

## Revision of the family Carabodidae (Acari: Oribatida) VI. Mangabebodes kymatismosi gen. nov., sp. nov. and Antongilibodes paulae gen. nov., sp. nov. from Madagascar

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## Revision of the family Carabodidae (Acari: Oribatida) VI. *Mangabebodes kymatismosi* gen. nov., sp. nov. and *Antongilibodes paulae* gen. nov., sp. nov. from Madagascar

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This is the sixth in a series of revisions on the family Carabodidae, in which we describe and illustrate two new genera, *Mangabebodes kymatismosi* gen. nov., sp. nov. and *Antongilibodes paulae* gen. nov., sp. nov., both from the island of Madagascar. The work is based on adult specimens studied with the aid of optical and scanning electron microscopy.

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**Keywords:** Acari; Oribatida; Carabodidae; *Mangabebodes kymatismosi* gen. nov., sp. nov.; *Antongilibodes paulae* gen. nov., sp. nov.; Madagascar

### Introduction

Over the last 3 years, large numbers of specimens and materials of the family Carabodidae, which form part of the extensive oribatid mite collection of the Muséum National d'Histoire Naturelle, Paris, France, have been studied.

In this paper, we embark on a study of a complex group of Carabodidae of which we have large amounts of materials, consisting of more than 30 groups of species. We encountered problems such as very superficial species descriptions, vagueness, mistaken structures and poor condition of type material from various Museums (possibly due to bleaching with caustic potash for study), and finally, in one instance, we were unable to secure a loan of type specimens. These challenges complicated the study of this group and we therefore established several conditions in order to produce accurate studies. These included abundance of specimens of high quality and availability of material for optical and Scanning Electronic Microscopy (SEM), as well as adequate material to do dissections. Finally, for material not available on loan, we decided to compare our optical observations and drawings with the most recently available original description.

In the present paper, we describe two new genera of Carabodidae from Madagascar (Coll. Betsch) (for details see Fernandez and Cleva 2010; Fernandez et al. 2010, 2013a).

### Materials and methods

Specimens studied with light microscopy were macerated in lactic acid and observed in the same medium using the open-mount techniques (cavity slide and cover slip) described by

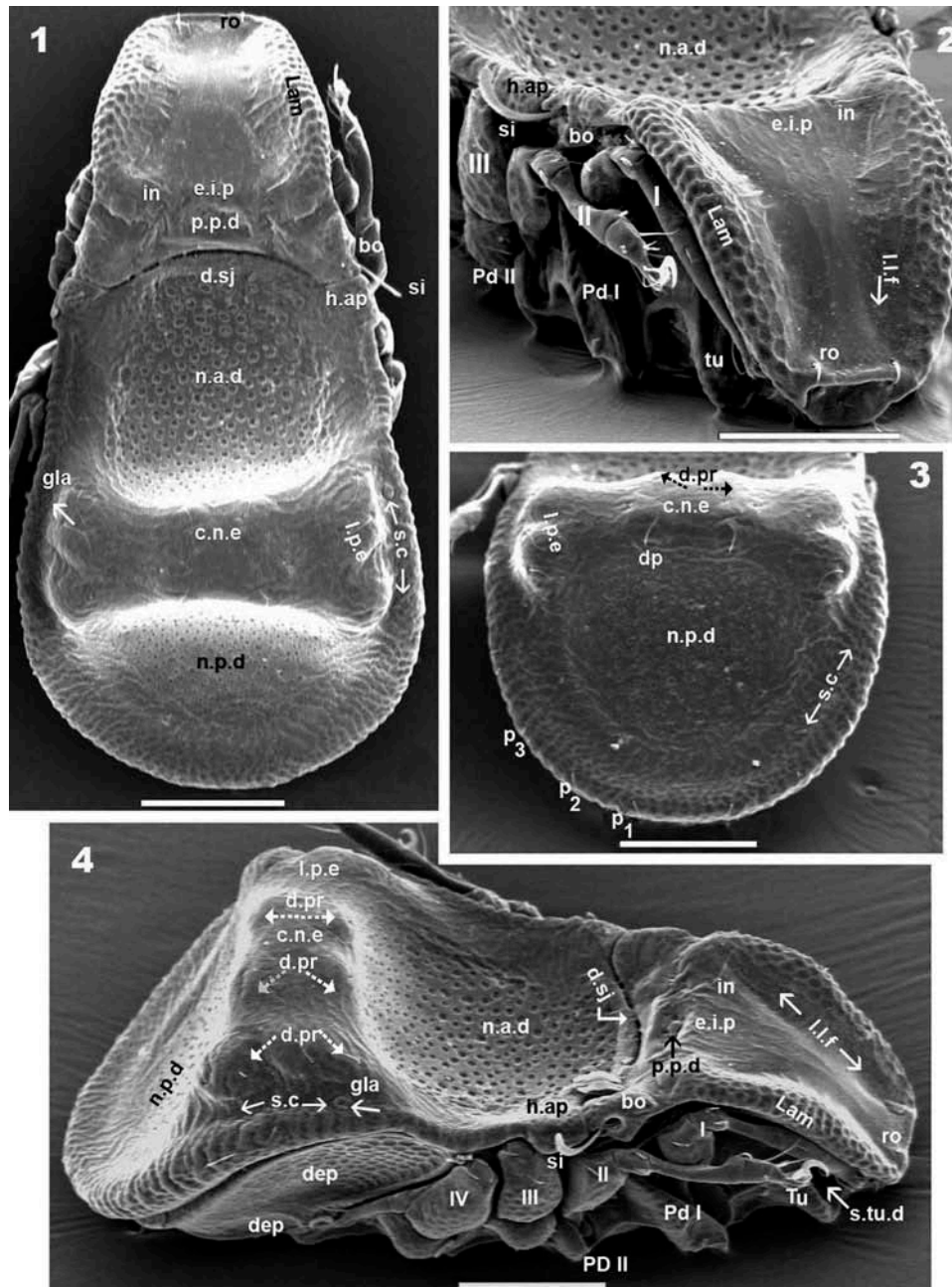
Grandjean (1949) and Krantz and Walter (2009). Drawings were made by use of an Olympus BHC compound microscope (Rungis, France), equipped with a drawing tube. Specimens were also studied under a scanning electron microscope (SEM). Specimens preserved in ethanol were carefully rinsed by sucking them several times into a Pasteur pipette, after which they were transferred to buffered glutaraldehyde (2.5%) in Sörensen phosphate buffer: pH 7.4; 0.1 M for 2 hours. After postfixation in buffered 2% OsO<sub>4</sub> solution for 2 hours and being rinsed in buffer solution; all specimens were dehydrated in a series of graded ethanol and dried in a critical point apparatus. After mounting on Al-stubs with double-sided sticky tape, specimens were gold-coated in a sputter apparatus (Alberti and Fernandez 1988, 1990a, 1990b; Alberti et al. 1991, 1997, 2007; Fernandez et al. 1991). Measurements taken: total length (tip of rostrum to posterior edge of notogaster) and width (widest part of notogaster), in micrometres (µm).

Setal formulae of the legs include the number of solenidia (in parentheses); tarsal setal formulae include the famulus (ε).

In order to study several structures (cornea superior medial eye, supratutorial depression, bothridial ring, lateral depressions), specimens were dissected and monitored during the lactic acid maceration process (in warm 70% lactic acid), before being stained with chlorazol black E (Coineau 1974).

### Morphological terminology

Morphological terms and abbreviations used are those developed by F. Grandjean (1928–1974) (cf. Travé & Vachon 1975); Norton and Behan-Pelletier (2009) and Fernandez et al. (2010).



Figures 1–4. *Mangabebodes kymatismosi* gen. nov., sp. nov., adult., SEM. 1. dorsal view ; 2. frontal anteroposterior view; 3. notogaster posterior view; 4. dorsal inclined lateral view. Abbreviations: see “Materials and methods”. Scale bars: 1–4 = 100  $\mu$ m.

For setal types Evans (1992) and for ornamentation of cuticular surfaces, Murley (1951 ex: Evans (1992)) were used.

Many different terms were previously used for corresponding structures in generic or species descriptions; thus we found it necessary to create a standardized (homogenized) terminology to use when comparing con-familial genera and species. We used the terms strictly in the sense proposed by the authors cited above.

A number of specific morphological characters have not previously been described in detail and no terminology and/or abbreviations exist. For these, we have included the following in the text and on the figures for the sake of clarity as interlamellar external expansion (*i.e.e.*).

Institution abbreviations: M.N.H.N, Muséum National d’Histoire Naturelle, Paris, France; M.H.N.G, Geneva Natural History Museum, Switzerland

#### *New taxon description*

#### *Mangabebodes* gen. nov.

#### *Etymology*

The generic prefix “*Mangabe*” derives from Nosy Mangabe Island, north-eastern Madagascar, place of origin of type material.

*Diagnosis adult*

Body shape ovoid.

*Prodorsum*. Slightly elevated interlamellar process; small halfmoon-shaped posterior prodorsal depression; complex anterior *ro* setae insertion zone.

*Notogaster*. Twelve pairs of setae. Anterior dorsal depression and posterior dorsal depression present, between them elevated zone, divided in a lateral paired elevation and a central notogastral elevation. Elevated zone with seven pairs of setae; five pairs positioned marginally. Tutorium large and long, spoon shaped, larger or equal in size to pedotectum I; pedotectum II and discidium present. Epimeric setae: 3-1-3-3; G: 4; Ag:1; Ad:3; An:2.

**Type species:** *Mangabebodes kymatismosi* **gen. nov., sp. nov.**

***Mangabebodes kymatismosi* gen. nov., sp. nov.**  
(Figures 1–38)

*Etymology*

The specific epithet is derived from “κυματισμός” Greek = undulation, related to the characteristics of the ventral body region.

*Material examined*

Holotype: female “Mad. 905. Madagascar nord-est. Province de Tamatave, Baie d’Antongil. Ile de Nosy Mangabe; alt. 30 m. FDHBA (Forêt dense humide de base altitude). Ao: 0–3 cm – J.M. Betsch coll. 17-vii – 1967.” deposited in the M.N.H.N., preserved in 70% ethanol. Four paratype adult females; two deposited in the M.N.H.N.; and two deposited in M.H.N.G., same locality and date as holotype. material studied by use of SEM: six specimens, not deposited.

*Diagnosis*

*Integumental microsculpture*. Complicated, varying according to body region.

*Setation*. Lanceolate: subcapitular *a*, *m*; lanceolate-bipectinate: *le*; other setae: simple.

*Prodorsum*. In setae situated anterior to bothridial level; lamellae dorsolateral; *le* setae situated far from lamellar tip, exceeding the lamellar tip in length; shallow lamellar furrow clearly visible; lamellar tip rounded; cornea superior medial eye present; *Tu* inclining forward, extending laterally; apically ribbed microsculpture.

*Notogaster*. Dorsosejugal furrow convex sagittal, antiaxially rectilinear, slightly concave. Anterior notogastral

depression ovoid, large; posterior notogastral depression crescent-shaped, medium size.

*Elevated zone*. One pair lateral elevated zones, each divided into two elongated promontories with *la*, *lm*, *lp*, *h*<sub>2</sub>, setae; central elevated zone dividing in two poorly developed, paired rounded promontories, with *da*, *dm*, setae; *dp* setae position variable.

*Lateral*. Supratutorial depression deep; bothridial ring well delimited, smooth; bothridial tooth, large; bothridial end penetrating humeral apophysis. Pedotectum I prominent; Pedotectum II small rounded apex; discidium small, clearly discernible. Several ovoid lateral depressions; particular small demarcated depression to hide leg IV during leg folding process.

*Ventral*. Epimeric zone topography complicated, with alternating elevated and depressed zones; sagittally conspicuous elongated depression. Epimeric chaetotaxy: setae *1a*, *3a* minuscule, other setae normal; anterior genital furrow deep; small deep cavity in narrowed posterior extremity of anterior genital furrow; behind genital opening a paired rounded depression; lateral anal opening polyhedral and ovoid depressions; behind IV acetabulum large prominence; *iad* well visible.

*Description*

*Measurements*: SEM:620 µm (560–700) × 310 µm (290–330) (material used for SEM studies not deposited).

Light microscopy: 620 µm (526–710) × 320 µm (270–360) (measurement of specimens deposited in M.N.H.N. and M.H.N.G. All specimens female.

*Shape*. Elongate oval (Figures 1, 5).

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

*Cerotegument*. Consistently very thin rough layer (±1 µm), covering body and legs, following cuticular irregularities, does not impede observation (Figures 9, 10).

*Integument*. Microsculpture complicated, varying according to body region (Figures 1, 2, 8, 9, 11–13, 19, 20–25, 27, 28). *Foveate*: very clearly delimited round-ovoid fovea, internally pocket-shaped (Figures 8, 10), situated on notogastral anterior depression (*n.a.d*) and notogastral posterior depression (*n.p.d*) (Figures 1, 2, 5, 16, 23); *reticulate-foveate*: fovea not clearly delimited, polyhedral, surrounded by cuticular thickening (Figures 9, 12), on prodorsum, antiaxial zone; lamellae (*Lam*); tutorium (*Tu*); bothridium (*bo*) dorsal zone; notogaster from near circumgastric furrow (*s.c*) to notogastral margin (*b.ng*); humeral apophysis (*h.ap*) and legs, principally on trochanter, femur and tibia (Figures 1, 2, 17, 19–21, 23); *reticulate-foveate with cuticular thickenings*: reticulate-foveate mixed with



