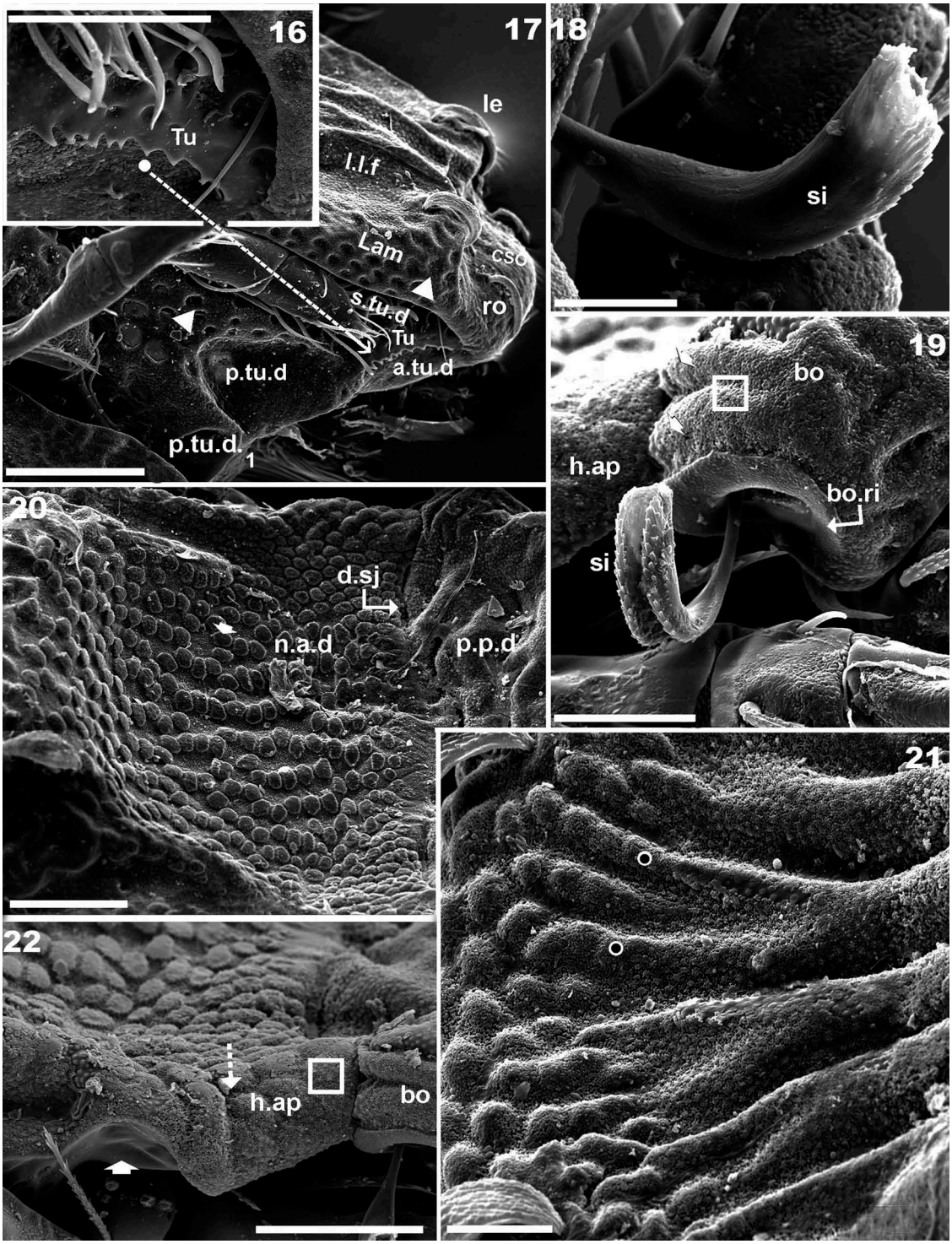
Medial epimeral depression indicated by small diamond ◆ ; *a.g.f* followed by depressed zone indicated by 💧; *e.i.p* V-shaped, central area, indicated by ⇨; *s.c* trajectory indicated by ●; sockets 🕳.

Foveate (Figures 2, 12, 17 indicated by solid black diamond, 23), very clearly delimited round-ovoid fovea, situated on lateral zone of lamellae (*Lam*) (Figures 1, 2, 12); tutorium (*Tu*) and posterior lateral tutorial depression (*p.tu.d*); pedotecta I (*Pd I*); femora I, II, III, IV (Figure 12); subcapitulum (Figure 29), and anal plate. Sulcate (Figures 12, 15, 35 indicated by ↑) posterior zone of ventral shield. Undulate ***(Figures I, 19, 22 indicated by black outlined square) bothridium (*bo*) and *h.ap* zones.



Figures 12–15. ***Costacarabodes turrialbai*** **gen. nov., sp. nov**. Adult female, SEM. **12**. lateral view; **13**. dorsal inclined, anteroposterior view; **14**. notogastral anterior depression, microsculpture, elevated surfaces, more or less circular, with scalloped edges; **15**. posterolateral microsculpture. Scale bars: 12, 13 = 100 µm; 15 = 50 µm; 14 = 5 µm.

*Integumental m*icrosculpture: Creased, indicated by ⇡; ***Wrinkled, hardly raised, with very shallow folds, indicated by ⇪; Aligned, ribbed, indicated by ⭘; Elevated, more or less circular shapes, with scalloped edges indicated by ➽; irregular ribbed zone divided into two zones by smooth polyhedral surface indicated by ❖; irregularly ribbed indicated by *; Sulcate indicated by ↑; colliculate microsculpture indicated by white solid ⇨;*e.i.p* V-shaped, central area, indicated by ⇨; *s.c*, trajectory indicated by ●.



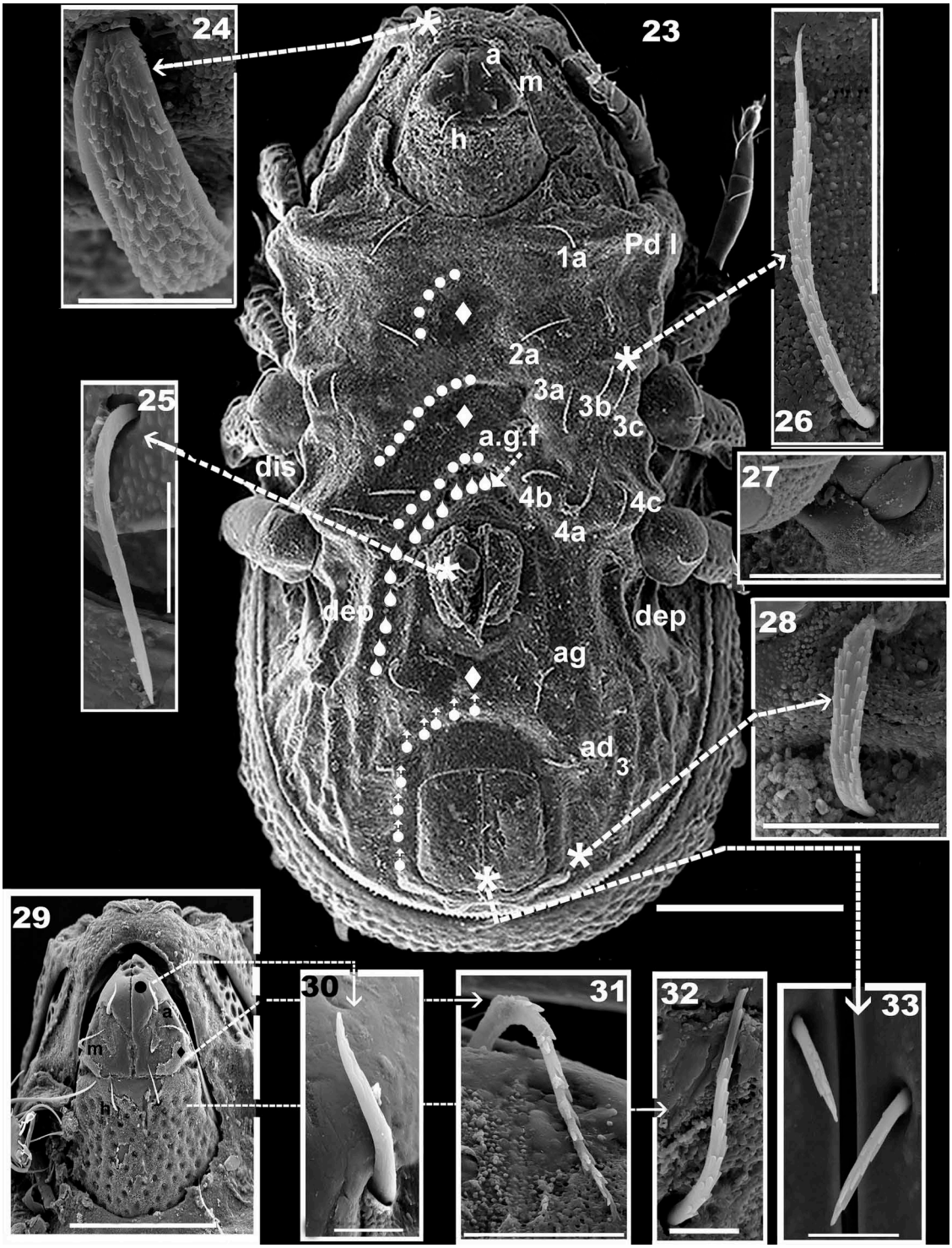
Figures 16–22. *Costacarabodes turrialbai* gen. nov., sp. nov. Adult female, SEM observations. **16**. tutorium detail, inferior zone with aligned teeth; **17**. anterolateral zone, prodorsum; **18**. sensillus, lateral view; **19**. sensillus, frontal view; **20**. notogastral anterior depression (*n.a.d*); **21**. notogastral posterior depression showing aligned ribs (indicated by ⭘); **22**. lateral *h.ap* zone. Scale bars: 17, 20 = 50 µm; 16 = 30 µm; 19; 21; 22 = 20 µm; 18 = 10 µm.

Elevated, more or less circular shapes, with scalloped edges indicated by ⬬; Aligned, ribbed, indicated by ⭘; Undulate indicated by □; *h.ap* transversal groove indicated by ⇢.