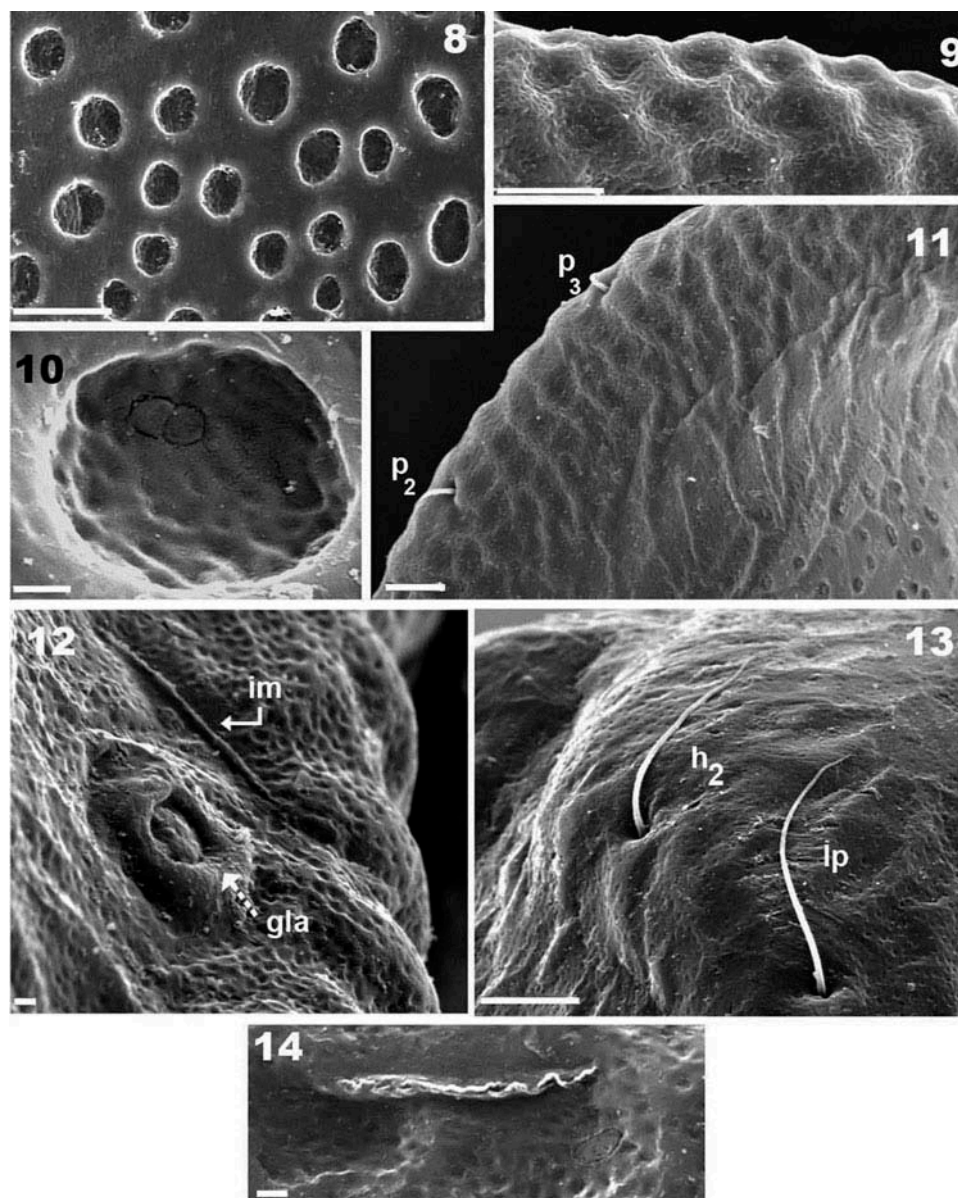


Figures 5–7. *Mangabebedes kymatismosi* **gen. nov., sp. nov.**, adult. 5. dorsal view; 6. ventral view; 7. lateral view. Abbreviations: see “Materials and methods”. Scale bars: 5–7 = 250  $\mu\text{m}$ .

ribbon-like rectilinear or irregular cuticular thickenings (Figure 11) from posterior notogastral margin to promontory zone (insertion zone of *la*, *lm*, *lp*, *h*<sub>2</sub> setae) (Figures 1, 3, 23); *erased reticulate-foveate*: reticulate-foveate microsculpture is flattened giving an impression of being “partly erased” (Figure 28) on epimeric zone, subcapitulum, around genital opening, anal plate (Figures 22, 23, 24, 26); *smooth*: flat microsculpture, on paraxial zone of prodorsum between lamellar furrows (*l.l.f*); bothridial ring (*bo.ri*) (Figures 1, 2, 4, 20); *smooth-rough*: flat microsculpture giving the appearance of a smoothed but poorly finished wall (Figure 13) on dorsal notogastral promontory at setae *da*, *dm*, *dp*, *la*, *lm*, *lp*, *h*<sub>2</sub> insertions (Figures 1, 4);

*reticulate*: (Figure 27) obvious in depression (*dep*) situated behind leg IV, slightly less pronounced in other *dep* near genital and anal opening (Figures 17, 22, 23); *pusticulate*: in front of *bo.ri* and internal lamellar margin, anterior to *le* setae insertions (Figures 20, 21); *ribbed*: ventral anterior zone of *Tu* (Figures 6, 15, 22, 23).

*Setation* (legs not included). *Simple*: rostral, interlamellar, notogastral, sub-capitular *h*, epimeric, genital, aggenital, anal, adanal; length: (measurements taken on six specimens used for SEM-studies. Lengths of setae are to be considered relative as, though preservation was good, these mites were preserved in alcohol for over 35 years



Figures 8–14. *Mangabebodes kymatismosi* gen. nov., sp. nov., adult, SEM. 8. notogastral ornamentation; 9. detail: notogastral margin depressions; 10. detail: ornamentation of Figure 8; 11. notogastral lateral margin ornamentation; 12. lateroabdominal gland and lyrifissure *lm*; 13. lateral view, notogastral setae; 14. lyrifissure *ih*. Abbreviations: see “Materials and methods”. Scale bars: 10, 12, 14 = 1  $\mu$ m; 8, 9, 11, 13 = 10  $\mu$ m.

and we cannot easily ascertain possible damage to setae tips); *ro* = 20  $\mu$ m (18–22); *in* = 30.5  $\mu$ m (28–33); *da*, *dm*, *dp*, *la*, *lm*, *lp*, *h*<sub>2</sub> = 26  $\mu$ m (22–30); *h*<sub>1</sub>, *h*<sub>3</sub>, *p*<sub>1</sub>, *p*<sub>2</sub>, *p*<sub>3</sub> = 10.5  $\mu$ m (9–12); subcapitular *h* = 20  $\mu$ m (18–22), *a* = 10  $\mu$ m (8–12), *m* = 6  $\mu$ m (5–7); epimeric = 19.5  $\mu$ m (16–23) (except *1a*, *3a* tiny); *g* = 15.5  $\mu$ m (12–19); *ag* = 20  $\mu$ m (26–17); *an* = 10  $\mu$ m (8–12); *ad*<sub>1</sub>, *ad*<sub>2</sub> = 15 (11–16), *ad*<sub>3</sub> = 20  $\mu$ m (17–22). *Lanceolate-bipectinate*: lamellar (Figure 21); length *le* = 40  $\mu$ m (45–38). *Lanceolate*: subcapitular *a*, *m* (Figure 29); length, *a* = 10  $\mu$ m (9–11) (setae *m*, measurements not given, their tips were mostly damaged).

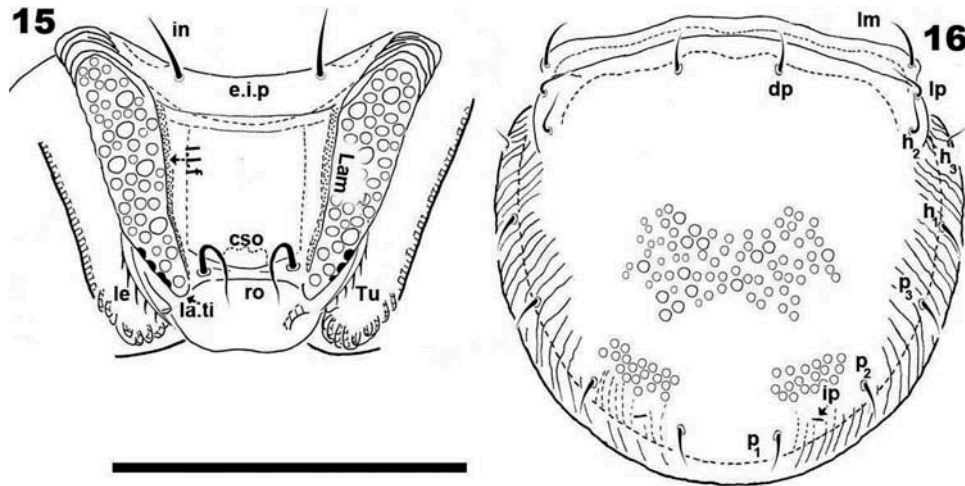
*Prodorsum*. Near dorsosejugal furrow (*d.sj*), situated on posterior medial zone, small ovoid *p.p.d* (Figures 1, 4).

Elevated interlamellar process (*e.i.p*), centrally elevated (Figures 2, 4, 7, 17) medially concave (in frontal view, Figure 15); setae *in* situated anterior to bothridial level, slightly antiaxially (Figures 2, 4, 5, 15).

Rostral margin rounded (Figure 15); *ro* curving anteriorly (Figure 15). *Lam* running dorsolaterally in dorsal zone of prodorsum, shallow furrow (*l.l.f*) (Figures 4, 5, 15) demarcating inner paraxial margin, furrow terminating in internal zone of lamellar apex (*la.ti*) (Figure 15). Small rounded *la.ti*; superior cornea of naso (*cso*) hardly discernible, situated slightly in front *ro* setal insertion level (Figures 5, 15).

In frontal observation spoon-like *Tu* clearly discernible (Figures 2, 15) (shape confirmed in lateral view, Figures 17, 19 – see below); ribbed microsculpture of tip (principally found ventrally) clearly visible (Figure 15).





Figures 15–16. *Mangabebodes kymatismosi* gen. nov., sp. nov., adult. 15. prodorsum frontal view; 16. notogaster posterior view. Abbreviations: see “Materials and methods”. Scale bars: 15–16 = 250  $\mu$ m.

Anterior to the *ro* setal insertion, the situation is very complicated (Figures 2, 15), with a transversal cuticular ribbon terminating near *la.ti*; this slightly elevated zone delimiting depressed zone extending to the aspis. Dissected material yielded rather poor results, fresh material is necessary in order to undertake the necessary ultrastructural studies.

*Notogaster*. Shape: ovoid (Figures 1, 5, dorsal view); *d.sj* well delimited (Figures 2, 10) by a large convex furrow in sagittal plane, rectilinear to slightly concave antiaxially (Figures 1, 4, 5).

Two conspicuous depressions: (1) *n.a.d* ovoid, large, extending from *d.sj* posteriorly to half the total notogastral length (2) *n.p.d* situated in the posterior third of notogaster (Figures 1, 5), in these figures *n.p.d* appears crescent-shaped due to positioning of specimens, in reality it is ovoid (Figure 3), but this is only evident during observation in posterior view.

Elevated zone between *n.a.d* and *n.p.d* with paired *l.p.e* (lateral paired elevations); each *l.p.e* dividing into two dorsal promontories (*d.pr*) with central notogastral elevated zones (*c.n.e*) (for *l.p.e*; *d.pr* and *c.n.e* see Fernandez et al. 2013d); *c.n.e* dividing into four poorly developed rounded parallel *d.pr*; two *d.pr* on each side. Central promontories hardly discernible in strictly dorsal position (Figures 1, 5); clear observation necessitates dorsal inclined position (Figure 4), posterior view (Figure 3) or lateral slightly inclined position (Figure 17).

The *d.pr* of *l.p.e* are more conspicuous than the *c.n.e* (Figures 1, 4, 5, 17) and have two pairs of setae each; anterior *la* and *lm* and posterior *lp* and *h<sub>2</sub>* setae. In *c.n.e* anterior *d.pr* has *da* setae and posterior *dm* setae (Figures 5, 7); position of *dp* setae variable, situated close to or far from *d.pr* depending on specimen. Precisely establishing the position of *dp* setae complicated by the shape of the area of occurrence due to convergence of *d.pr* and *n.p.d*

margin as well as due to slight variability found amongst specimens (Figures 1, 3, 5, 16).

Twelve notogastral setae, seven situated in elevated zone (described above) and another five pairs *h<sub>3</sub>*, *h<sub>1</sub>*, *p<sub>1</sub>*, *p<sub>2</sub>*, and *p<sub>3</sub>* situated on notogastral margin (Figure 11). No setae in *n.a.d*. The first marginal notogastral seta (*h<sub>3</sub>*) is found between the level of *lp* and *h<sub>2</sub>* setae (Figures 5, 16).

Four pairs of lyrifissures visible: *im*, *ih*, *ips* and *ip* (Figures 7, 12, 14, 16). Numerous dissections of the *h.ap* zone were executed in order to find evidence of lyrifissure *ia*, without results.

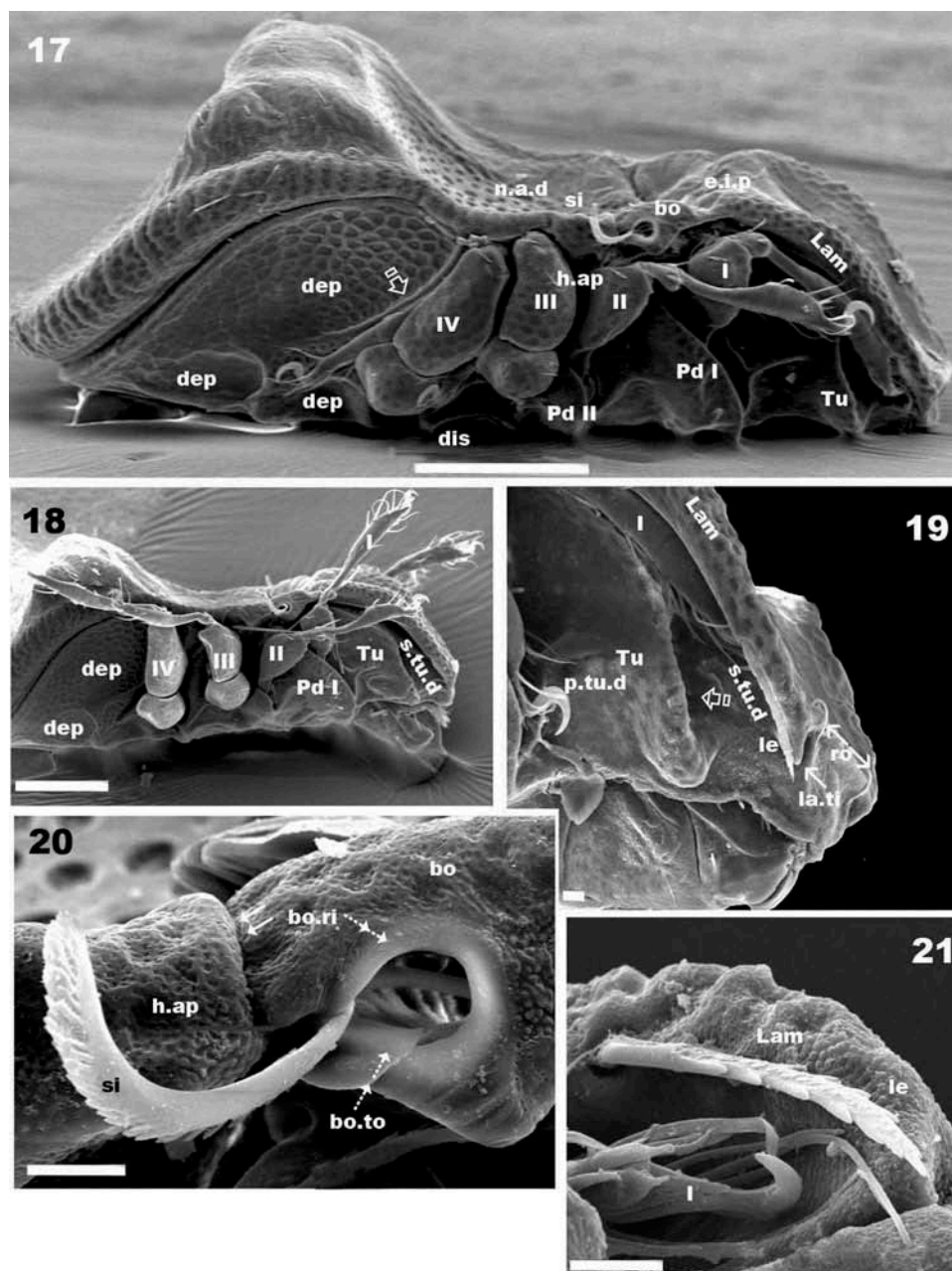
Clearly visible *gla* with characteristic shape (Figure 12), situated near lyrifissure *im*.

The *s.c* is easily discernible from near *h.ap* to *gla*, *im* level (Figure 4); posterior to this level it exists, but is difficult to distinguish (Figure 3).

*Lateral region*. Observation in lateral view is central to understanding of several structures, but observations at different positions are necessary in order to show these particular structures (Figures 2, 4, 7, 17, 18, 19, 20). *Lam* well visible (Figures 2, 7, 4, 15, 17–19). Interior convex zone clearly observed (Figure 21) along with the protection given to leg I; *la.ti* small and rounded (Figure 15); *le* setae insertions situated far from narrowed *la.ti* zone (Figures 7, 19). Large *le* setae exceeding *la.ti*, despite the large distance between insertion and *la.ti* (Figure 19).

Very particular *Tu*, large and long, spoon-shaped, similar or larger in size than *Pedotectum* I (Figures 2, 4, 7, 17, 18, 19, 20). *Tu* structure inclining forwards (in lateral view), extending laterally (Figures 15, 17, 19); ribbon thickenings (situated mainly ventrally), visible in frontal and lateral views in anterior part of structure (Figures 4, 15). Spoon shape is more pronounced on the apical zone (Figure 19).

Deep *s.tu.d* (Figures 7, 18, 19) with anterior and posterior pocket depressions (*a.tu.d*; *p.tu.d*) (Figure 7);



Figures 17–21. *Mangabebodes kymatismosi* gen. nov., sp. nov., adult, SEM. 17. lateral view; 18. lateral view, legs displaced; 19. lateral view, anterior prodorsum zone; 20. bothridium and humeral apophysis, lateral view; 21. apical zone lamellae, ventral, inclined view. Abbreviations: see “Materials and methods”. Scale bars: 17–18 = 100  $\mu$ m; 19–21 = 10  $\mu$ m.

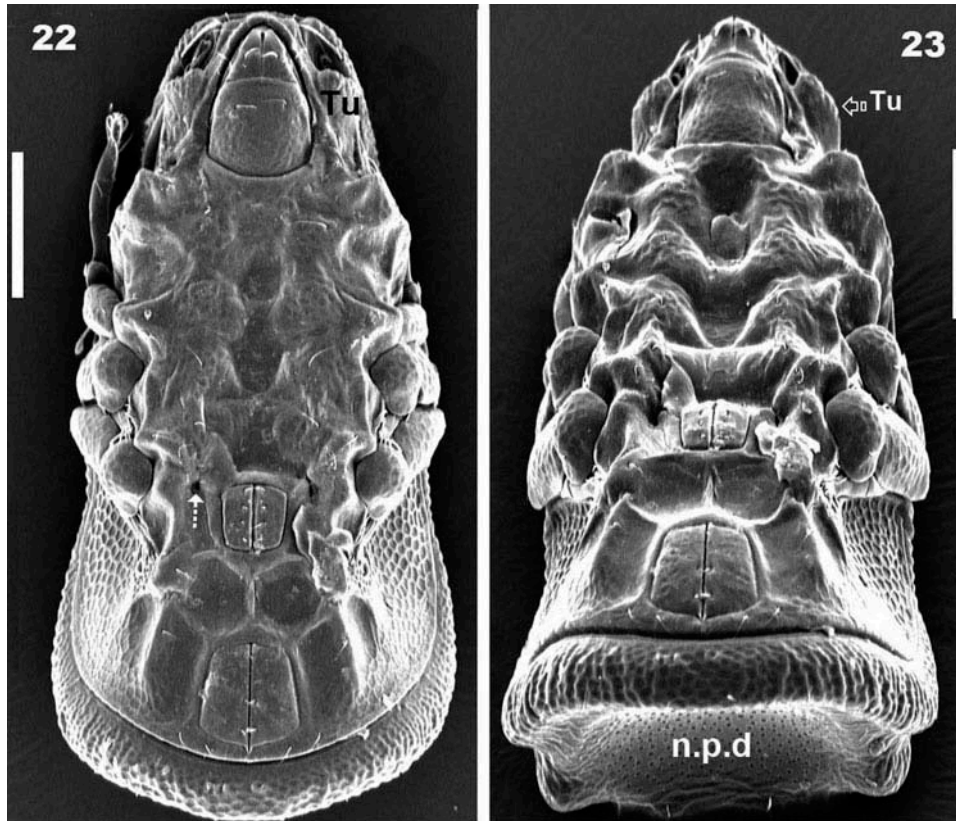
internally presenting a shallow semi-circular depression (indicated with specific arrow in Figure 7).

A particular *bo* (Figures 2, 4, 7, 17, 20) with different cuticular microsculpture in dorsal and ventral zones (see integument); *bo.ri* well delimited, smooth cuticular surface and *bo.to* large (Figure 20); inferior margin of bothridia striated cuticular microsculpture (Figure 20). Bothridial posterior tip rounded, penetrating *h.ap* anterior margin (Figure 20); *h.ap* medium sized, anterior zone rectangular (Figure 20), penetrated by the posterior bothridial tip. Upper margin slightly elevated; almost flat; inferior margin ovoid (Figures 4, 7, 17, 18). *Pd I* prominent extended

lamina; *Pd II* lamina small, apex rounded (Figures 7, 17, 18); *dis* easily discernible, (Figures 7, 17). Lyrifissures *im*, *ih*, *ips* clearly discernible (Figure 7); *im* near *gla*, situated below at level between *la* and *lm* setae; *ih* situated between *h*<sub>1</sub> and *h*<sub>2</sub>, near *b.ng*; *ips* situated between *h*<sub>1</sub> and *p*<sub>3</sub> setae near *b.ng*; *ip* only visible in posterior view (Figure 16) situated between *p*<sub>1</sub> and *p*<sub>2</sub> setae.

Many conspicuous *dep*: large reticulate microsculpture, situated behind legs IV, ovoid, and limited interiorly by depression which hide distal segments of legs IV during folding process (indicated by specific arrow Figures 7, 17); others smaller, ovoid, situated at level of anal





Figures 22–23. *Mangabebodes kymatismosi* gen. nov., sp. nov., adult., SEM. 22. ventral view; 23. ventral inclined posterior anterior view. Abbreviations: see “Materials and methods”. Scale bars: 22–23 = 100  $\mu$ m; 19–21 = 100  $\mu$ m.

opening. Behind genital opening, ventral cavity visible due to transparency (indicated in Figure 7 by double arrow) (see “Ventral region” and “Remarks”). Lyrifissure *iad* hardly discernible at level of *ad*<sub>3</sub> setae (Figure 7). Setae *ad*<sub>1</sub>, *ad*<sub>2</sub>, *ad*<sub>3</sub> and *ag* easily discernible (Figure 7).

**Ventral region.** Figures 22 and 23 is of the same specimen, with only a slight inclination to illustrate complexity of the ventral region; we decided to label the structures only in Figure 6.

Prominent *Tu* visible, expanding laterally up to prodorsal margin, reaching forward to level of *m* subcapitular setae and close to *le* insertion level (Figures 22, 23); anterior margin with longitudinal cuticular thickening (Figures 15, 22). *Tu* comparable with *Pd I* in size (Figure 23). *Pd I*, *Pd II*, *dis* well visible.

Epimeric zone complex; in flat observation (Figure 22) impossible to understand the “topography” of epimeric zone, Figure 23 inclined antero-posteriorly to aid understanding.

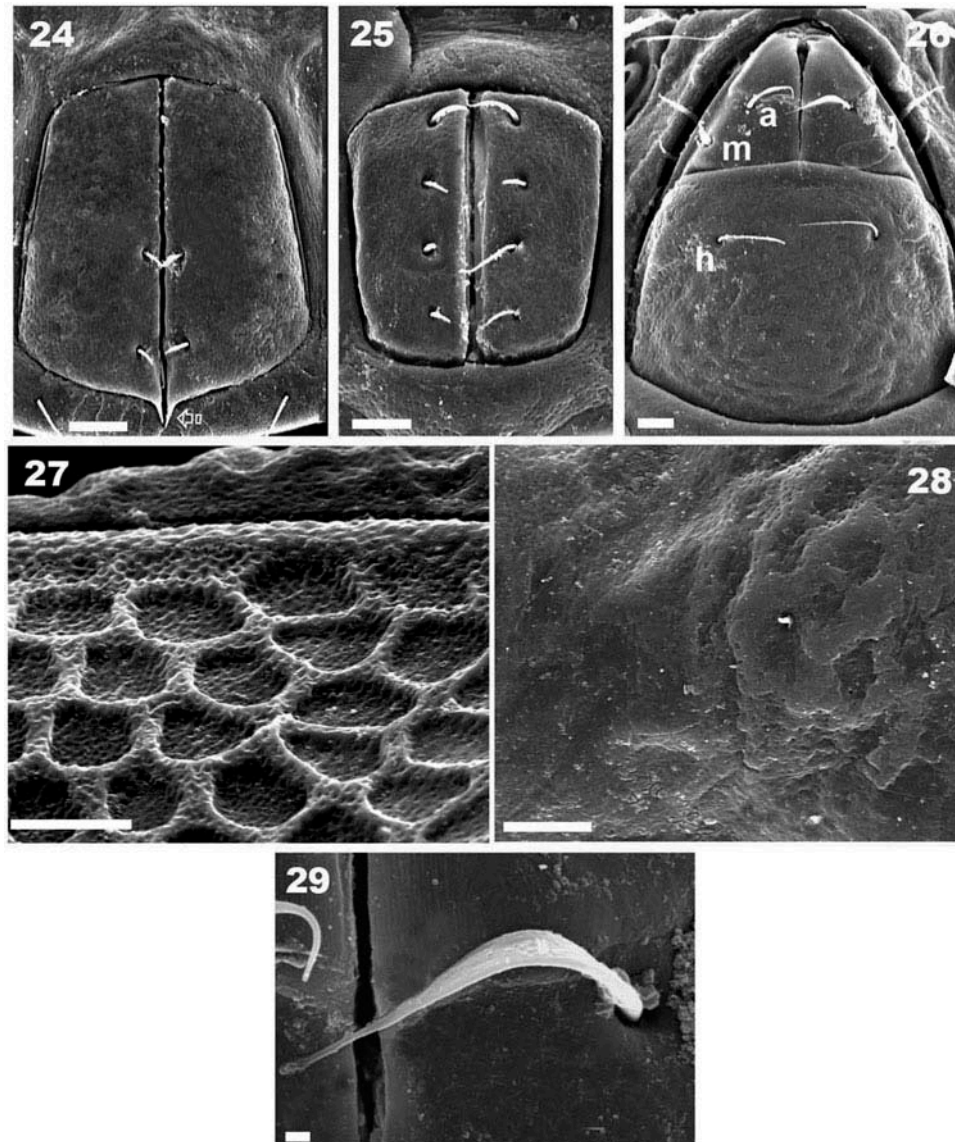
Furrows distinctly define epimera. Conspicuous longitudinal depression (Figure 23) present, with undulations at level of apodemata in zone of sagittal plane, at level of epimeres I, II, III; epimere IV without depression; *bo.1*, *bo.2*, *bo.sj* and *bo.3* clearly visible as shallow furrow (Figures 6, 23).

Epimeral chaetotaxy 3-1-3-3; setae *1a* and *3a* small (Figure 6); other epimeric setae of similar length.

Complex genito-anal zone; narrow elevated cuticular thickening surrounding genital opening; simple curved anterior thickening, and between them and epimere IV, *a.g.f* very deep semicircular depression (Figures 6, 22). In each *a.g.f* extremity, a cavity with particular shape (indicated by double arrow in Figures 6, 7 and by dotted arrow in Figure 22).

This cavity is clearly discernible from a lateral view (Figure 7), but is a little displaced due to the complicated shape of specimens making it difficult to place in strictly lateral position due to rotation. Narrow lateral thickening immediately leading to a deep furrow directed towards the cavity. Posterior thickening more or less polyhedral (Figure 22), delimited anteriorly by two rounded depressions situated between the genital and anal opening, paraxial and behind aggenital setae insertions (Figures 6, 22, 23). Cuticular thickenings surrounding rounded depressions.

Cuticular thickening surrounding anal opening delimiting two lateral polyhedral depressions (Figures 6, 22), *ad*<sub>3</sub> setae situated in marginal zone. Antiaxially to these depressions a medium-sized ovoid depression exists, continuing to lateral margin, forming a large, shallow depression with reticulate microsculpture.



Figures 24–29. *Mangabebodes kymatismosi* **gen. nov., sp. nov.**, adult., SEM. 24. anal plate; 25. genital plate; 26. subcapitulum; 27. ventral ornamentation; 28. epimeric ornamentation; 29. subcapitular setae. Abbreviations: see the section “Materials and methods”. Scale bars: 29 = 1  $\mu$ m; 24–28 = 10  $\mu$ m.

Behind acetabulum IV a prominence (indicated by specific arrow in Figure 6).