Setation (excluding legs). Genital, aggenital (*ag*) setae simple (Figures 23, 25); genital setae length 22 (20–24); *ag* setae (Figure 23) length 20 (19–22). Notogastral (*ng*), lamellar (*le*), rostral (*ro*), adanal (*ad*) setae lanceolate-barbate. Dorsal *ng* setae (Figures 1, 12, 13) (59–64), marginal *ng* setae (Figures 1, 5) 30 (27–31), *ro* setae (Figure 4) 22 (21–23), *le* setae (Figure 6) 29 (27–30) and *ad* setae (Figure 28) 19 (20–22). Interlamellar setae (*in*) (Figure 3) lanceolate-barbate with central vein 63 (61–64). Epimeral setae (Figure 26) elongate barbate 32 (30–35). Subcapitular setae *a* (Figures 29, 30) spiniform, curved 11 (9–12). Subcapitular setae *h, m* (Figures 31, 32) serrate-barbate 16 (14–20). Anal setae (Figures 23, 33) spiniform with small barbs 8 (9–11).

Prodorsum. Conspicuous polyhedral prodorsal posterior depression (*p.p.d*) between elevated interlamellar processes and *d.sj* (Figures 1, 9, 12, 13, 20);*e.i.p* complex, with depressed V-shaped, central area (Figures 1, 2, 9, 11, 12, 13 indicated by ⇨). Setae in situated slightly towards the posterior on *e.i.p* (Figures 1, 2, 12, 13), directing forward, surpassing *e.i.p; le* setae situated dorsally on lamellae, close to *ro* setae.

Shape and characteristics of *in* setae differ vastly to *le, ro* setae (Figures 1, 3, 4); relative length *in>le>ro*. Dorsolaterally developed *Lam* lacking sharp cuspis; *le* setae dorsally situated (Figure 1); two clearly visible *l.l.f* (Figures 2, 9) with well-defined, triangular to polyhedral zone of creased cuticular microsculpture between them



Figures 23–33. ***Costacarabodes turrialbai*** **gen. nov., sp. nov**. Adult female, SEM. **23**. ventral view; **24**. *ro* setae; **25**. genital setae; **26**. epimeral setae; **27**. pedotecta II; **28**. adanal setae ad_3; **29**. subcapitulum; **30**. subcapitular seta *a*; **31**. subcapitular seta *m;* **32**. subcapitular seta *h*; **33**. anal setae. Scale bars: 23 = 140 µm; 24 = 8 µm; 25, 26 = 20 µm; 27 = 40 µm; 28 = 20 µm; 29 = 50 µm; 30 = 5 µm; 31 = 10 µm; 32 = 5 µm; 33 = 5 µm.

Conspicuous longitudinal medial epimeral depression indicated by □; semicircular cuticular thickening indicated by □; *a.g.f* followed by depressed zone indicated by □.

(Figures 1, 2 indicated by ⇡). Polyhedral *bo* (Figures 12, 19) with elongate promontories; downward directed opening; large, smooth bothridial ring (*bo.ri*) (Figure 19). Sensillus (*si*) complex, curved, directing upwards (Figures 12, 13), in lateral view horn-shaped (Figure 18), in frontal view directing upwards, U-shaped (Figure 19).

Notogaster. Well delimited dorsosejugal furrow with irregular trajectory (Figures 1, 13). Polyhedral *n.a.d*, extending posteriorly from *d.sj* to more or less a third of total notogastral length, to starting point of central elevation (Figures 1, 12).

Eight pairs of setae, four pairs situated on central elevated zone and four pairs situated marginally; the central four pairs are not nominated and the lateral four pairs are tentatively named h_3, p_1, p_2, p_3 (see Remarks). Rectangular to polyhedral zone between *d.sj* and elevated central zone; *h.ap* polyhedral (Figures 1, 12, 22); posterior zone of *h.ap* with semicircular depression (Figure 22 indicated by solid black arrow), concealing femur-genu during leg folding; *h.ap* with transversal groove (Figure 22 indicated by dashed arrow); polyhedral elevated central zone (with four pairs of central notogastral setae); notogaster incompletely surrounded by *s.c*, as ribbed microsculpture of *p.p.d* impedes and interrupts *s.c* (Figures 1, 13).

Posterior aspect of notogaster (Figure 13). Elevated central zone with notogastral setae delimited laterally by the *s.c*, trajectory clearly indicated by solid doton Figure 13; elevated central zone posteriorly

delimited by aligned ribs (Figure 13 ⭘). Position of lateral notogastral setae clearly discernible on colliculate microsculpture.

Lateral region. Cuticular bar connecting *Lam* to prodorsum (Figures 7, 12, 17); elevation anterior of *Lam* descending abruptly; *Lam* limited interiorly by *l.l.f* (Figures 12, 17); *le* setae inserted on *Lam*, slightly behind the zone where it descends abruptly; *ro* setae anterior to *le* setae, situated on either side of CSO (Figure 17). Slightly developed *Tu* (Figures 7, 16, 17) with aligned teeth (dentition) in inferior zone (Figure 16). Supra tutorial depression (*s.tu.d*) observed between *Tu* and *Lam*. *Pd I* with large blade, rounded apex. Three pocket depressions *a.tu.d, p.tu.d, p.tu.d*$_1$ (Figures 12, 17) between *Pd I* and *Tu*. Very small *Pd II* (Figures 7, 39); triangular *dis* with rounded apex (Figure 17). Bothridium with rounded elongate elevations (Figure 19 indicated by solid arrow); bothridial opening directing downwards (Figures 12, 19); *bo.ri* smooth, wide, surrounding bothridial opening, *h.ap* polyhedral (Figure 12); *h.ap* anterior zone overlapping posterior bothridial zone; transversal groove present (Figure 22 indicated by ⇢); posterior *h.ap*. zone with semicircular depression (Figure 22 indicated by solid arrow).

Ventral region. Clearly visible polyhedral *Pd I; Pd II* small, with difficult to distinguish ovoid projection; discidium (*dis*) digitiform projection (Figure 23). Epimeral chaetotaxy 1-1-3-3 (Figures 8, 23); large elongate barbate setae, all more or less the same size; *3b, 3c* closely adjacent and parallel. Conspicuous longitudinal medial epimeral depression (Figure 23 indicated by small diamond); clearly demarcated more or less semicircular cuticular thickening observed (Figures 8, 23 indicated by large solid dot). Apodemes *apo.1, apo.2, apo.dj, apo.3* clearly visible, epimeral borders hardly discernible (Figure 8).

Genital plate ovoid, with four pairs of setae (Figures 8, 23, 25); genital opening situated on elevated zone (Figure 23), surrounded anteriorly by aggenital furrow (*a.g.f*) followed by depressed zone (Figures 8, 23, indicated by teardrop); this depressed zone extends towards the posterior, connecting with irregular ribbed microsculpture. Depressed polyhedral zone between genital and anal openings (Figure 23 indicated by large solid diamond); elevated ridge surrounding anal area (Figures 8, 23); between this ridge and anal opening, depressed area surrounding the genital opening (Figure 23). Setae *ad* situated externally to elevated ridge (Figure 23). Two pairs of *dep* are present posterior to legs IV (Figure 23); genital plate smaller than anal plate (Figures 8, 23). Anal opening situated in elevated zone; anal plate rectangular to polyhedral, terminating in small sharp tip (Figures 8, 35 indicated ⇨); two pairs of small anal setae.

Legs (Table 1). The genu-tibial dorsal side socket articulation observed in legs III and IV is an important characteristic not previously observed in Carabodidae (Figures 10, 40, 41). Another particularity is the presence of a series of depressions on ventral areas of femur I and II (Figure 23, and in 38 indicated by ↪). The solenidia of tibia IV, genu III, tibia III; genu II and tibia II are digitiform (Figures 40–46); unguinal (*u*) setae U-shaped anteriorly (Figure 45).

Table 1. Provisional leg setae, solenidia and claws of *Costacarabodes turrialbai* gen. nov., sp. nov.

	Femur	Genu	Tibia	Tasus	Claw
Leg I					
Setae	*d,v*	*l'v*	*d,v*	*(ft),ε,(tc),(it),(p),(u),(a),s,pv'*	1
Solenidia		*Σ*	φ_1,φ_2	ω_1,ω_2	
Leg II					
Setae	*dp,da,l''*	*(l),v*	*d,(v)*	*(pv),s,(a),(u),(p),(it),(tc),(ft)*	1
Solenidia		*σ*	*φ*	ω_1, ω_2	
Leg III					
Setae	*d,l',v*	*l'*	*l',v*	*(pv),s,(a),(u),(p),(it),(tc),ft'*	1
Solenidia		*Σ*	*φ*	–	
Leg IV					
Setae	*d,v*	*d,l'*	*l',v*	*(pv),s,(a),(u),(p),(tc),ft'*	1
Solenidia		–	*φ*	–	

Provisional setal formulae I (1-2-2-2-15-1) (1-2-2); II (1-3-3-3-15-1) (1-1-2); III (2-3-1-2-14-1) (1-1-0); IV (1-2-2-2-12-1) (0-1-0).

Note. In order to nominate all notogastral setae with certainty, ontogenetic studies would have to be completed; however, only the adult stage was available in this study. The semicircular depression on the posterior zone of *h.ap*. conceals the genu and part of tibia III during leg folding; therefore, leg setae of these segments are difficult to observe.

Tuberocepheus Balogh & Mahunka, 1969 ***Tuberocepheus kompsosis* sp. nov**. (Figures 47–75)

Etymology

The specific epithet "kompsosis" is derived from the Greek κομψός, meaning elegant, due to the characteristics of the specimens.

Diagnosis. (adult female)

Microsculpture. Foveate: notogaster anterior depression, notogastral posterior depression; pusticulate: anterior marginal prodorsal zone, rostral zone, humeral apophysis, lateral lamellae, epimeral zone; punctate: subcapitular zone; rugose: humeral apophysis zone; sulcate: between circumgastric furrow and notogastral border; undulate: central notogaster zone; and smooth zone between low lamellar furrow and anterior posterior prodorsal depression.