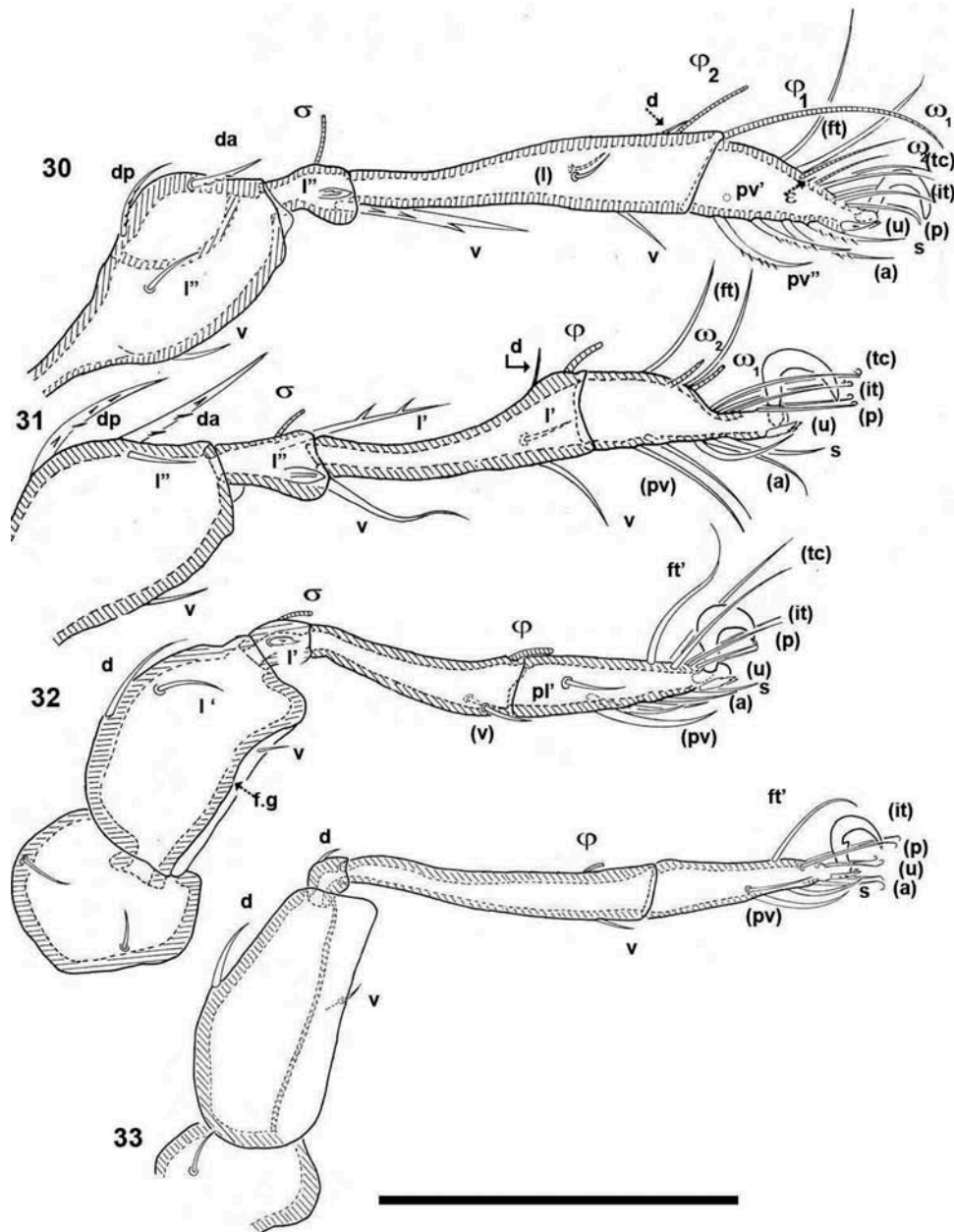
One pair of aggenital setae situated laterally to rounded depressions; three pairs of adanal setae; *iad* well discernible.

**Gnathosoma and palp.** Conspicuous diarthric subcapitulum; subcapitular setae *h*, *m*, *a* clearly visible, varying in shape (see “Setation”). Characteristic palp (Figure 34), *sul*, (*ul*), *acm* eupathidium, solenidion  $\omega$  long, easily discernible.

**Posterior aspect.** Due to the very complicated shape establishing an inclination in order to obtain only one SEM image or to make an illustration was difficult. We have included three Figures (3, 16, 23) with different views.

**Shape.** Ovoid. **SEM observations:** Figure 3: *l.p.e* with two paired protuberances; *c.n.e* with two pairs of protuberances; *s.c* well discernible; the origin of *n.p.d*, setae *dp* and ornamentation clearly discernible; in Figure 23: *l.p.e* (only one pair of protuberances) and *n.p.d* visible. **Optical observation:** Figure 16: *dp* setae, *n.p.d*, lyrifissure *ip* and all marginal setae.

**Legs** (Figures 30–33). claws without teeth; all legs more or less equal length. Femur of each leg differing (Figure 30–33), principally III and IV, with important role in “leg folding” process (see Fernandez et al. 2013a); genu III and IV small, hinge-like articulation with femur (Figures 32, 33); tibia I, IV long; II medium length and III short tarsi; I and II, very different; III and IV similar in shape and length.

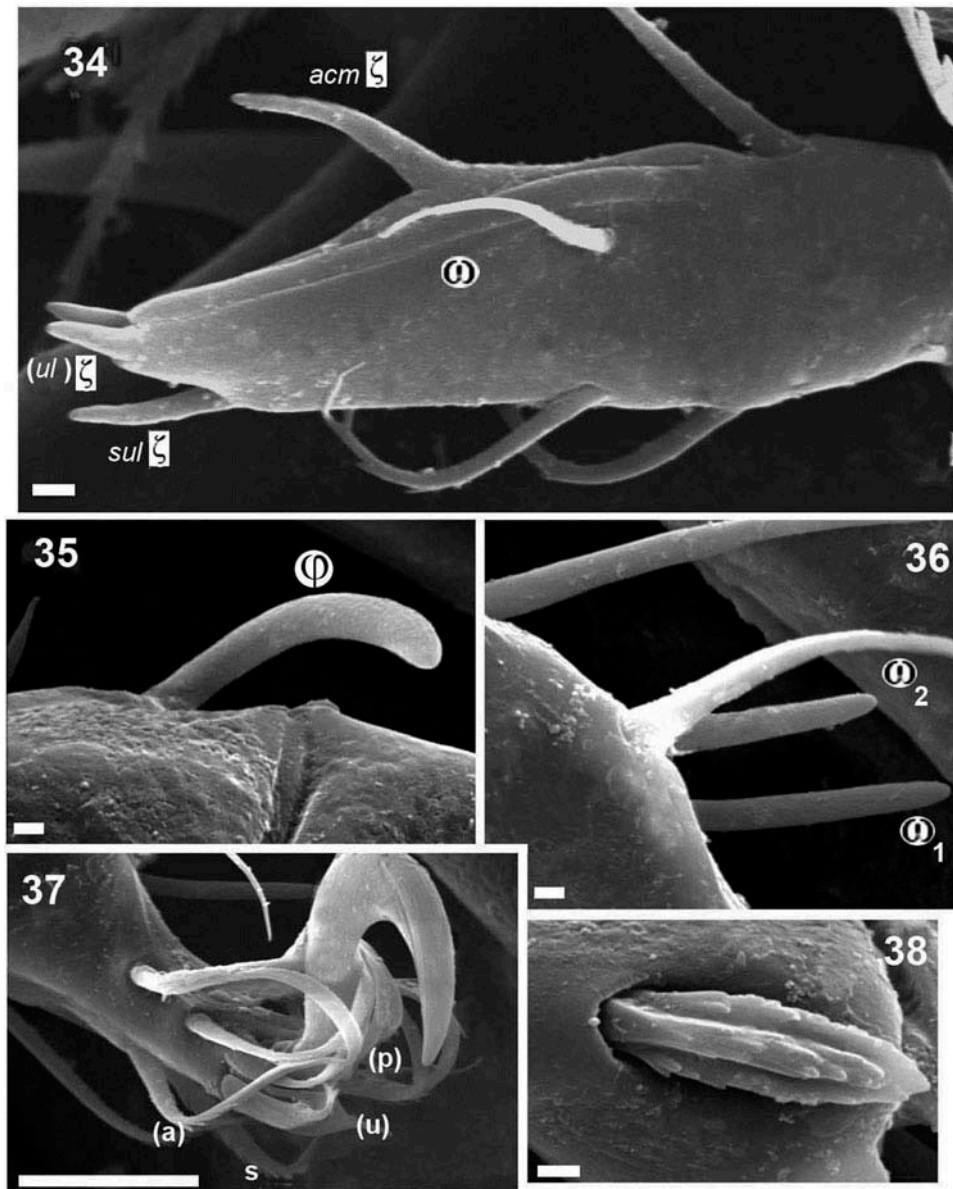


Figures 30–33. *Mangabebodes kymatismosi* gen. nov., sp. nov., adult. 30. leg I; 31. leg II; 32. leg III; 33. legs IV; Abbreviations: see “Materials and methods”. Scale bars: 30–33 = 70  $\mu$ m.

Table 1. *Mangabebodes kymatismosi* gen. nov., sp. nov. setae and solenidia.

	Femur	Genu	Tibia	Tarsi	Claw
Leg I					
Seta	<i>dp, da, l'', v</i>	<i>l'', v</i>	<i>(l), d, v</i>	<i>(ft), (tc), (it), (p), (a), s, (pv), <math>\varepsilon</math></i>	1
Solenidia	—	$\sigma$ —	— $\phi_1, \phi_2$ —	— $\omega_1, \omega_2$ —	
Leg II					
Seta	<i>da, dp, l'', v</i>	<i>(l), v</i>	<i>d, l', v</i>	<i>(ft), (tc), (it), (p), (u), (a), s, (pv)</i>	1
Solenidia	—	— $\sigma$ —	— $\phi$ —	— $\omega_1, \omega_2$ —	
Leg III					
Seta	<i>d, l, v</i>	<i>l'</i>	<i>(v)</i>	<i>ft', (tc), (it), (p), (u), (a), s, (pv), pl'</i>	1
Solenidia	—	— $\sigma$ —	— $\phi$ —	—0—	
Leg IV					
Seta	<i>d, v</i>	<i>d</i>	<i>v</i>	<i>ft', (it), (p), (u), (a), s, (pv)</i>	1
Solenidia	—	—0—	— $\phi$ —	—0—	





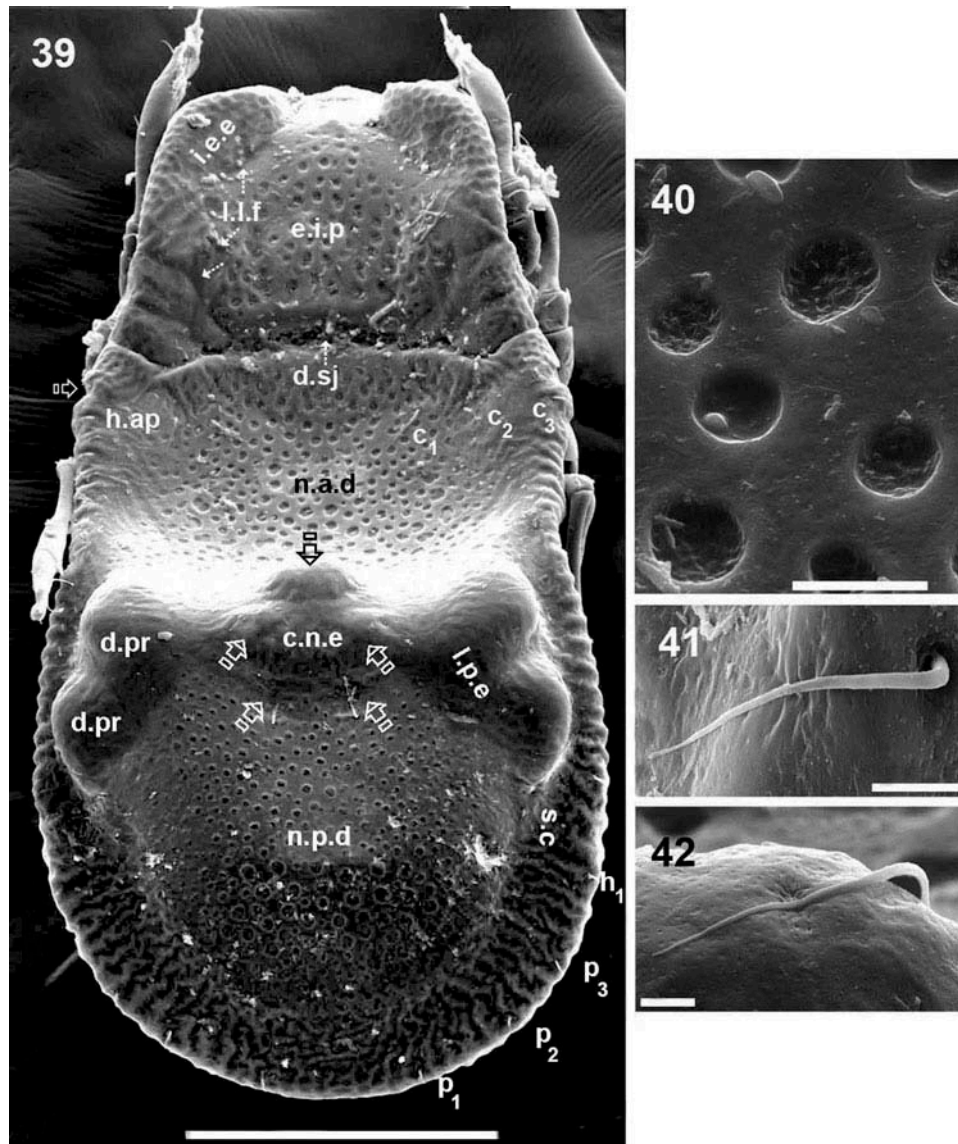
Figures 34–38. *Mangabebodes kymatismosi* **gen. nov., sp. nov.**, adult, SEM. 34. Palp, antiaxial view; 35. solenidium tibia II; 36. solenidia tarsus II; 37. tarsus II antiaxial; 38. seta *l''* genu II. Abbreviations: see “Materials and methods”. Scale bars: 37 = 10  $\mu\text{m}$ ; 34–36, 38 = 1  $\mu\text{m}$ .

*Leg I* (Figure 30). Femur long; basal zone narrow; depressed antiaxial zone hardly discernible; paraxial at level *da*, *dp*, setae ovoid zone (Figure 30), possibly a porose area. Genu, setae *v* large, barbed; *l''* particular shape (Figure 38); solenidia  $\sigma$  baculiform, short; tibia with  $\varphi_1$  long, setiform, tactile, situated on apophysis;  $\varphi_2$  baculiform, medium length, with setae *d* not associated but close. Tarsus with  $\omega_1$ ,  $\omega_2$  setiform and  $\varepsilon$  small; setae (*u*) typical shape as in tarsus II (Figure 37).

*Leg II* (Figure 31). Genu particular shape; setae *v* long and *l''* as in genu I (Figure 38); *l'* long, strongly barbed; solenidium  $\sigma$  baculiform, short. Tibia particular shape; solenidium  $\phi$ , baculiform, small (Figure 35); seta *d* present but not associated with solenidium. Tibiotarsus articulation

small synarthrodial skin, permitting limited movement. Tarsus size and shape similar to tarsus I. Solenidia  $\omega_1$ ,  $\omega_2$  baculiform, small (Figure 36); setae (*u*) and (*p*) particular (Figure 37).

*Leg III* (Figure 32). Trochanter: ovoid. Femur unlike all others, with characteristics and function typically related to “leg folding”; polyhedral in shape; basal slightly antiaxial, more or less rectangular shaped femoral groove (*f.g*); *v* setae situated on interior of small inner groove. Genu:  $\sigma$  baculiform, small; only *l'* setae, similar shape as in genu I and II (Figure 38), but smaller. Tibia small size;  $\phi$  baculiform, small; paired *v* setae. Tarsus normal shape; chaetotaxy normal but with one additional *pl'* seta.



Figures 39–42. *Antongilibodes paulae* gen. nov., sp. nov., adult., SEM. 39. dorsal view; 40. Ornamentation, notogastral anterior depression; 41. interlamellar seta; 42. notogastral seta. Abbreviations: see “Materials and methods”. Scale bars: 38 = 1  $\mu$ m; 39 = 200  $\mu$ m; 40 = 10  $\mu$ m; 41,42 = 5  $\mu$ m; arrow see text.

*Leg IV* (Figure 33). Trochanter: polyhedral. Femur, prominent basal blades with  $\nu$  setae. Genu small, only one  $d$  seta. Tibia long, thin;  $\phi$  small, baculiform. Tarsus normal, without ( $tc$ ) setae.

Setal formulae (trochanter to tarsus) and solendia:

I (1-4-2-4-16-1) (1-2-2); II (1-4-3-3-15-1) (1-1-2); III (2-3-1-2-15-1) (1-1-0); IV (1-2-1-1-12) (0-1-0) (Table 1).

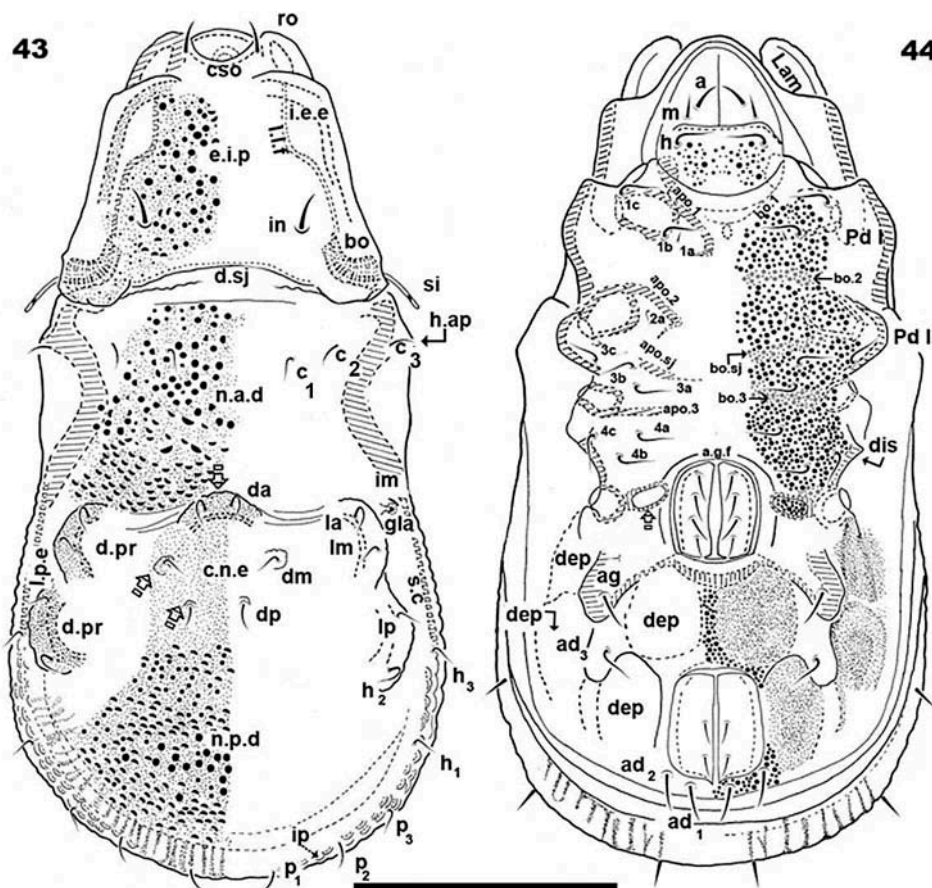
#### Remarks

In optical microscopy, finding a position and inclination from which to study these specimens was complicated due to their shape. For this reason dissection was necessary. The use of SEM was critical to understanding certain structures. With a small number of specimens it would be almost impossible to undertake such studies, while

larger numbers of available specimens may illustrate more appropriate morphological variability.

*Tutorium*. This structure is normally (in many Carabodidae) a prominent cuticular thickening, delimiting a supratutorial depression, permitting concealment of leg I underneath the spoon-shaped lamellae during the leg folding process (Fernandez et al. 2013a). In these specimens the tutorium is a large, long, forward projecting structure, expanded laterally. Firstly understanding the shape of the structure in lateral position is necessary, so as to not to confuse it with Pedotectum I. The tutorium shape, the supratutorial depression and the interior part of the lamella (spoon-shaped), results in an open lateral tube, which permits protection of leg I when concealed under the lamellae.

Another interesting characteristic is the depression situated behind acetabulum IV, giving additional protection



Figures 43–44. *Antongilibodes paulae* gen. nov., sp. nov., adult. 43. dorsal view; 44. ventral view. Abbreviations: see “Materials and methods”. Scale bars: 43–44 = 200  $\mu$ m.

when the distal segment of leg IV is partially concealed behind trochanter and femur. The particular tutorium combined with the depression are small adaptations that improve the protection mechanism (Fernandez et al. 2013a).

The ventral region of this specimen is bizarre, and slight inclination (Figures 22, 23) completely changes its appearance. The epimeric zone resembles a series of valleys and mountains.

Genital and anal openings are slightly elevated, surrounded by depressions. On the border of the anterior genital depression, a large cavity is observed.

Most of these observations were primarily made on specimens in inclined positions and with SEM; observations on the level plane gave no indication of the complexity of the structures.

### New taxon description

#### *Antongilibodes* gen. nov.

#### Etymology

The generic prefix “*Antongi*” derives from “Baie d’Antongil”, Nosy Mangabe Island, north-eastern Madagascar, place of origin of type material.

#### Diagnosis adult

Body shape, ovoid.

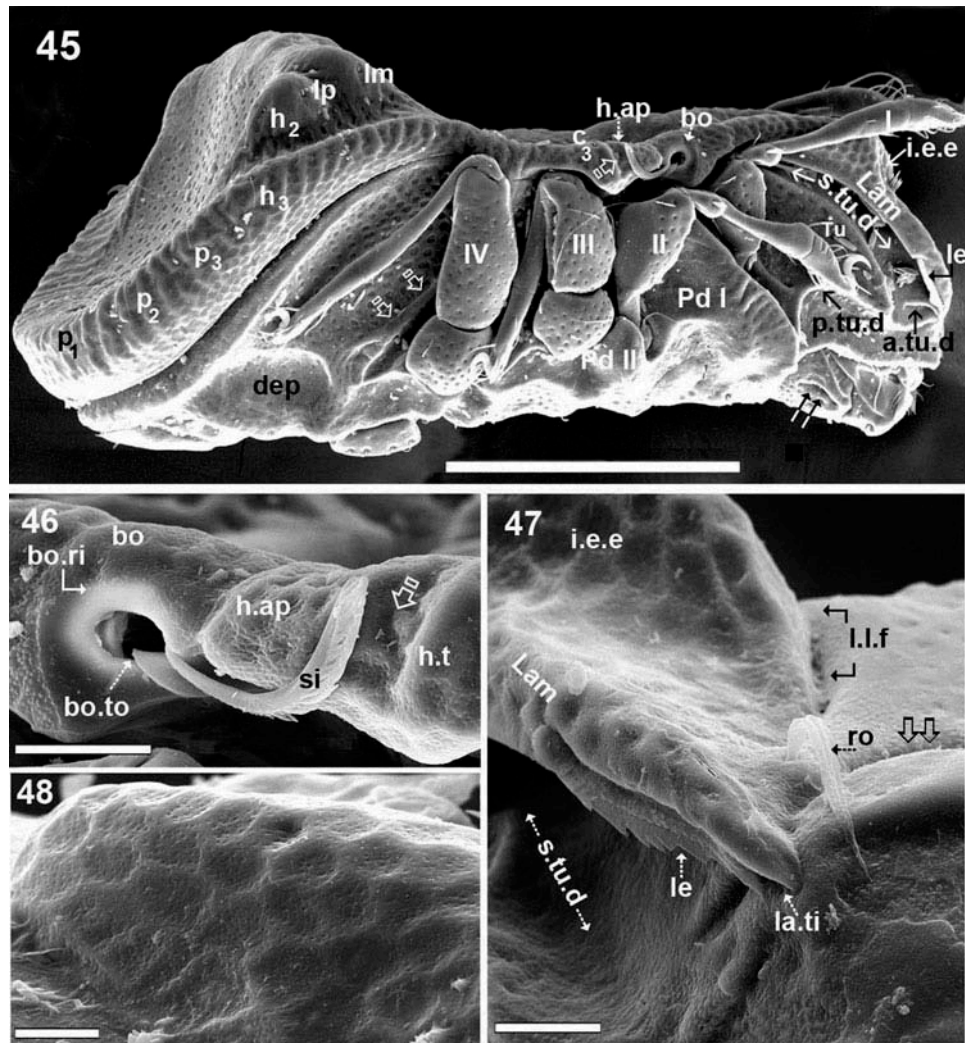
**Prodorsum.** Elevated interlamellar process terminating in paired external elevations; zone anterior insertion *ro* setae complex.

**Notogaster.** Anterior dorsal depression and posterior dorsal depression present, elevated zone between them, divided in lateral paired elevations and central notogastral elevation with unpaired central elevation, paired medial elevations and faintly demarcated posterior medial elevations. Fifteen pairs of setae, *c*<sub>1</sub>, *c*<sub>2</sub>, *c*<sub>3</sub> inner notogastral anterior depression; *da*, *dm*, *dp*, *la*, *lm*, *lp*, *h*<sub>2</sub> in central region and *p*<sub>1</sub>, *p*<sub>2</sub>, *p*<sub>3</sub>, *h*<sub>1</sub>, *h*<sub>3</sub>. Tutorium, pedotectum I; pedotectum II and discidium present as normal. Epimeric setae: 3-1-3-3; G:4; Ag:1; Ad:3; An:2. Ventral region with a paired bean-shaped depression in anterior genital zone.

**Type species:** *Antongilibodes paulae* gen. nov., sp. nov.

Related genus *Tuberocephus* Balogh & Mahunka, 1969 (See “Discussion”)





Figures 45–48. *Antongilibodes paulae* . gen. nov., sp. nov., adult., SEM. 45. lateral view; 46. humeral apophysis and bothridium; 47. lamellar anterior zone, 48. interlamellar external expansion, ornamentation. Abbreviations: see “Materials and methods”. Scale bars: 45 = 200  $\mu$ m; 46 = 20  $\mu$ m; 47 = 20  $\mu$ m; 48 = 10  $\mu$ m.

***Antongilibodes paulae* gen. nov., sp. nov.**

***Etymology***

The specific epithet is dedicated in homage to Dr Paula A. Rodriguez Moreno, Deputy Manager of Marine Invertebrate Collection of Technical Team and Assistant Curator of Crustacean Collection; Collection Department, Muséum National d'Histoire Naturelles, Paris, France; for her friendly collaboration and assistance in several technical projects.

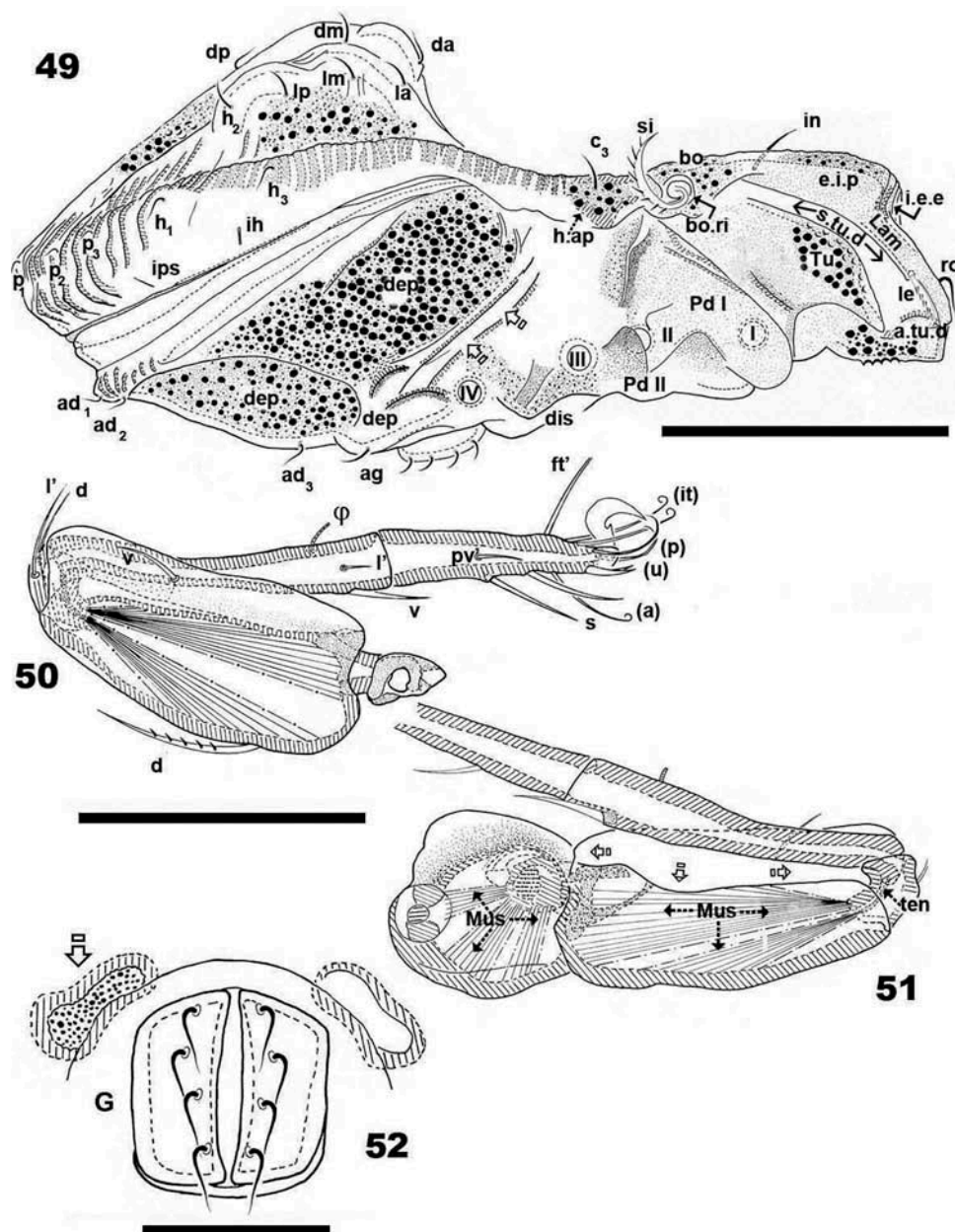
***Material examined***

Holotype: female “Mad. 906. Madagascar nord-est. Province de Tamatave, Baie d’Antongil. Ile de Nosy Mangabe; alt. 300m. FDHBA (Forêt dense humide de base altitude). Litière – J.M. Betsch coll.16-vii – 1967.” deposited in the Collection of the M.N.H.N, preserved in 70% ethanol. Paratypes: two adult females “Mad. 906. Madagascar nord-est. Province de Tamatave, Baie

d’Antongil. Ile de Nosy Mangabe; alt. 300m. FDHBA (Forêt dense humide de base altitude). Litière – J.M. Betsch coll.16-vii – 1967.” deposited in the Collection of the M.N.H.N, preserved in 70% ethanol; Paratypes: two, from same locality and date ; preserved in 70% ethanol, deposited in Collection of M.H.N.G. Material studied in S. E.M: six specimens, not deposited.