Prodorsum. Polyhedral elevated interlamellar processes, V-shaped depressed central area, and large bothridial tooth, beak-shaped. Notogaster. Twelve pairs of notogastral setae, rectangular, rugose humeral apophysis. Lateral region. Supratutorial depression deep, with three pocket depressions. Ventral zone. Anterior genital furrow forming a semicircular depression, followed by depressed area surrounding genital opening; large paired ovoid depressions between genital and anal openings, genital plate smaller than anal plate; aggenital seta and adanal seta, ad_3 more or less of similar shape and length, situated close to each other in elevated zone.

Material examined

Holotype: Female "CR 0978 TU 15. Costa Rica Turrialba forêt naturelle du Catie 560 m. Tamisage d'humus. Pied d'arbre à contrefort 11/X/1978 Leg. P.Werner" deposited in the Collection of the Museum of Natural History Geneva, Switzerland, specimen preserved in 70% ethanol. Three other specimens, female, observed under SEM, not deposited; all from type locality: CATIE Turrialba forest, Costa Rica.

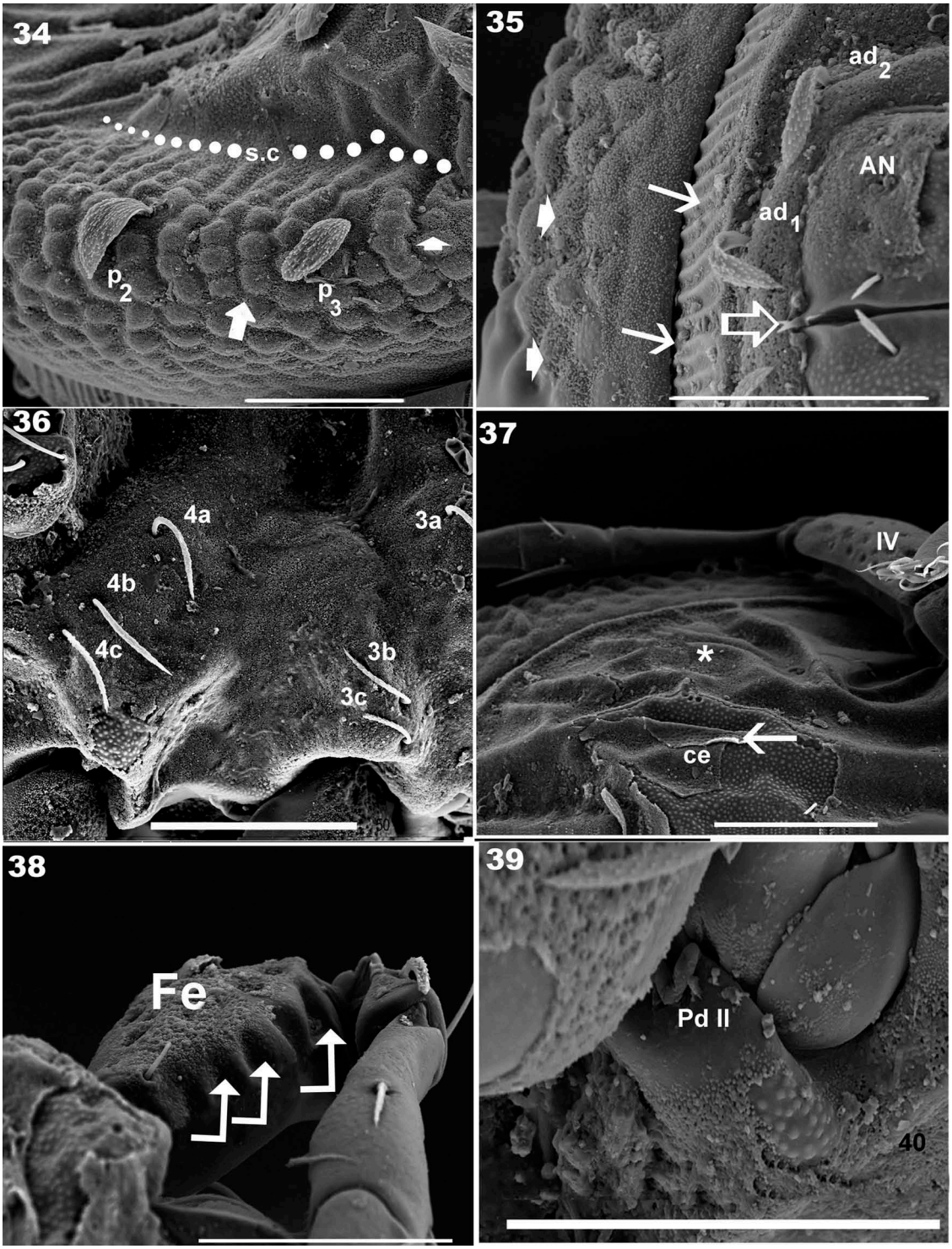
Description

Measurements. SEM 614 (585–640) × 223 (207–240) (n: 3). Light microscopy: 635 × 243 (n: 1); all specimens female.
Shape. Oval (Figure 47).

Colour. Specimens without cerotegument: brown; slightly shiny when observed in reflected light.

Cerotegument. With consistently thick porous granulate layer (3–5 μm) (Figures 50, 52).

Integument. Microsculpture complicated, varying according to body region.
Foveate (Figure 48, indicated by small diamond), very clearly delimited round-ovoid fovea, internally pocket-shaped: *n.a.d, n. p.d* (Figures 47, 57 indicated by ♦); pusticulate (Figure 50): anterior marginal prodorsal zone, rostral zone, *h.ap* ventral zone (Figure 61 indicated by asterisk), lateral lamellae (Figure 62, indicated by asterisk), epimeral zone (Figure 63, indicated by asterisk). Reticulate-foveate: *e.i.p*, posterolateral prodorsal zone (Figures 47, 59, indicated by large solid square); anterior marginal zone of ventral shield (Figure 59, indicated by large solid square).



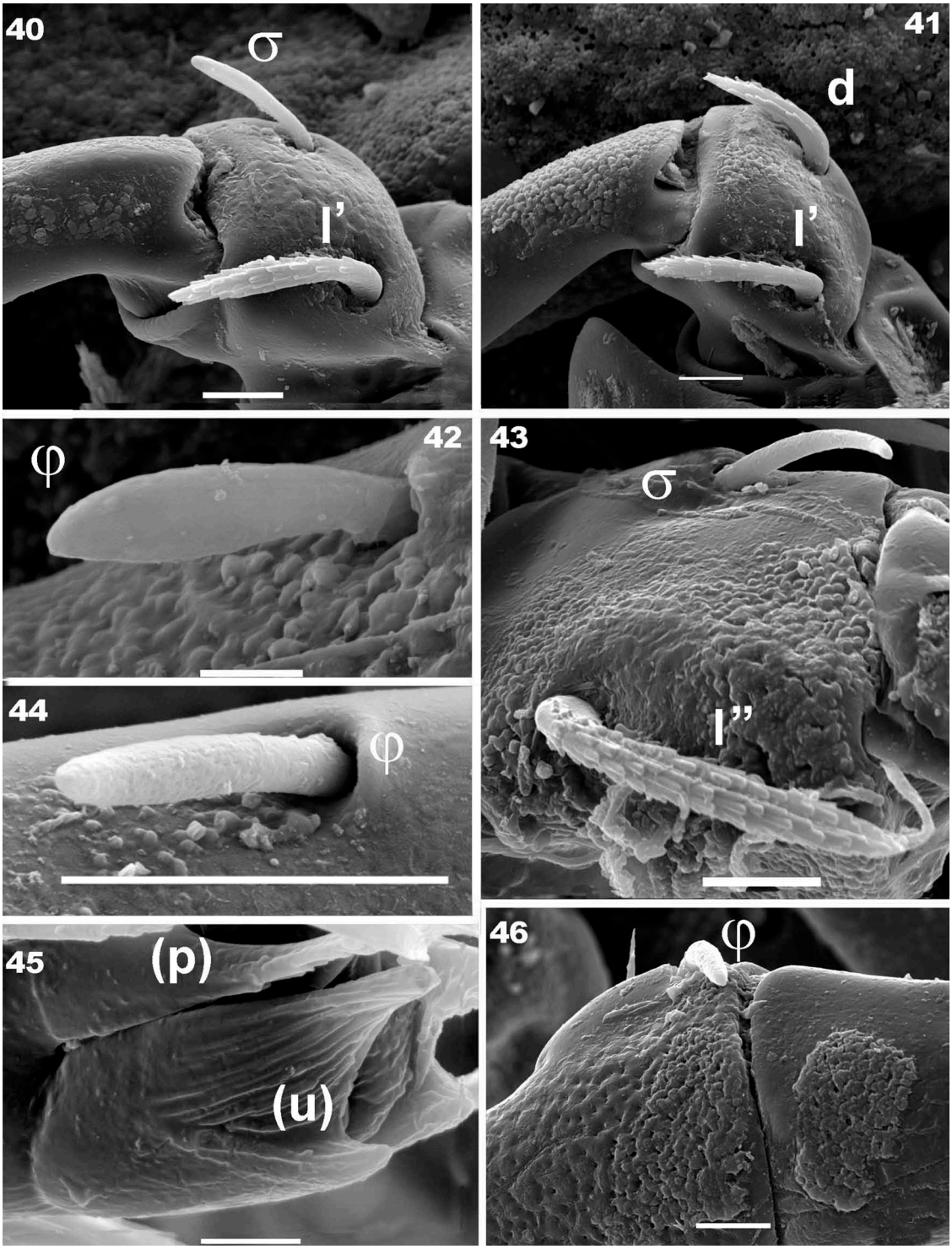
Figures 34–39. ***Costacarabodes turrialbai* gen. nov., sp. nov**. Adult female, SEM. **34**. notogastral posterolateral dorsal view; **35**. ventral posterior shield; **36**. epimeral zone; **37**. ventral region with cerotegumental layer and irregularly ribbed cuticular microsculpture; **38**. femur with transversal depressions; 39. leg II (partial) with reduced *Pd* II. Scale bars: 34, 37 = 50 µm; 35, 36, 38, 39 = 40 µm.

s.c trajectory indicated by ●; colliculate microsculpture indicated by white solid ⇨; small anal sharp tip indicated transparent ⇨; sulcate microsculpture indicated by ↑;depressions on ventral areas of femur I and II, indicated by ⮑; irregularly ribbed indicated by *.

Punctate: (Figure 64, indicated by ⇡) subcapitular zone (Figure 65, indicated by ⇡). *Rugose: h.ap* zone posterior to transversal depression (Figure 52 indicated by ◯). Sulcate: between *s.c* and *b.ng* (Figures 47, 59, indicated by ❖). Undulate: promontories zone on notogaster (Figures 47, 53, 55 indicated by teardrop). Smooth: zone between *l.l.f* and anterior zone of *p.p.d* (Figure 47, indicated by ⌘). Smooth (or displaying slight rugosities): anterior prodorsal zone delimited by *l.l.f*, in zone where *e.i.p* is divided in two, and *p. p.d* (Figure 47)

Setation (legs not included). Simple: genital, aggenital, anal, adanal, subcapitular *m, h* (Figures 66, 70, 72, 73). Simple with small dentitions (Figures 51, 51′): epimeral, notogastral, *ro, in* (Figures 49, 51, 51′, 53, 63, 68, 69). Simple, basally inflated: subcapitular *a* setae (Figure 67). Elongate, pectinate: *le* setae (Figures 60, 62).

Prodorsum. Polyhedral *e.i.p* with depressed V-shaped central area (Figures 47, 57 indicated by solid black arrow) defining two lateral triangular to polyhedral areas. Polyhedral *p.p.d; l.l.f* very shallow but discernible (Figures 47, 57); *in* setae length 47 (45–49), situated internally to *e.i.p* on the smooth cuticle (Figures 47, 57), and anteriorly to *bo* level; rostral margin rounded; *ro* setae

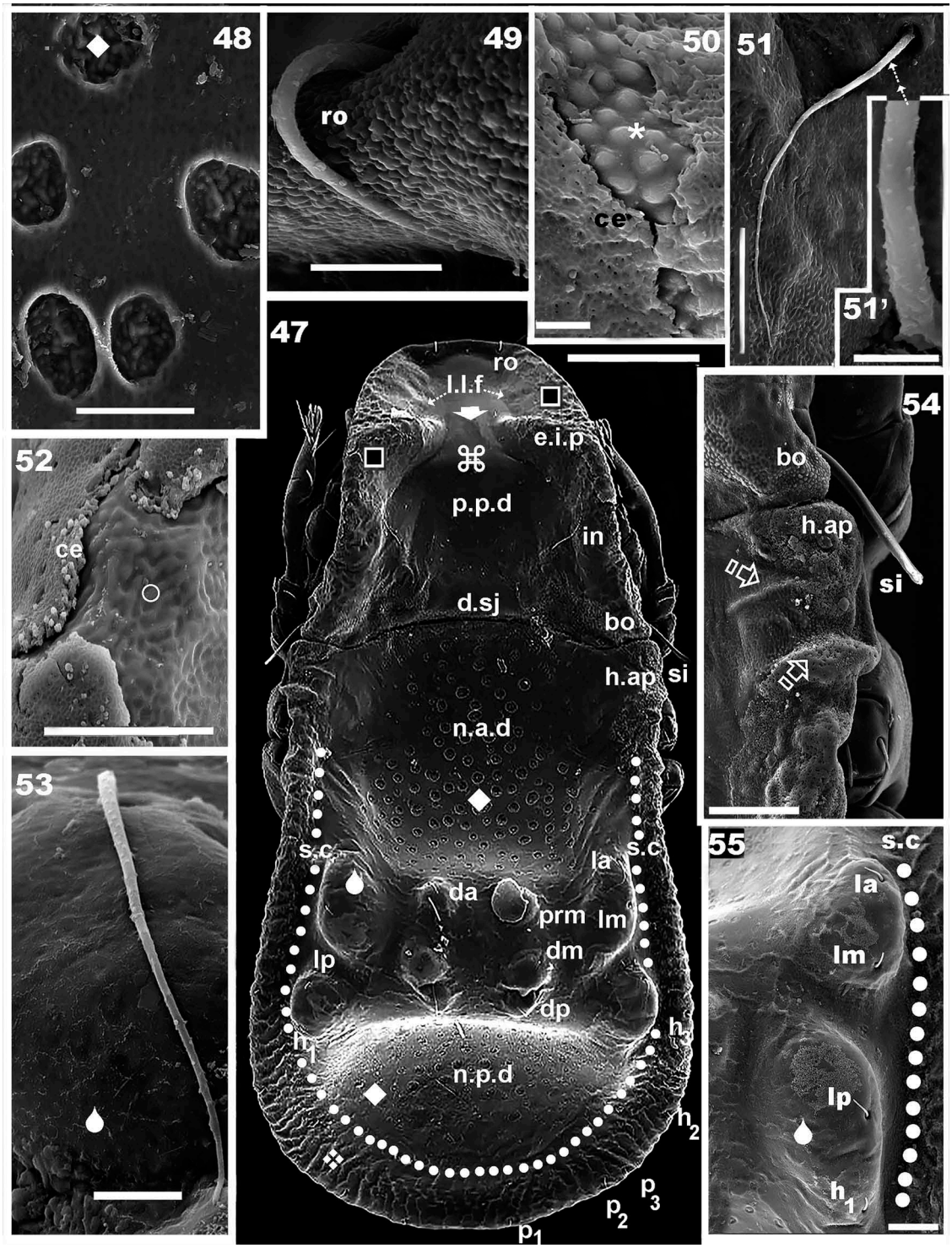


Figures 40–46. ***Costacarabodes turrialbai*** **gen. nov., sp. nov**. Adult female, SEM. **40**. genu, tibia III; **41**. genu, tibia IV; **42**. solenidion tibia IV; **43**. genu II; **44**. solendion tibia III; **45**. setae *(p), (u)* tarsus II; **46**. tibia II. Scale bars: 40, 41, 42, 43, 46 = 5 µm, 45 = 2 µm.

length 12 (10–14) curving towards anterior, directing downwards (Figures 47, 49, 57); *d.sj* convex; *bo* complex (Figure 61); *bo.ri* surrounding bothridial opening; surface smooth, but irregular, with some sectors wide and others narrow; *bo.to* large, bulb-shaped (Figures 56, 61); *si* elongate barbate, directing backwards (Figure 61).

Notogaster. Shape. Rectangular to polyhedral *h.ap* zone (Figures 54, 57), zone behind *h.ap* bulb-shaped (Figures 47, 57); *d.sj* clearly delimited (Figures 47, 57). Large polyhedral *n.a.d* extending posteriorly from *d.sj* to more or less half the total notogastral length. Posterolateral *n.a.d* zone with cuticular ridges (Figures 47, 57), rectangular central area near elevated zone (Figures 47, 57); foveate cuticula clearly visible (Figures 47, 48, 57); *n.p.d* crescent-shaped. Elevated zone between *n.a.d* and *n.p.d* with five paired elevations: three central and two lateral. Two rounded to ovoid anterior central paired promontories (Figures 47, 57), the third semicircular; *da* setae situated on first pair, *dm* setae on second pair, and *dp* setae on third pair (Figures 47, 57, 53). First lateral paired promontories large, ovoid, with *la, lm* setae; second pair medium-sized, ovoid, with *lp* and h_1 setae (Figure 55).

Twelve pairs of notogastral setae, length 22 (20–23), seven situated in elevated zone (described above) and another five pairs h_3, h_2, p_1, p_2, and p_3 situated on notogastral margin (Figures 47, 57). The first marginal notogastral seta (h_3) occurs between the level of *lp* and h_1 setae (Figure 57). Clearly discernible *s.c* surrounding notogaster from *h.ap* posterior zone (Figures 47, 55, 57 indicated by large solid dot) forming a conspicuous