***Diagnosis***

**Integument microsculpture.** *Foveate*: elevated interlamellar region, partially lamellae, dorsal humeral apophysis, notogastral anterior depression, notogastral posterior depression, ventral region and depressions, tutorium; legs, trochanter, femur; *reticulate-foveate*: prodorsal interlamellar external expansion, elevated interlamellar expansion laterally, bothridium, dorsal anterior zone; notogaster near *bng* at setal level  $h_3$ ,  $p_1$ - $p_3$ ; *ribbon-like cuticular thickenings*: notogastral margin from *s.c* to a distance from *bng*; *smooth irregular*: dorsal promontories, some depressions around anal and genital opening.



Figures 49–52. *Antongilibodes paulae* gen. nov., sp. nov., adult. 49. lateral view. 50. leg IV with muscles, antiaxial. 51. leg IV paraxial; 52. depressed zone in anterior genital depression. Abbreviations: see “Materials and methods”. Scale bars: 49 = 200  $\mu$ m; 50, 51 = 50  $\mu$ m; 52 = 100  $\mu$ m.

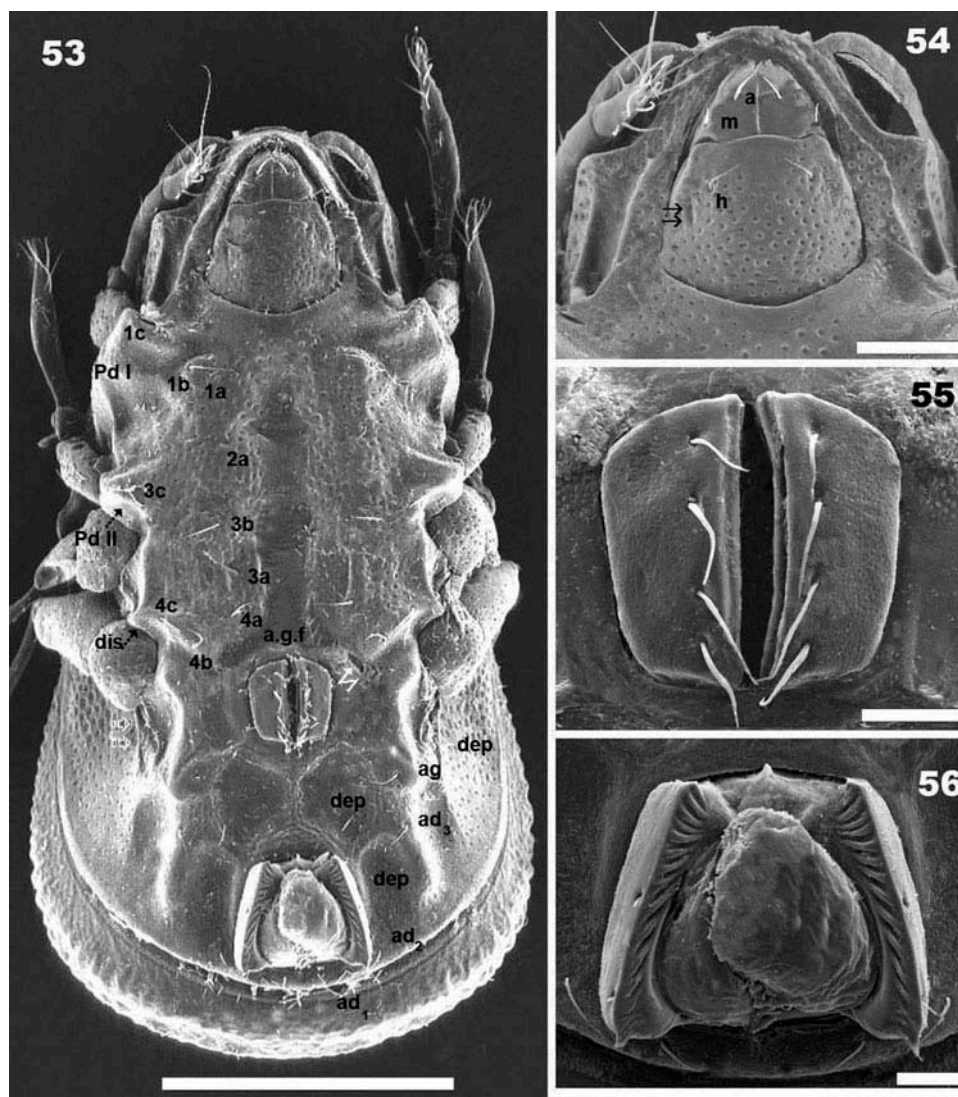
**Setation.** *Simple*: interlamellar; notogastral; sub-capitular; epimeric; genital; aggenital, anal, adanal. *Lanceolate*: ro. *Pectinate*: le.

**Prodorsum.** Posterior prodorsal depression not discernible; elevated interlamellar process conspicuous, terminating forwards in an oblique interlamellar external elevation, not continuing in medial prodorsal zone; shallow lamellar furrow clearly discernible, terminating near ro setae; transverse convex furrow, terminating near lamellar tip. Seta in inserted in front of bothridial level; rostral margin rounded; ro curving forward (Figure 47). Lam running dorsolaterally; lamellar tip small, wide sharpened apex.

**Notogaster.** Dorsosejugal furrow well delimited, middle zone slightly convex to rectilinear, antiaxial zone rectilinear. Notogastral anterior depression ovoid, up to more than half of total notogastral length; notogastral posterior depression ovoid, situated on posterior third of notogaster.

Between the depressions an elevated zone with: paired lateral elevated zone each divided into two dorsal promontories with la, lm, lp, h<sub>2</sub> setae; one central notogastral elevation with anterior unpaired promontory with da setae; one pair of central promontories with dm setae, one pair of small posterior depressions, sometimes difficult to observe, with dp setae.

Fifteen pairs of notogastral setae: c<sub>1</sub>, c<sub>2</sub>, c<sub>3</sub> situated in notogastral anterior depression; seven pairs da, dm, dp, la,



Figures 53–56. *Antongilibodes paulae* gen. nov., sp. nov., adult., SEM. 53. ventral view; 54. subcapitulum; 55. genital plate; 56. anal plate. Abbreviations: see “Materials and methods”. Scale bars: 53 = 200  $\mu$ m; 54 = 50  $\mu$ m; 55, 56 = 20  $\mu$ m.

*lm*, *lp*, *h*<sub>2</sub> situated on central notogastral zone; five pairs *h*<sub>3</sub>, *h*<sub>1</sub>, *p*<sub>1</sub>, *p*<sub>2</sub>, *p*<sub>3</sub> situated in notogastral margin; four pairs lyrifissures: *im*, *ih*, *ips*, *ip*; latero-abdominal gland and circumdorsal furrow, well discernible.

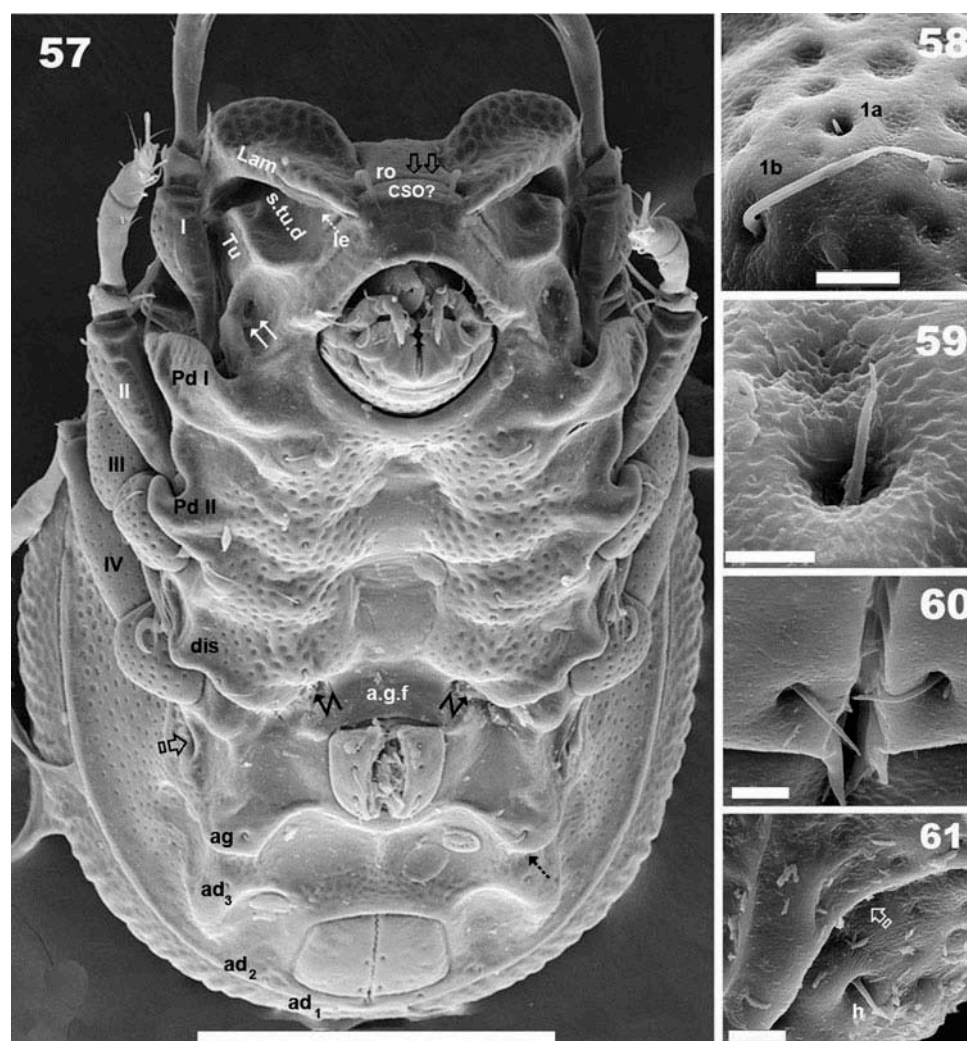
*Lateral region.* *Tu* normal, strongly curving cuticular thickening; supra tutorial depression antiaxially deep open tube, with anterior and posterior tutorial depression; *le* large; setal insertions far from lamellar tip. Bothridium ovoid; bothridial ring poorly delimited, smooth; bothridial tooth large; bothridial posterior tip penetrating humeral apophysis; pedotecta I, II, and discidium present. Dorsal margin pedotetum I with rectilinear cuticular thickening; tarsus II, similar thickening. Many conspicuous depressions: one pair, large with foveate microsculpture, behind acetabulum IV; one pair deep, longitudinal cuticular channel situated behind acetabulum IV; paired semicircular depressions situated near end of cuticular channel. Lyrifissure *iad* not discernible.

*Ventral region.* paraxial subcapitular setae *h*, semicircular slit. Epimeric zone complex, with elevations and depressions; broad longitudinal furrow in central zone; interrupted at sejugal apophysis and setae *4a* level. Epimeral chaetotaxy 3-1-3-3; *1a*, *2a* setae small; deep aggenital furrow, halfmoon-shaped; conspicuous bean-shaped cavity; paired depressions lateral to genital opening; posterior genital opening, paired polyhedral depression; aggenital seta situated on ear-like process. Ovoid to polyhedral depressed zone situated antero and lateral to the anal opening. Four pairs of genital setae; one pair of aggenital setae; three pairs of adanal setae; two pairs of anal setae; anal plate terminating in sharp tip.

#### Description

*Measurements.* SEM: 671  $\mu$ m (630–720)  $\times$  425  $\mu$ m (339–488) (material used for SEM studies, not deposited).





Figures 57–61. *Antongilibodes paulae* gen. nov., sp. nov., adult, SEM. 57. ventral inclined anteroposterior view; 58. epimeric zone; 59. seta 1a, detail; 60. posterior zone anal plate; 61. incision near subcapitular setae *h*. Abbreviations: see “Materials and methods”. Scale bars: 57 = 200  $\mu$ m; 58 = 10  $\mu$ m; 59 = 2  $\mu$ m; 60 = 2  $\mu$ m; 61 = 5  $\mu$ m.

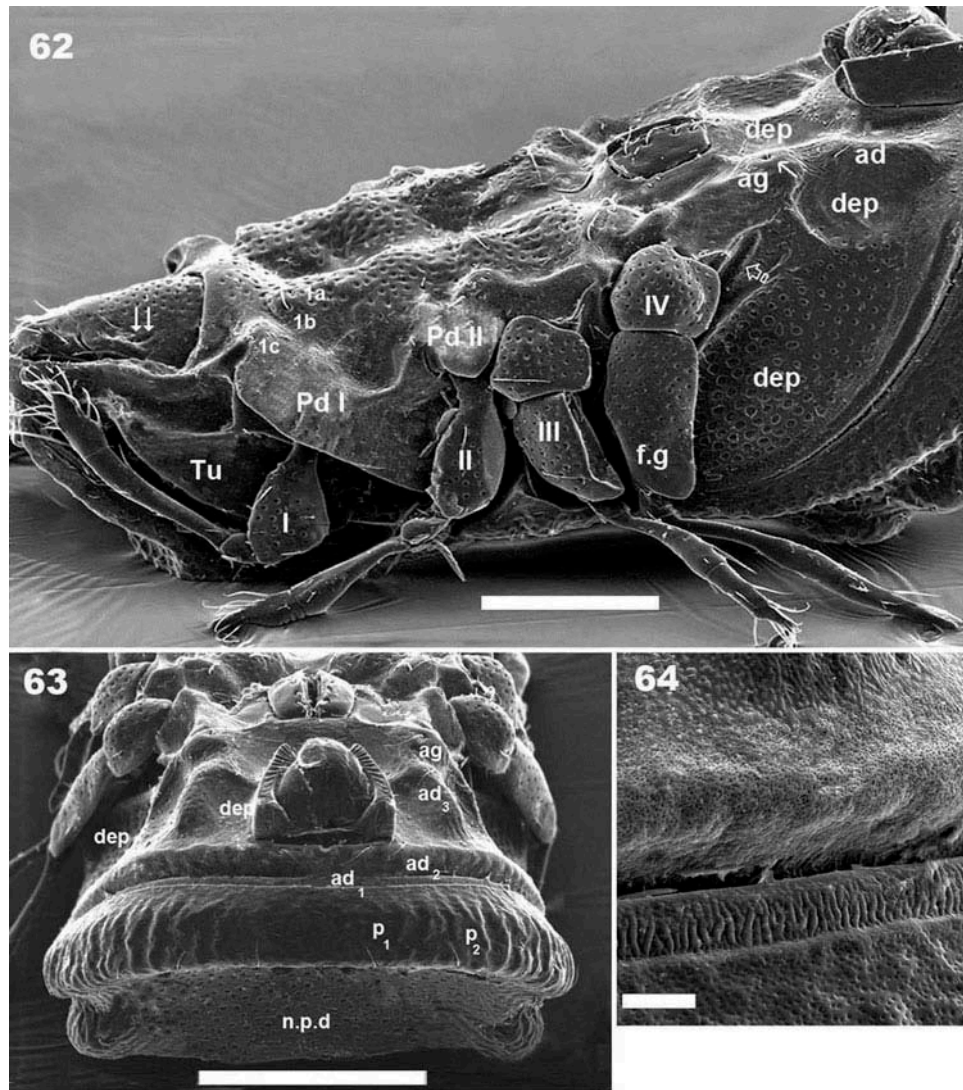
Light microscopy: 692  $\mu$ m (680–710)  $\times$  432  $\mu$ m (360–485) (measurement of specimens deposited in M.N.H.N and M.H.N.G). All specimens female.