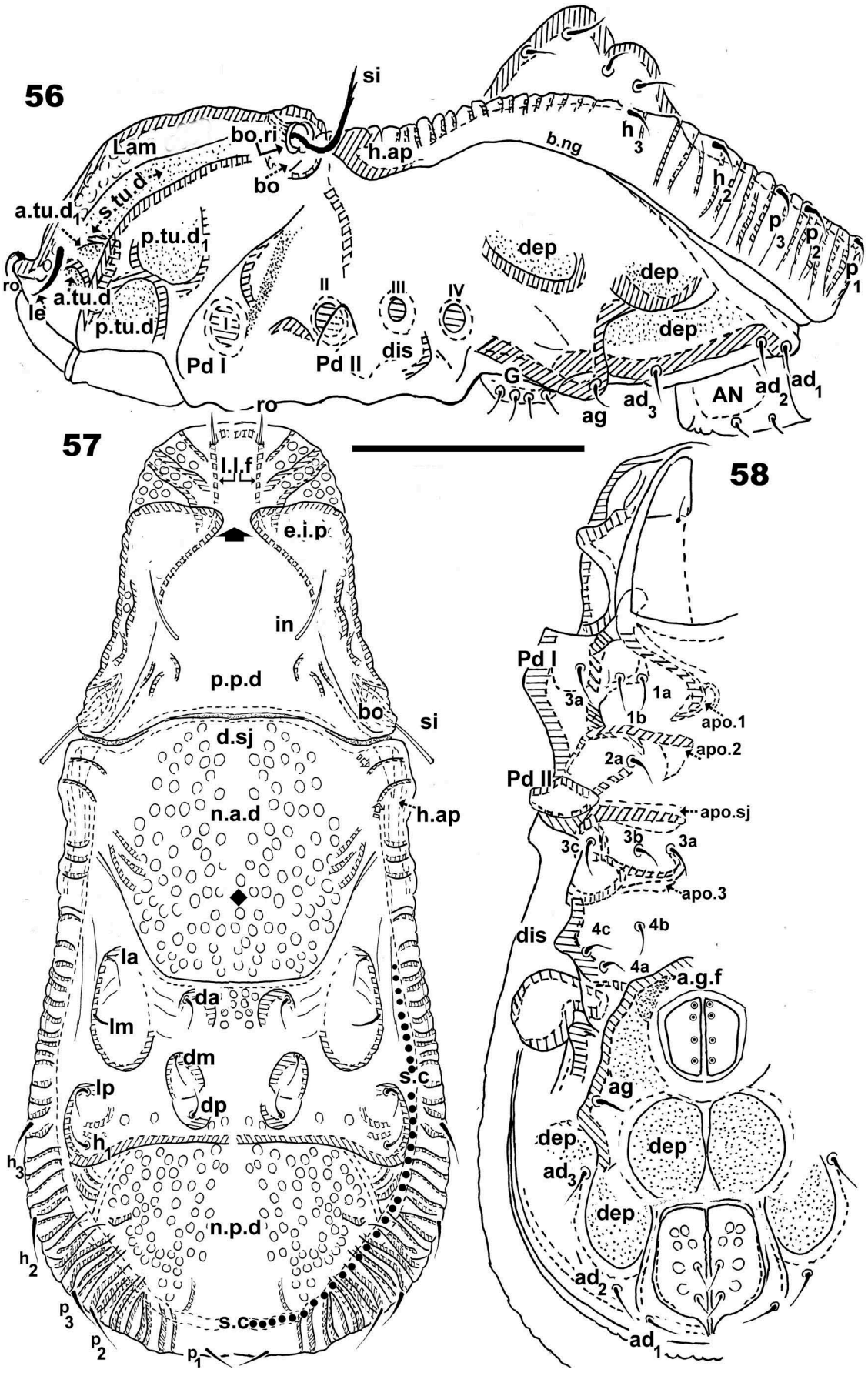


Figures 47–55. ***Tuberocepheus kompsosis*** **sp. nov**. Adult female, SEM. **47**. dorsal view; **48**. cuticular microsculpture on *n.a.d*; **49**. *ro* setae; **50**. prodorsum, rostral zone; cuticular microsculpture and cerotegumental layer; **51**. *in* setae; 51′. detail, *in* setae; **52**. *h.ap* zone, cuticular microsculpture and cerotegumental layer; **53**. notogastral setae *da*, on promontories; **54**. *h.ap*, depressed zone; **55**. lateral promontories and *s.c*. Scale bars: 47 = 100 µm; 48 = 10 µm; 49 = 5 µm; 50 = 2 µm; 51 = 30 µm; 51′ = 5 µm; 52 = 10 µm; 53 = 5 µm; 54 = 20 µm; 55 = 20 µm.

Foveate micrsoculpture indicated by □; pusticulate microculpture indicated by *; reticulate-foveate microsculpture indicated by □; rugose microsculpture indicated by □; sulcate microsculpture indicated by □; Undulate microsculpture indicated by □; smooth (or displaying slight rugosities) cuticle indicated by □; *s.c* trajectory indicated by □.

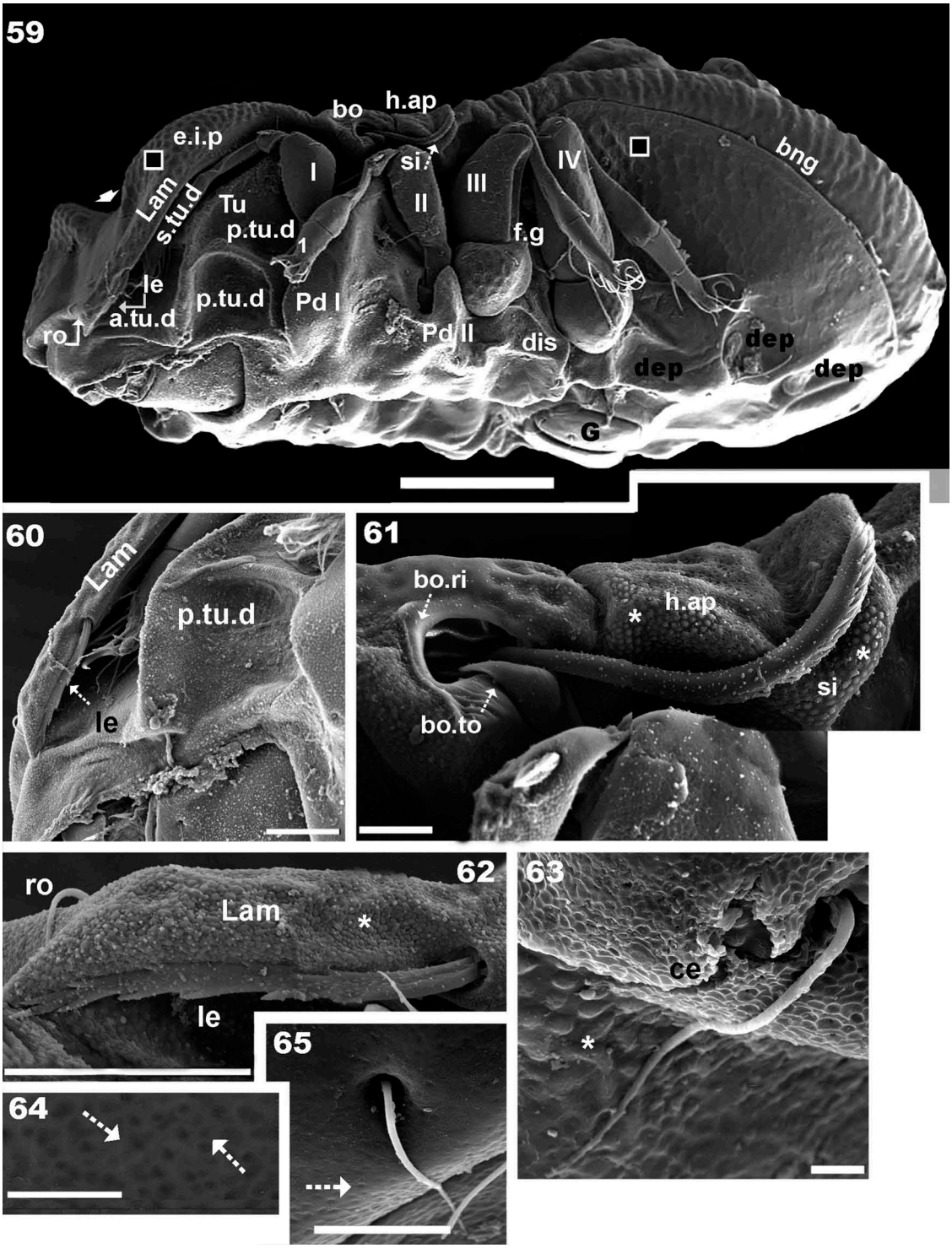
furrow; *h.ap* (Figure 52) rectangular (Figure 54 indicated by thick dashed arrow).

Lateral region. Dorsally elevated *Lam* (Figures 56, 59, 60); *le* setae length 48 (46–51), situated far from anterior apical zone, sharp apical tip absent (Figures 60, 62); *le* setae with wide barbs (Figures 60, 62). Large, curved ridge formed by *Tu* (Figure 59), deep *s.tu.d* (Figures 56, 59, 60) with medium-sized pocket depression *a.tu.d* (Figures 56, 59); two other depressions observed behind *Tu*: large *p.tu.d*, curving superior margin; *p.tu.* d_1, less visible, situated above *p.tu.d*. (Figures 56, 59, 60). Oblong *bo* (Figure 61), opening incomplete; *bo.ri* smooth, narrow in certain zones and wide in others (Figure 61); *bo.to* (Figure 61) an unusual beak-shape; *h.ap* polyhedral, with large V-shaped posterior depression (Figure 61 indicated by solid arrow). This zone shelters the *si* when protection mechanism is activated (see Fernandez et al. 2013a). Posterior zone of *bo* extends into the anterior area of *h.ap* (Figure 61). Pedotectum I with large blade, rounded apex (Figures 56, 59); *Pd II* medium-sized, more or less triangular with convex anterior part, directing upwards



Figures 56–58. *Tuberocepheus kompsosis* sp. nov. Adult female, Optical microscopy. 56. lateral view; 57. dorsal view; 58. ventral view. Scale bars: 56, 57, 58 = 200 µm.

Foveate microsculpture indicated by □; *e.i.p* depressed V-shaped central area indicated by □; *s.c* trajectory indicated by □.

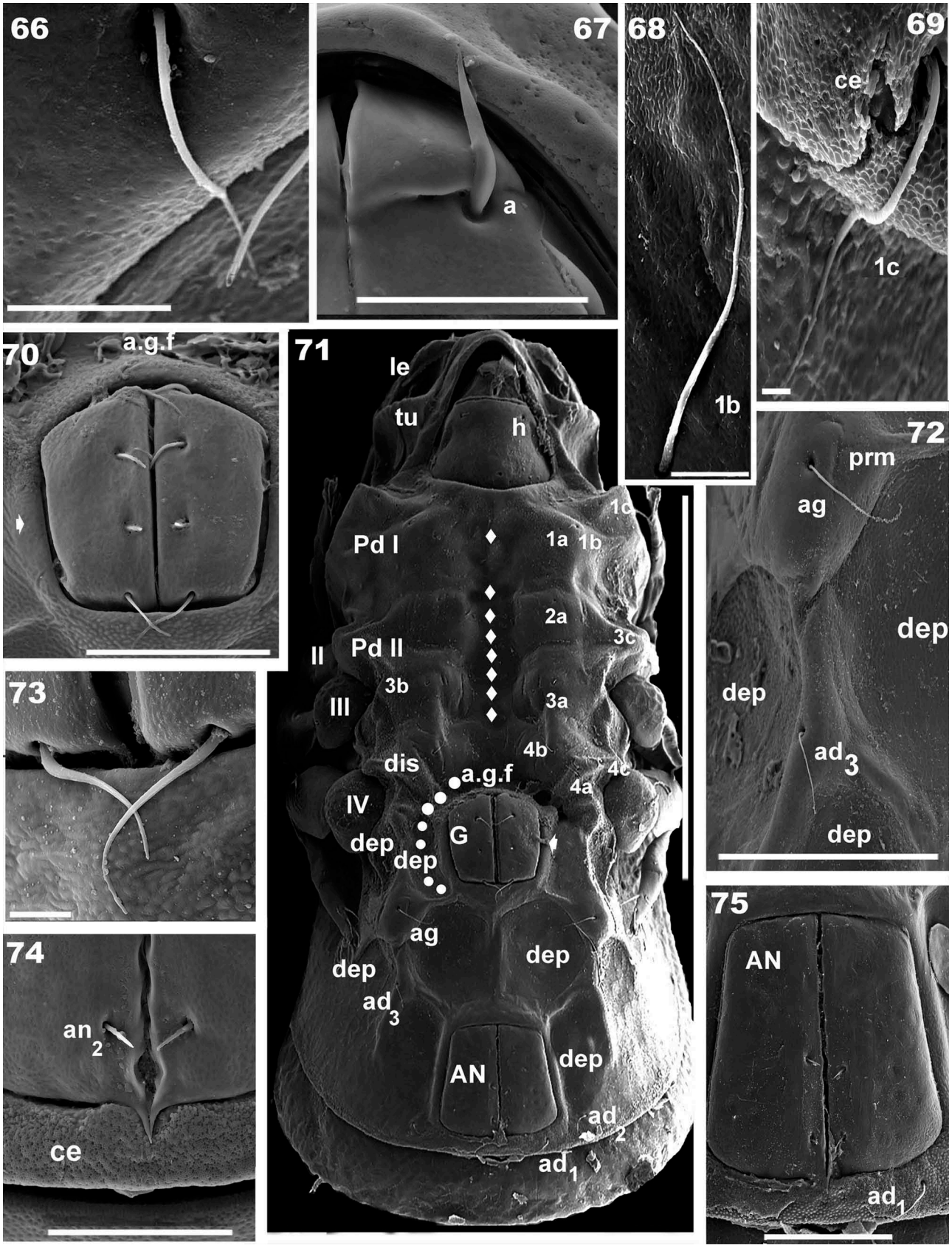


Figures 59–65. ***Tuberocepheus kompsosis* sp. nov** Adult female, SEM. **59**. lateral view; **60**. anterolateral prodorsal zone; **61**. *bo* zone and *h.ap*; **62**. lamellar apical zone and le setae; **63**. epimeral cerotegumental layer and epimeral setae; **64**. punctate microsculpture; **65**. epimeral setae*1a*. Scale bars: 59 = 100 µm; 60 = 20 µm; 61 = 10 µm; 62 = 30 µm; 63 = 2 µm; 64 = :10 µm; 65 = 2 µm.

e.i.p depressed V-shaped central area indicated by □; pustuliculate microculpture indicated by *; reticulate-foveate microsculpture indicated by □; punctate microsculpture, indicated by □.

(Figures 56, 59); *dis* clearly discernible; *ag* setae situated posterior to genital opening on oblong promontories (Figures 56, 72); ad_3 setae some distance from *ag* setae, similar shape (Figure 56). Many conspicuous *dep* present; large ovoid structure situated behind leg IV, at level of genital opening and anterior to anal opening (Figures 56, 59). Anal plate sharply tipped (Figure 56).

Ventral region. Conspicuous longitudinal medial epimeral depression present (Figure 71 indicated by small diamond). Apodemes *apo.1, apo.2, apo.dj, apo.3* clearly visible (Figure 58), none crossing bilateral symmetry plane; epimeral borders easily discernible (Figure 71), epimeres 3-4 fused, epimeral chaetotaxy 3-1-3-3, epimeral setae length 15 (13–17) (Figure 71). Genital opening situated on elevated area, with narrow surrounding zone (Figures 70,71 indicated by solid arrow); *a.g.f* forming a semicircular depression situated anterior to genital opening, followed by depressed area surrounding the genital plate (Figure 71, indicated by large solid dot), situated externally to narrow elevated zone surrounding genital plate. Several *dep* lateral to genital and anal openings (Figure 71); large paired ovoid *dep* (Figure 71) between genital and anal openings, lateral to anal opening and separated by cuticular ribbons from large paired ovoid-polyhedral *dep* (Figure 71).



Figures 66–75. ***Tuberocepheus kompsosis*** **sp. nov**. Adult female, SEM. 66. subcapitular setae *h*; 67. subcapitular setae a; 68. epimeral setae *1b*; 69. epimeral seta *1c*; 70. genital plate; 71. ventral view; 72. aggenital, adanal zone; 73. genital setae g*4*; 74. anal plates with sharp tip; 75. anal plate, general view. Scale bars: 66 = 20 µm; 67 = 20 µm; 68 = 10 µm; 69 = 2 µm; 70 = 40 µm; 71 = 200 µm; 72 = 50 um; 73 = 5 µm; 74 30 µm; 75 = 50 µm.

Conspicuous longitudinal medial epimeral depression indicated by □; genital opening situated on elevated area, indicated by □; *a.g.f* semicircular depression, followed by depressed area indicated by □.

Genital plate smaller than anal plate (Figure 71). Polyhedral genital plate (Figures 70, 73), four pairs of genital setae, length 19 (16–20). Anal plate (Figure 75) trapezoidal, anal setae length 6 (5–7), two pairs of aligned anal setae situated in central posterior zone (Figure 75). Anal plate terminating in short sharp tip (Figure 74), with a rounded depression situated anterior to these tips; *ag* setae, length 37 (35–39), situated on oblong promontories (Figures 71, 72); three pairs of *ad* setae, length 26 (25–

31); *ag* setae on elevated zone situated externally to depression surrounding genital opening and superior externally of ovoid paired *dep*, between genital and anal openings (Figures 71, 72); ad_3 setae situated on cuticular ribbon delimiting lateral posterior ovoid paired *dep*; distance between *ag* and ad_3, two and a half times length of *ag* setae (Figure 72). Gnathosoma: conspicuous diarthric subcapitulum (Figure 71); subcapitular setae *h, m* (Figure 67) and *a* (Figure 66) very different in shape.

Legs. I, II, III more or less equal in length, IV longer. Provisional setal formulae (trochanter to tarsus) and solenidia: I (1-4-2-4-16-1) (1-2-2); II (1-4-2-3-16-1) (1-1-2); III (2-3-1-2-14-1) (1-1-0); IV (1-2-2-2-12) (0-1-0).

Discussion

The authors compared the genus type specimens studied thus far as part of the revision of the Carabodidae family. The fascinating new genus from Costa Rica, *Costacarabodes* **gen. nov**. presents some characteristics in common with *Congocepheus* Balogh 1958; (Fernandez et al. 2013a, 2013b, 2014a, 2014b, 2016a, 2016b); *Tuberocepheus* Balogh & Mahunka, 1969 (Fernandez et al. 2015b); *Mangabebodes*, (Fernandez et al. 2014c); and *Antongilibodes*, (*Fernandez* et al. 2014c) and *Cubabodes* Balogh & Mahunka 1974.

The comparison with *Cubabodes* deserves a little clarification. We studied the type material of *Cubabodes hexagonalis* Balogh & Mahunka 1974, a paratype on loan from the Hungarian Natural History Museum, Budapest. The following complications arose: (1) labels were almost illegible, but after suggestions from a number of colleagues, we understood the label to read: "Paratypus Cubabodes exagonalis n.g. n.sp. 1969.X. 28. Leg. A.Borhidi Cuba. Sierra Maestra. Gran Piedra. det. J.Balogh – S.Mahunka".

This text corresponds (mostly) with the text and information in the species description by Balogh and Mahunka (1974). (2) The material was extremely lightened, causing difficulty in detailed observation. (3) Legs were impossible to study, as they were broken or had disintegrated. Finally we decided to use the description of the genus by Mahunka in 1986b: 90 and Figures 22–24, as this description in many instances gave clearer information than our study of the type material, which was not well preserved.

Elevated interlamellar process

In *Costacarabodes*, the elevated interlamellar process (*e.i.p*) is present, as in *Congocepheus, Tuberocepheus, Mangabebodes, Antongilibodes*, and *Cubabodes*. However, important differences exist between them. In *Costacarabodes*, this process is observed as a central V shaped depressed area and two triangular to polyhedral lateral areas.

In *Congocepheus*, the shape of the *e.i.p* is variable; while in *Co. heterotrichus* Balogh, 1958, it is undivided, slightly elevated; in *Co. velatus* Mahunka 1986a, it is medially elevated, with a small flat medial depression; *Co. orientalis* Mahunka 1987 is complete (undivided), with medial depressed zone; *Co. involutus* Mahunka, 1997 is slightly elevated, undivided; *Co. ektactesi* Fernandez, Theron, Rollard, Tiedt 2013, is medially elevated, very small medial depression; *Co. gabonensis* Fernandez, Theron, Rollard, Tiedt 2013 is prominent, elevated, small medial depression, rounded lateral end; *Co. germani* Fernandez, Theron, Rollard, Castillo 2014 is slightly elevated, undivided, lacking medial depression; *Co. rwandensis* Fernandez, Theron, Leiva 2016 is elevated with a medial depression and two rounded elevated lateral zones; *Co. kayovae* Fernandez, Theron, Leiva 2016, is elevated, flattened dorsally; *Co. kardiae*, Fernandez, Theron, Leiva 2016 is elevated, complete, lacking depression; *Co. camerunensis* Fernandez, Theron, Leiva, Tiedt 2017, is medially elevated with rounded medial depression.

In *Tuberocepheus*, the *e.i.p* is present as two lateral ear-like processes with medial depression in *T. longus* (Balogh, 1962), and in *T. kompsosis* sp. nov. (present paper), a depressed V-shaped central area and two lateral triangular to polyhedral areas.

In *Mangabebodes*, species *M. kymatismosi* Fernandez, Theron, Leiva, Rollard, Tiedt 2014, the *e.i.p* is slightly elevated, medially concave. In *Antongilibodes*, species *A. paulae* Fernandez, Theron, Leiva, Rollard, Tiedt 2014, the *e.i.p* is slightly elevated, convex, terminating in an oblique interlamellar external elevation. In *Cubabodes* (*Cu. exagonalis* Balogh & Mahunka 1974, based on our observations of type material), the *e.i.p* is slightly elevated; medially concave.

Posterior prodorsal depression

Costacarabodes has a posterior prodorsal depression (*p.p.d*) in common with *Congocepheus Tuberocepheus* and *Mangabebodes*. In *Costacarabodes*, this process is deep, polyhedral, with irregular longitudinal or oblique cuticular ridges.

In *Congocepheus*, this depression varies in shape, while in *Co. heterotrichus*, it is observed as an ovoid depressed zone of reduced size; in *Co. velatus*, a large, deep polyhedral area is present. The *p.p.d* is observed as a large rounded depression in *Co. orientalis*; in *Co. involutus* as a small depressed polyhedral area; *Co. ektactesi* a small depressed polyhedral area; *Co. gabonensis* an ovoid depressed area; *Co. germani*, a slightly depressed zone; *Co.rwandensis*, a large ovoid depressed area; *Co. kayovae* an ovoid depressed zone with more or less smooth surface; *Co. gabonensis* an ovoid depressed area; *Co. kardiae* a large, deep, rounded area; and in *Co. camerunensis* as a deep triangular to polyhedral area. In *Tuberocepheus* (*T. longus; T. kompsosis*), a conspicuous, deep polyhedral area is observed, in *Mangabebodes* (*M. kymatismosi*) a small half-moon-shaped area is visible.