*Shape.* ovoid (Figures 39, 43).

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

*Cerotegument.* A consistently very thin layer ( $\pm 0.5$   $\mu$ m), covering body and legs and following cuticular irregularities; do not impede observations; with different characteristics: *rough*: epimeric zone (Figure 58), under high magnification the roughness appears *crumpled* (Figure 59); *porous*: dorsal prodorsum (Figures 48, 42), notogaster, dorsal promontories; *granulate*: *s.t.u.d* zone at *le* setal insertion; *h.ap* anterior part and bothridium anterior part (Figures 47, 46).

*Integument.* Microsculpture complicated, varying according to body region (Figures 39, 40, 43–49, 53–55, 57, 58, 61–64, 67, 68); *foveate*: clearly delimited round-ovoid fovea, internally pocket-shaped (Figure 40), highly variable in size and shape (Figures 39, 43, 44, 53, 54, 57, 62, 63), situated on: prodorsum, *e.i.p* (Figures 39, 43); *Lam* between *le* setal insertion and *la.ti* (Figure 47); dorsal *h.ap*, near *d.sj* (Figure 39) notogaster, *n.a.d*, *p.p.d* (Figures 39, 43, 45); ventral region, subcapitulum (Figures 44, 53, 54), around ventral zone (Figures 53, 54); epimeric zone and *dep*, principally behind acetabulum IV, in others *dep*, less pronounced or absent (Figures 44, 45, 49, 53, 54, 57, 58, 62); *Tu* more or less pronounced in different specimens (Figures 45, 62), legs: trochanter, femur (Figures 45, 62, 67); *reticulate-foveate*: fovea not clearly delimited, polyhedral, surrounding cuticular thickening (Figure 48), found on: prodorsum, interlamellar external expansion (*i.e.e*) (Figures 39, 45, 47, 48, 57), lateral *e.i.p* (Figure 45); bothridium, dorsal anterior zone (Figure 45); notogaster, near *bng* at setal level *h*<sub>3</sub>, *p*<sub>1</sub>, *p*<sub>2</sub>, *p*<sub>3</sub> (Figures 45, 57);



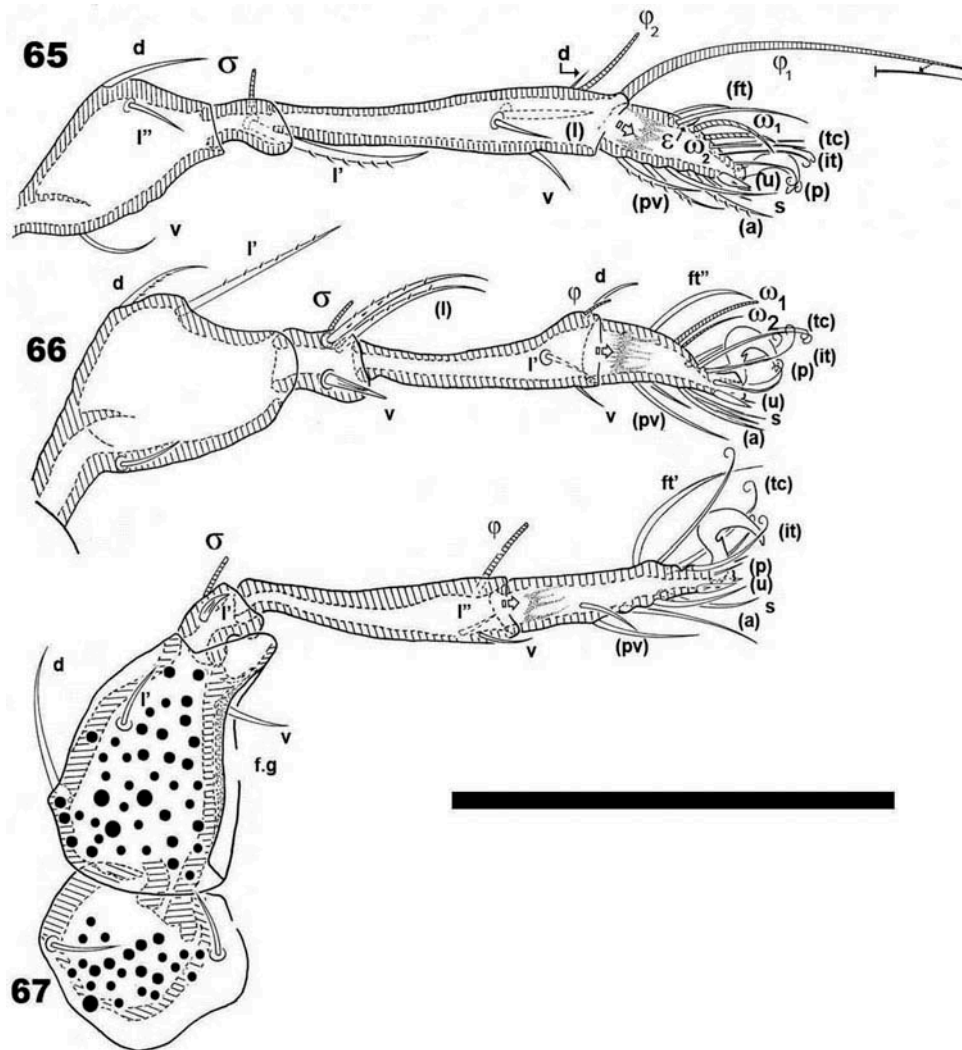
Figures 62–64. *Antongilibodes paulae* gen. nov., sp. nov., adult, SEM. 62. lateral inclined view; 63. posterior general view; 64. microsculpture posterior notogaster ventral zone. Abbreviations: see “Materials and methods”. Scale bars: 62,63 = 100  $\mu$ m 64 = 10  $\mu$ m.

*ribbon-like cuticular thickenings*: notogastral margin from *s.c* to a distance from *bng* (Figures 39, 43, 45, 64); *smooth irregular*: *d.pr*, *dep*, around anal and genital opening, microsculpture more or less smooth with small, not properly delimited fovea or faint ribbon cuticular thickening (Figure 39, 42, 43, 45, 53, 57, 62, 63).

*Setation* (legs not included). *Simple*: interlamellar (Figure 41); notogastral (Figure 42); subcapitular (Figure 54); epimeric (Figures 53, 58, 59, 61); genital (Figure 55); aggenital (Figure 53), anal (Figures 56; 60), adanal (Figures 53, 56). *Lanceolate*: *ro* (Figure 47). *Pectinate*: *le* (Figures 46, 47). Lengths: (measurements from six specimens used for SEM studies; consideration should be given to the fact that these mites were preserved in alcohol for more than 35 years (preservation very good), and the length of setae is relative as we cannot be certain that tips are not damaged) *ro* = 40  $\mu$ m (43–37); *in* = 17.5  $\mu$ m (22–15); *le* = 58.8  $\mu$ m (61–57); *h*<sub>1</sub>, *h*<sub>2</sub>, *h*<sub>3</sub>, *da*, *dm*, *dp*, *la*, *lm*,

*lp*, *h*<sub>2</sub> = 36.7  $\mu$ m (33–43); *h*<sub>1</sub>, *h*<sub>3</sub>, *p*<sub>1</sub>, *p*<sub>2</sub>, *p*<sub>3</sub> = 18.7  $\mu$ m (14–22); subcapitular = 12.5  $\mu$ m (11–14); epimeric = 26  $\mu$ m (19–32) (except *1a* and *2a*); *1a* = 3.3  $\mu$ m (3.5–3.7); *2a* never found complete; *g* = 18.3  $\mu$ m (23–15); *ag* = 28  $\mu$ m (31–22); *an* = 3.4  $\mu$ m (3–5) (only measured in two specimens, others broken); *Ad* = 18  $\mu$ m (14–24).

*Prodorsum*. *p.p.d* (Figures 39, 43) not discernible; *e.i.p* elevated (Figures 39, 45, 48) terminating in an oblique interlamellar external elevation (*i.e.e*), not continuing in medial prodorsal zone (Figures 47, 57), ear-like appearance in ventral anterior posterior inclined view (Figure 57); *l.l.f* clearly discernible in SEM (Figures 39, 47, 57) or due to transparency (Figure 43); *l.l.f* delimiting anterior *i.e.e*, terminating near *ro* setae, seems to reach *la.ti* (Figure 47), but the *ro* insertion and transversal convex furrow which terminate near *la.ti* makes the situation confusing. Seta *in* inserted anterior to *bo* level and far from *i.e.e* (Figures 43, 49)(see “Remarks” and “Discussion”).



Figures 65–67. *Antongilibodes paulae* gen. nov., sp. nov., adult. 65. leg I antiaxial; 66. leg II antiaxial; 67. leg III antiaxial. Abbreviations: see “Materials and methods”. Scale bars: 65–67 = 150  $\mu$ m.

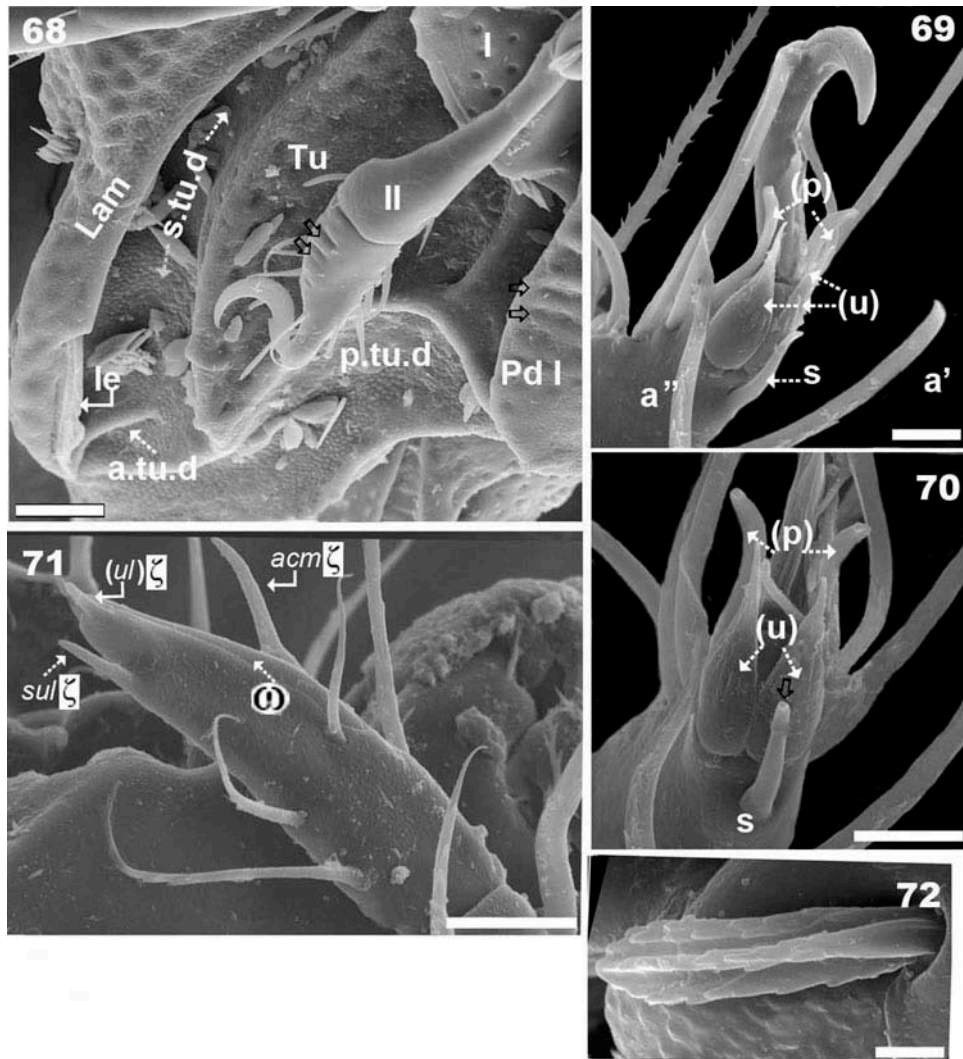
Table 2. *Antongilibodes paulae* gen. nov., sp. nov. setae and solenidia.

	Femur	Genu	Tibia	Tarsus	Claw
Leg I					
Setae	<i>d, l'', v</i>	<i>l'</i>	<i>(l), d, v</i>	<i>(ft), (tc), (it), (p), (a), s, (pv), <math>\epsilon</math></i>	1
Solenidia	—	$\sigma$ -	$-\phi_1, \phi_2-$	$-\omega_1, \omega_2-$	
Leg II					
Setae	<i>d, l', v</i>	<i>(l), v</i>	<i>d, l', v</i>	<i>ft', (tc), (it), (p), (u); (a), s, (pv)</i>	1
Solenidia	—	$-\sigma-$	$-\phi-$	$-\omega_1, \omega_2-$	
Leg III					
Setae	<i>d, l', v</i>	<i>l'</i>	<i>l'', v</i>	<i>ft', (tc), (it), (p), (u), (a), s, (pv), pl'</i>	1
Solenidia	—	$-\sigma-$	$-\phi-$	—0—	
Leg IV					
Setae	<i>d, v</i>	<i>d, l'</i>	<i>l', v</i>	<i>ft', (it), (p), (u), (a), s, (pv)</i>	1
Solenidia	—	—0—	$-\phi-$	—0—	

Rostral margin rounded (Figures 47, 57) but very complex, with a transversal convex furrow parallel to rostral margin; CSO not discernible; *ro* curving forward (Figure 47). *Lam* running dorsolaterally, in dorsal zone of prodorsum, shallow furrow (*l.l.f*) (Figures 39, 47, 57)

clearly demarcating inner paraxial margin of lamellae; this furrow probably terminates in the internal zone of lamellar apex (*la.ti*) (Figure 47), but the insertions of *ro* setae obstruct clarifying observation; *la.ti* small, wide sharpened apex (Figure 47).





Figures 68–72. *Antongillobodes paulae* gen. nov., sp. nov., adult, SEM. 68. anterior prodorsal zone, lateral view; 69. tarsus I tip, antiaxial view; 70. tarsus I tip, frontal view; 71. palp antiaxial view; 72. seta *l'* genu III. Abbreviations: see “Materials and methods”. Scale bars: 68 = 20  $\mu$ m; 69,70 = 5  $\mu$ m; 71 = 10  $\mu$ m; 72 = 2  $\mu$ m.

Ventral anteroposterior view (Figure 57) clearly indicating the position of several structures (*rostrum*, *la.ti*, *le* setae, *ro* setae, *s.tu.d*, *i.e.e*, *Tu*).