Notogastral anterior depression

Costacarabodes has the presence of a notogastral anterior depression in common with *Congocepheus, Tuberocepheus, Mangabebodes*, and *Antongilibodes*.

In *Costacarabodes*, a large polyedral area is observed. This depression is of variable shape in *Congocepheus*: in *Co. heterotrichus* ovoid and conspicuous; *Co. velatus* absent or very reduced; *Co. orientalis* an ovoid, extended area; *Co. involutus* ovoid, deep; *Co. ektactesi* polyhedral, deep; *Co. gabonensis* a small, deep ovoid depression; *Co. germani* a conspicous extended area; *Co. rwandensis* polyhedral, small; *Co. kayovae* small half-moon-shaped area; *Co. kardiae* small, deep, half-moon-shaped structure; *Co. camerunensis* deep half-moon-shaped structure; *Tuberocepheus* (*T. longus; T. kompsosis*) a large ovoid to polyhedral depression. In *Mangabebodes* (*M. kymatismosi*), the depression is large, ovoid, extending from *d.sj* to half the total notogastral length. In *Antongilobodes* (*A. paulae*), this depression forms a large ovoid area, extending from the *d.sj* to more than half of the total notogastral length.

Notogastral promontories. Insertions notogastral setae

In *Costacarabodes*, notogastral promontories related to the notogastral setae are absent. An elevated zone is situated between the area of the notogastral anterior depression and the notogastral posterior depression zone, where the four pairs of central notogastral setae are situated. In this zone, the microsculpture of the integument is complex: wrinkled, hardly raised, with very shallow folds. This differs greatly from other related genera with the exception of *Cubabodes*. In *Cubabodes hexagonalis*, neither the notogastral anterior depression nor the notogastral posterior depression is present. It is not indicated if the setae are situated on an elevated zone, and the presence of promontories is not indicated either. Only the number of notogastral setae is similar in these two genera, but their placement is not the same.

Table 2. Comparison between *Costacarabodes, Congocepheus, Tuberocepheus, Mangabebodes, Antongilibodes*, and *Cubabodes.*

Characters	*Costacarabodes*	*Congocepheus*	*Tuberocepheus*	*Mangabebodes*	*Antongilibodes*	*Cubabodes*
Lamelar setae	Dorsal close to *ro* setae	Lateral on lamellae anterior zone	Lateral on anterior Lamerlar zone	Lateral, situated far from lamellar tip	Lateral on anterior Lamerlar zone	Dorsal
Lamelar tip	Absent	Round to small sharp tip	Round without tip	Small rounded	small, wide sharpened apex	Sharp cuspis
Elevated interlamelar process	With depressed V-shaped central area; two lateral triangular to polyhedral areas	Variable shape	Divided in two ear-like processes	Present slightly elevated; medially concave	Elevated terminating in oblique interlamellar external elevation	Concave medially
Tutorium shape	Slightly develop; Aligned teeth	Strongly develop, curving lamina	Stronly develop, curving lamina	Large lamina spoom-shaped	Strongly curving cuticular thickening	Absent
Prodorsal Posterior depression	Present polyhedral shape	Present variable shape	Conspicuous, polyhedral	Present small, ovoid	Not discernible	Absent
Number notogastral setae	Eight pairs	Fourteen pairs	Twelve pairs	Twelve pairs	Fifteen pairs	Eight pairs
Notogastral anterior depression	Large polyhedral	Variable shape	Ovoid, large	Large, ovoid	Notogastral anterior depression ovoid	Absent
Pedotectum II	Diminute hardy discernible	Small; well discernible	Medial size; well discernible	Small lamina, round apex	Normal size; well discernible	Normal size; well discernible
Epimeral chaetotaxy	1-1-3-3	3-1-3-3	3-1-3-3	3-1-3-3	3-1-3-3	1-1-3-3
Notogastral posterior depression	Present, interrupted by ribbed microsculpture	Absent	Present, large, conspicuous crescent shape, not interrupted by ribbed microsculpture	Present, conspicuous, ovoid shape.	Anterior zone polyhedral; posterior zone rounded.	Absent
Circumgastric furrow	Present, interrupted by ribbed microsculpture in posterior notogastral zone	Completely surrounding notogaster	Completely surrounding notogaster	Present in anterior zone near *h.ap* and on posterior notogatral zone	Completely surrounding notogaster	??
Notogastral promontories. Insertions of notogastral setae	Not present	Present or absent	Present	Partially present	Two dorsal promontories with *la, lm, lp, h2* setae; anterior unpaired with *da* setae; one pair central with *dm* setae	Not present
Articulation genu-tibial III,IV	With sockets	Lacking sockets	Lacking sockets	Lacking sockets	Lacking sockets	Lacking sockets

Promontories and notogastral setae observed in *Congocepheus* are more complex but very different to those observed in *Coscacarabodes*. *Costacarabodes* has in common with *Congocepheus* the presence of notogastral anterior depression, but where in *Costacarabodes* the posterior notogastral depression is present, it is absent in *Congocepheus*. Due to the absence of this depression, no elevated zone delimited by anterior and posterior notogastral depressions is observed.

Notogastral promontories observed in *Congocepheus* are present in *Co. orientalis, Co. ektactesi*, and *Co. gabonensis*.

Promontories are also absent in *Co. heterotrichus*, *Co. velatus*, *Co. involutus*, *Co. germani*, *Co. rwandensis*, *Co. kayovae*, *Co. kardiae*, *Co.*

Table 3. Comparison between *Tuberocepheus komposis* sp. nov. and *Tuberocepheus longus* (Balogh 1962).

	Tuberocepheus komposis sp. nov.	*Tuberocepheus longus* (Balogh 1962)
Microsculpture	**Foveate**: *n.a.d, n.p.d* . **Pusticulate**: antero-marginal prodorsal zone; rostral zone; *h.ap* ventral zone; *Lam* lateral zone; epimeric zone. Reticulate-foveate: *e.i.p*, posterolateral zone; ventral shield, antero-marginal zone. **Punctate**: subcapitum. **Rugose**: *h.ap*, zone posterior to transversal depression. **Sulcate**: between *s.c* and *b.ng*. **Undulate**: notogaster promontories . **Smooth**:bothridial ring, bothridial tooth, zone between *l.l.f* and anterior zone of *p.p.d*. **Smooth (or displaying slight rugosities)**: anterior prodorsal zone delimited by *l.l.f*, in zone where *e.i.p* is divided in two, and *p.p.d*.	**Foveate**: *p.p.d, l.l.f, n.a.d; n.p.d*; zone between central and lateral notogastral promontories. **Reticulate-foveate**: (fovea not clearly delimited, polyhedral, surrounded by cuticular thickening): antiaxial prodorsal zone; *bo*; posterior dorsal zone; notogaster near *s.c*. **Polyhedral foveate network**: *e.i.p* zone, between lamellar border and *l.l.f, Tu, Pd l*; ventral depressions. **Erased reticulate-foveate**: epimeric zone, subcapitulum near zone *h* setae. **Smooth**: bothridial ring, bothridial tooth, subcapitulum, zone *a, m* setae **Smooth-rough**: elevated zones of notogastral promontories near setal insertions *da, dm, dp*, La, *lm, lp,* h_1 **Reticulate-foveate** (with cuticular thickenings reticulate-foveate mixed with ribbon-like rectilinear or irregular cuticular thickenings): posterior notogastral margin posterior to *h.ap*; near *s.c* up to *b.ng*.
Setation	**Simple**: genital, aggenital, anal, adanal, subcapitular *m, h*. **Simple with small dentitions**: epimeric, notogastral, *ro, in*. **Simple, basally inflated**: subcapitular *a*. **Elongate, pectinate**: *le.*	***Simple****: ro, in*, notogastral, sub- capitular, epimeric, genital, aggenital, anal, adanal. ***Lanceolate-pectinate***: *le*.
Elevated interlamellar process	Polyhedral with depressed V-shaped central area defining two lateral triangular to polyhedral areas.	Complex, with depressed central area, defining two ear-like structures
Notogastral anterior depression	Large polyhedral shape. Posterolateral zone with cuticular ridges.	Ovoid, large shaped,
Tutorial depressions	*a.tu.d, p.tu.d,* $p.tu.d_1$	*a.tu.d; p.tu.d*

camerunensis, but the situation is very different as elevated zones, extending between the notogastral anterior depression towards the back of the notogaster, are observed in these species. Also, the observed number of setae in all cases exceeds four pairs.

For: lamellar setae; lamellar tip; tutorium shape; number of notogastral setae; pedotectum II; epimeral chaetotaxy; notogastral posterior depression; circumgastric furrow; and articulation of genu-tibia III, IV, see Table 2.

Tuberocepheus kompsosis sp. nov.

For the characteristics of the genera *Mangabebod*es and *Tuberocepheus*, we took into consideration Balogh (1962) the footnote in Balogh and Mahunka (1969: 9), the revision of the family Carabodidae by Mahunka (1986b), and the comparative analysis in Fernandez et al. (2015b). After in-depth analysis, we concluded that this is a new species of the genus *Tuberocepheus*. The classification by Subias (2004 updated 2017) included *Mangabebodes* as a subgenus of *Tuberocepheus*, but since no clarification was given as to the relationship between *Mangabebod*es and *Tuberocepheus*, it was not used as part of this comparison

For comparison of this new species, we considered the original description of *Machadocepheus longus* Balogh (1962) and the redescription in Fernandez et al. (2015b) as *Tuberocepheus longus* (Balogh 1962) (see Table 3).

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References

Alberti G, Fernandez N. 1990a. Aspects concerning the structure and function of the lenticulus and clear spot of certain oribatids (Acari: oribatida). Acarologia. 31:65–72.

Alberti G, Fernandez N. 1990b. Fine structure and function of the lenticulus and clear spot of Oribatids (Acari: oribatida). In: Andre HM, Lions J-CL, editors. L'ontogènese et le concept de stase chez les arthropodes. Agar: Wavere. p. 343–354.

Alberti G, Fernandez N, Coineau Y. 2007. Fine structure of spermiogenesis, spermatozoa and spermatophore of *Saxidromus delamarei* (Saxidromidae, Actinotrichida, Acari). Arthropod Structure Development 36:221–231.

Alberti G, Fernandez N, Kümmel G. 1991. Spermatophores and spermatozoa of oribatid mites (Acari: oribatida). Part II. Functional and systematical considerations. Acarologia. 32:435–449.

Alberti G, Norton R, Adis J, Fernandez N, Franklin E, Kratzmann M, Moreno A, Ribeiro E, Weigmann G, Woas S. 1997. Porose integumental organs of oribatid mites (Acari: oribatida). Zoologica. 48:33–114.

Balogh J. 1958. Oribatides nouvelles de l'Afrique tropicale. Revue De Zoologie Et Botanique Africaine. 58:1–34.

Balogh J. 1962. Recherches sur la faune endogeé de Madagascar. VII.Oribates (Acariens) Nouveaux.II. Naturaliste Malgache. 13:121–151.

Balogh J, Mahunka S. 1969. The scientific results of the Hungarian soil zoological expedition to South America.10 Acari: oribatids collected by the second expedition. I. Acta Zoologica Hungarica. 15:1–21.

Balogh J, Mahunka S. 1974. A Foundation of the Oribatid (Acari) Fauna of Cuba. Acta Zoologica Academiae Scientiarum Hungaricae. 20:1–25.

Evans GO. 1992. Principles of acarology. Wallingford (UK): C.A.B International Cambridge. p. 563 p.

Fernandez N, Alberti G, Kümmel G. 1991. Ultrastructure of the spermatophores and spermatozoa of some Oribatid mites (Acari: oribatida) Part I. Fine structure and histochemistry. Acarologia. 32:261–286.

Fernandez N, Theron P, Leiva S. 2016a. Revision of the family Carabodidae (Acari, Oribatida) V. Fourth part. Two new species of the genus *Congocepheus* from the Republic of Rwanda: *congocepheus rwandensis* sp. n., and *Congocepheus kayoveae* sp. n. ZooKeys 19–41. doi: 10.3897/zookeys.435.8071.

Fernandez N, Theron P, Leiva S. 2016b. Revision of the family Carabodidae (Acari: oribatida) XI. *Congocepheus kardiae* sp. nov. and *Zimbabweae pluosiae* gen. nov., sp. nov. from the Republic of Zimbabwe. International Journal of Acarology 42:341–357.

Fernandez N, Theron P, Leiva S, Jordaan E. 2017a. Revision of the family Carabodidae (Acari, Oribatida) V. Fifth part. Redescription of *Congocepheus latilamellatus* Mahunka 1984, with complementary studies of. *C. ornatus* Mahunka 1983. Description of *Tanzaniacepheus* gen. nov. and *Zimbabwecepheus* gen. nov. Zootaxa. 4324:315–330. Available from: http://www.mapress.com/j/zt//10.11158/saa.22.11.4

Fernandez N, Theron P, Leiva S, Rollard C, Rodrigo Castillo E. 2014d. Revision of the family Carabodidae (Acari, Oribatida) VII. Redefinition of the genus *Malgasodes*; redescription of *M. curvisetus* Mahunka, 2000; and complementary description of *M. hungarorum* Mahunka, 2010. Phylogenetic relationships between *Malgasodes, Bovicarabodes, Afticarabodes, Congocepheus* and *Cavaecarabodes* are discussed. ZooKeys. 25–48. doi: 10.3897/zookeys.435.8071.

Fernandez N, Theron P, Leiva S, Rollard C, Tiedt L. 2014c. Revision of the family Carabodidae (Acari: oribatida) VI. *Mangabebodes kymatismosi* gen. nov., sp. nov. and *Antongilibodes paulae* gen. nov., sp. nov. from Madagascar. International Journal of Acarology 40:296–319.

Fernandez N, Theron P, Rollard C. 2013a. The family Carabodidae (Acari: oribatida) I. Description of a new genus, *Bovicarabodes* with three new species, and the redescription of *Hardybodes mirabilis* Balogh, 1970. International Journal of Acarology 39:26–57.

Fernandez N, Theron P, Rollard C. 2013b. Revision of the family Carabodidae (Acari: oribatida) II. Redescription of Austrocarabodes ensifer (Sellnick, 1931), *Aokiella florens* Balogh & Mahunka, 1967 and *Singabodes rarus* Mahunka, 1998. International Journal of Acarology 39:181–199.

Fernandez N, Theron P, Rollard C. 2013d. Revision of the family Carabodidae (Acari: oribatida) IV. *Afticarabodes anjavidilavai* gen. nov. sp. nov., *Rugocepheus joffrevillei* sp. nov., and redescription of the genus *Rugocepheus* Mahunka, 2009. International Journal of Acarology 39:462–480.

Fernandez N, Theron P, Rollard C. 2013e. Family Carabodidae (Acari: oribatida) V. The genus *Congocepheus* Balogh, 1958 (second part), with a redescription of *Congocepheus involutus* Mahunka, 1997, and descriptions of *two new species*.

Zoosystema. 35:551–579Available from: http://www.bioone.org/doi/abs/10.5252/z2013n4a8

Fernandez N, Theron P, Rollard C, Leiva S. 2013c. Revision of the family Carabodidae (Acari: oribatida) III. Redefinition of *Meriocepheus peregrinus* Aoki, 1973. 1973; *Bathocepheus concavus* Aoki, 1978; and *Opisthocepheus kirai* Aoki, 1976. International Journal of Acarology 39:327–340.

Fernandez N, Theron P, Rollard C, Leiva S. 2014a. The family Carabodidae (Acari: oribatida) V. The genus *Congocepheus* (first part) with redescriptions of *Congocepheus heterotrichus* Balogh 1958, *Congocepheus orientalis* Mahunka 1987 and *Congocepheus hauseri* Mahunka 1989. International Journal of Acarology 39:600–614.

Fernandez N, Theron P, Rollard C, Leiva S. 2014e. The family Carabodidae (Acari, Oribatida) VIII. The genus *Machadocepheus* (first part) *Machadocepheus leoneae* sp. n. and *Machadocepheus rachii* sp. n. from Gabon. ZooKeys 1–28. doi:10.3897/zookeys.456.8570.

Fernandez N, Theron P, Rollard C, Leiva S. 2015a. The family Carabodidae (Acari: oribatida) IX. Redescription of *Carabodella calcarata* Mahunka, 1986 and *Hardybodes penicillatus* Mahunka, 1995. International Journal of Acarology 41:551–562.

Fernandez N, Theron P, Rollard C, Leiva S, Tied L. 2017b. Revision of the family Carabodidae (Acari, Oribatida) XII. *Yoshiobodes camerunensis* sp. n. and *Rugocepheus costaricensis* sp. n. ZooKeys. 706: 31–50. doi: 10.3897/zookeys.706.14807 http://zookeys.pensoft.net

Fernandez N, Theron P, Rollard C, Leiva S, Tiedt L. 2015b. Revision of the family Carabodidae (Acari: oribatida) X. *Bovicarabodes jacquelinae* sp. nov., redefinition of the genus *Tuberocepheus* Balogh & Mahunka, 1969 and redescription of *Tuberocepheus longus* (Balogh, 1962). International Journal of Acarology 42:79–91.

Fernandez N, Theron P, Rollard C, Leiva S, Tiedt L. 2017c. Revision of the family Carabodidae (Acari, Oribatida) XIII. *Congocepheus camerunensis* from Cameroon and *Synkrotima zimbabwae* gen. nov. sp. nov. from the Republic of Zimbabwe. Systematic & Applied Acarology 22:1822–1842.

Fernandez N, Theron P, Rollard C, Leiva S, Tiedt L. 2017d. Revision of the family Carabodidae (Acari: oribatida) XIV. *Phyllocarabodes costaricensis* sp. nov. from Costa Rica and *Zimbabweae kenyaensis* sp. nov. from Kenya. International Journal of Acarology 43:518–533.

Fernandez N, Theron P, Rollard C, Rodrigo Castillo E. 2014b. Revision of the family Carabodidae (Acari: oribatida) V (third part). Redefinition of *Congocepheus*, definition of *Cavaecarabodes* gen. nov., and descriptions of three new species, *Congocepheus germani* sp. nov., *Cavaecarabodes pulchritude* gen. nov., sp. nov., and *Cavaecarabodes anouchkae* gen. nov., sp. nov. International Journal of Acarology. 40:535–555.

Grandjean F. 1949. Formules anales, gastronomiques, génitales, aggénitales du développement numérique des poils chez les Oribates. Bulletin Société Zoologique France. 74:201–225.

Krantz G, Walter D. 2009. A manual of acarology. 3rd ed. ed. Lubbock (TX): Texas Tech University Press. p. 807.

Mahunka S. 1997. Oribatids from Madagascar III. (Acari: oribatida). Revue Suisse De Zoologie. 104:115–170.

Mahunka S. 1986a. Oribatids from Africa (Acari: oribatida)III. Folia Entomologica Hungaricae. 47:41–76.

Mahunka S. 1986b. A survey of the family Carabodidae, C.L. Koch, 1836 (Acari: oribatida). Acta Zoologica Hungarica. 32:73–135.

Mahunka S. 1987. Neue und interessante Milben aus dem Genfer Museum LX. Oribatids from Sabah (East Malaysia) II. (Acari: oribatida). Revue Suisse Zoologie. 94:765–817.

Norton R, Behan-Pelletier V. 2009. Suborder Oribatida. In: Krantz GW, Walter DE, editors. A manual of acarology. 3rd ed. ed. Lubbock (TX): Texas Tech University Press. p. 430–564.

Subias L. 2004. Listado sistemático, sinonímico y biogeográfico de los ácaros oribátidos (Acariformes: oribatida) del mundo (excepto fósiles). Graellsia, 60. 3–305. Online version accessed in February 2017, 598 pp. http://graellsia.revistas.csic.es/index.php/graellsia/article/view/218/

Travé J, Vachon M. 1975. François Grandjean 1882–1975 (Notice biographique et bibliographique). Acarologia. 17:1–19.