Complex rostrum, but in front of *ro* setae, a transversal furrow visible, running parallel to aspis; exceeding *la.ti* and reaching inner zone of *s.tu.d* (Figure 47); transversal furrow running behind a convex zone, probably the *cso* (indicated in Figure 57 as *cso*); *s.tu.d* is conspicuous as a deep antiaxially open tube. *Tu* not exceeding lamellar margin, completely different to Pd I (see below, Lateral region).

*Notogaster*. Shape: ovoid; *d.sj* well delimited as slightly convex to rectilinear furrow, antiaxial zone rectilinear (Figures 39, 43).

Two conspicuous depressions: (1) *n.a.d*: ovoid, large, extending from the *d.sj* posteriorly up to more than half of the total notogastral length. (2) *n.p.d*: situated in the posterior third of notogaster (Figures 39, 43); ovoid.

Raised zone between *n.a.d* and *n.p.d*. Elevated zone with a pair of *l.p.e*; each *l.p.e* divided in two *d.pr* and a *c.n.e*. Each *l.p.e* presenting one large anterior *d.pr*, rounded, directing antiaxially to paraxially and slightly displaced to paraxial in relation to the posterior *d.pr*. Ovoid posterior *d.pr* situated paraxially to anterior *d.pr*. (Figures 39, 43, 45). Anterior *d.pr* with *la*, *lm* setae and posterior *lp*, *h<sub>2</sub>* setae.

The *c.n.e* with rounded unpaired anterior promontories with *da* setae (Figures 39, 43); a pair of central promontories small in relation to the anterior, with *dm* setae (Figure 39); sometimes tiny posterior *d.pr* with *dp* setae present; but in other cases these promontories are almost invisible or absent. Promontories of *c.n.e* never exceed level of *l.p.e* promontories.

The *n.p.d* extends to *c.n.e* zone, exceeding *dp* setae insertion level (Figures 39, 43, 45); foveate microsculpture of *n.p.d* exceeding tiny *d.pr* with *dp* setae, visible in Figure 39.

Total number of notogastral setae: 15, 3 pairs  $c_1$ ,  $c_2$ ,  $c_3$  situated in *n.a.d*; 7 situated in elevated zone (described above) and another 5 pairs  $h_3$ ,  $h_1$ ,  $p_1$ ,  $p_2$  and  $p_3$  situated in notogastral margin (Figure 43).

Only four pairs of lyrifissures visible *im*, *ih*, *ips* and *ip* (Figures 43, 49).

Clearly visible *gla*, characteristic shape, situated anterior to *d.pr* of *l.p.e*.

*Lateral region.* *Lam* clearly visible (Figures 45, 49, 62); *le* setal insertions situated far from *la.ti* (Figure 47), this zone is narrowed. Setae *le* large, reaching to level of *la.ti* (Figure 47), *Tu* normal, clearly visible as a strongly curved cuticular thickening (Figures 45, 49).

Deep *s.tu.d* with anterior and posterior pocket depressions (*a.tu.d*; *p.tu.d*) (Figures 45, 49, 68).

Ovoid *bo*; *bo.ri* poorly delimited, smooth cuticular surface, conspicuous *bo.to* (Figure 46). Bothridial posterior tip penetrating *h.ap* anterior margin (Figures 45, 46); *h.ap* medium-sized, anterior zone ovoid (Figures 45, 46); clearly visible depression concealing the sensillus during leg folding processes (Figure 46).

*Pd I*: prominent extended lamina (Figures 45, 47, 49, 57, 62); a series of rectilinear cuticular thickenings present in anterior margin (Figures 45, 57), tarsus II (Figures 46, 68) displaying similar type of thickening (Figure 68) (see "Remarks"). *Pd II*: small triangular lamina, rounded apex (Figures 45, 49, 57, 62) in Figure 57, from a different angle, *Pd II* appearing digitiform; clearly discernible small triangular *dis*, rounded end (Figures 49, 57). Lyrifissures *ih*, *ips*, *ip* easily discernible (Figure 49).

Many conspicuous *dep*: one large, with foveate microsculpture, situated behind acetabulum IV, others situated laterally to genital and anal opening and between them (Figures 45, 49, 62). Very interesting depressed area situated behind acetabulum IV, forming a deep longitudinal channel (Figures 45, 49, 57, 62; indicated with double specific arrow). This depression always occurs, but never this deep and robust. Semicircular depression situated slightly towards the termination of the channel (Figures 45, 49, 62). Longitudinal channel and semicircular depression combined with a particular depression on femur IV (see below) play a role in the leg folding process (see "Remarks").

Lyrifissure *iad* not discernible, probably exists, but observation hindered by microsculpture and depressions.

*Ventral region.* Observation of different inclinations of specimens permits better understanding of several structures in the complex ventral region (Figures 44, 53, 57).

Paraxial to subcapitular setae *h*, there is a semicircular slit (Figure 61, indicated by double arrow Figures 45, 54, 62).

Epimeric zone complex; flat observation (Figures 44, 53) permitting gathering of important information but not on the topography of this zone, which Figure 57 helps us interpret.

Epimera: General aspects visible as a series of elevations and depressions; central broad longitudinal furrow, interrupted at level of *apo.sj* by a transversal elevation and at level of setae *4a* by small transversal elevation (Figure 57).

Epimeres well defined by *bo.1*, *bo.2*, *bo.sj* and *bo.3* and well delimited furrows (Figures 44, 53, 57).

Epimeral chaetotaxy 3-1-3-3; all setae inserted in a rounded depression (Figures 57, 58); setae *1a* and *2a*, short (Figures 44, 58, 59); other epimeric setae large, similar in length (Figures 53, 57, 58).

Narrow cuticular thickening surrounding genital opening, which is situated on elevated zone. Immediately surrounding this zone, a depressed zone: (1) *a.g.f* (Figures 44, 52, 53, 57, 62) deep, semicircular; internally exhibiting a bean-shaped cavity, position variable, generally directed towards acetabulum IV (Figure 44, 57 indicated by special arrow) or parallel to *a.g.f* margin (Figure 52); (2) laterally to genital opening a paired depression (indicated by arrow Figures 53, 57); (3) posterior to genital opening, prominent polygonal elevation and below that a paired polyhedral depression (Figures 53, 57); aggenital seta situated marginally to this depression on an ear-like process (Figure 57, 62 indicated by arrow). Anterior and lateral to anal opening, ovoid to polyhedral depressed zone (Figures 44, 53, 57, 62).

Four pairs of genital setae (Figure 55); one pair of aggenital setae; three pairs of adanal setae; two pairs of anal setae and sharply tipped anal plate (Figure 56, 60); *iad* not discernible.

*Gnathosoma and palp.* Conspicuous diarthric subcapitulum; subcapitular setae *h*, *m*, *a* clearly visible; zone *m*, setae, conspicuous microsculpture (Figures 44, 53, 54). Characteristic palp (Figure 71), *sul*, (*ul*), *acm* eupathidic, solenidium  $\omega$  long, clearly discernible, similar to preceding species description.

*Posterior aspect* (Figure 63). To permit understanding of the complicated topography of posterior notogastral zone and ventral region from anal to genital opening. Shape: ovoid; *dep* situated around anal and genital opening are delimited by elevated cuticular structures.

*Legs* (Figures 50, 51, 65–67; 69–71). Legs monodactyl, claw with tooth; all legs more or less similar length. Tarsi I, II, III with particular arborescent structure (indicated by specific arrow Figures 65–67); less visible on tarsus IV. Femur shaped differently in each leg (Figures 62, 65–67), III and VI with special adaptations for their role in leg folding (see Fernandez et al. 2013a); genu more or less equal in length; tibia I, IV, long; III medium length; II small.

*Leg I* (Figure 65). Femur long; basal zone narrow; depressed antiaxial zone hardly discernible. Genu *l'* long, barbed setae; solenidium  $\sigma$  baculiform. Tibia long with dorsal anterior promontory;  $\phi_1$  long setiform situated on

promontory,  $\phi_2$  medium length, baculiform, setae *d* not associated with but close to solenidium. Tarsus  $\omega_1$ ,  $\omega_2$  setiform, medium length;  $\varepsilon$  small; setae (*p*) smooth, particular shape (Figures 69, 70) apical pore apparent (indicated by arrow Figures 69, 70); setae (*u*) conical shape, slightly barbed (Figures 69, 70), setae *s* small, smooth, nearly tubular in shape, with apparent apical pore (indicated by arrow Figure 70); setae *s* situated in front of (*a*) (Figures 65, 69, 70).

**Leg II** (Figure 66). Femur large; genu, solenidium  $\sigma$  baculiform, short, setae *v* particular, similar shape to *l'* setae of genu III (Figure 72). Tibia with tibiotarsus articulation by means of small synarthrodial skin, permitting limited movement; solenidium  $\phi$  baculiform, small; setae *d* present, large, not associated with solenidium. Tarsus size and shape similar to tarsus I, but with particular ribbon-like cuticular thickening in dorsal zone (Figure 68) (see "Remarks"). Solenidia  $\omega_1$ ,  $\omega_2$  setiform, medium size; seta (*u*), (*p*), *s*, (*a*), similar characteristics to tarsus I (Figures 69, 70).

**Leg III** (Figure 67). Trochanter polyhedral; polyhedral femur unlike all others; *f.g* clearly visible, with prominent anterior tip; genu small;  $\sigma$  baculiform; setae *l'* particular (Figure 72); tibia narrow, solenidium  $\phi$  baculiform, medium size. Tarsus long, position of setae (*p*), (*u*), *s*, (*a*) similar to tarsus I.

**Leg IV** (Figures 50, 51). Paraxial side of trochanter and femur was dissected, in order to observe the depressed zone and to accurately determine the position of muscles and tendon, Figure 51 is a final reconstruction of different dissections of this zone. Trochanter: polyhedral with large basal blade. Femur: prominent basal blade, with conspicuous depression paraxially (Figure 51), similar in shape to tibia, permitting concealment of this segment during leg folding process. Genu is a hinge, partially concealed by femur. Trochanter muscles are inserted on opposite side of ventral blade (dorsally), all are connected to basal part of femur (Figure 51); the femur with two groups of muscles, one situated basally near the depressed zone, inserted on posterior extremity of femur and genu; the second inserted in medial posterior dorsal zone of femur, innervating a tendon (*ten*) that reaches the posterior part of tibia. The two muscles are very prominent and appear powerful.

Tibia long, thin;  $\phi$  small, baculiform. Tarsus normal shape, but reduced number of setae with only one *ft'* and *pv'*, the absence of (*tc*) is normal to the four tarsi.

I (1-3-2-4-16-1) (1-2-2); II (1-3-3-3-14-1) (1-1-2); III (2-3-1-2-14-1) (1-1-0); IV (1-2-2-2-11) (0-1-0) (Table 2)

#### Remarks

**Protection mechanism:** *Antongilibodes paulae* **gen. nov., sp. nov.** exhibits a series of particularities related to protection mechanisms, principally on legs II and IV. Usually leg II, when mechanisms are activated (See Fernandez

et al. 2013a, Figures 76–80), is concealed by pedotectum I with the antiaxial depression of femur I effortlessly permitting entry of tarsus II under the protection of pedotectum I, but in this case pedotectum I and the dorsal zone of tarsus II are similar in shape and position, with the ribbon-like cuticular thickening (Figure 68, indicated by arrow) probably allowing better anchoring of the tarsus behind this protection.

Leg IV presents other particular characteristics: the ventral paraxial femoral depression, similar in shape to tibia; ventral blade of the trochanter and the channel and semicircular depression on lateral cuticular surface behind acetabulum IV (Figures 45, 49–51, 57, 62). The cuticular channel depression permits lodging of the apical part of the tibia with the tarsus, and semicircular cuticular depression accommodates the claw. Once the genu, tibia, tarsus and the claw are concealed in depressions on the lateral cuticular body surface, and by the ventral trochantral blade in conjunction with the femoral paraxial depression; these two last segments function similarly to the lid of a box.

**The cavities:** In the complex ventral region (Figures 44, 52–54, 57, 61), a semicircular slit close to the *h* subcapitular setae; and in the anterior aggenital furrow zone, a bean-shaped cavity were observed; these are almost certainly sensorial organs but ultrastructural studies are necessary for confirmation.

**Tarsal setae (*a*) and *s*:** Tarsal setae are particular, principally (*a*) and *s*; unusually, (*a*) are situated behind *s*. These setae have a smooth surface and appear to have an apical cavity (Figures 69, 70).

#### Discussion

For the study of this group of species (see "Introduction"), it was important to obtain specimens of the genus *Tuberocephus* Balogh & Mahunka, 1969 from Madagascar, to permit adequate comparison.

Initially we considered there to be a high probability of finding this genus in our collection of more than 4000 specimens, due to the fact that the description by Dr J. Balogh (1962) was based on samples sent to him by Professor M.R. Paulian.

This task proved very difficult, however, due to the superficial nature of the original genus and species descriptions (text and figures).

*Problems with Tuberocephus longus* (Balogh, 1962) *Machadocephus longus* Balogh, 1962; *Tuberocephus* Balogh & Mahunka, 1969, type species *Tuberocephus longus* (Balogh, 1962)

- (1) We were unable to secure the type species on loan from the Museum (Budapest) in which it was deposited. We determined that the original material was made available by the team of M.R. Paulian. In his original introduction to the paper in 1962, J. Balogh stated: "M.R. Paulian, Directeur-adjoint de l'Institut de Recherches



Scientifiques de Madagascar, m'a remis pour examen un matériel d'Oribates, riche en nouvelles espèces, dont la présente publication constitue la deuxième série de descriptions" Balogh (1962). (2) At least 30 groups of species exist where *Tuberocephus* could be found. (3) Descriptions of *Machadocephus longus* by Balogh in 1962; Balogh and Mahunka's description of the new genus *Tuberocephus* (1969); and descriptions in Mahunka's revision of Carabodidae (1986) are all different and the drawings are of little value.

Within this series of limitations, the original description by Mahunka (1986) was considered to contain sufficient elements to make a comparison: The newly established genus *Mangabebodes* differs from *Tuberocephus* in terms of: elevated interlamellar process without anterior expansion; presence of posterior prodorsal depression. Anterior dorsal notogastral depression and posterior dorsal notogastral depression present, between them an elevated zone with different distributions of promontories. Tutorium large, long, spoon-shaped, larger or of equal size to pedotectum I.

Characters in common with *Tuberocephus*: 12 pairs of notogastral setae and elevated notogastral central area.

Genus *Antongilibodes* presents a series of characters dissimilar to *Tuberocephus* such as anterior dorsal notogastral depression and posterior dorsal notogastral depression present; elevated central notogastral zone with central anterior unpaired elevation; paired medial elevations and faintly demarcated posterior medial elevations. Fifteen pairs of setae,  $c_1$ ,  $c_2$ ,  $c_3$  anterior notogastral depression;  $da$ ,  $dm$ ,  $dp$ ,  $la$ ,  $lm$ ,  $lp$ ,  $h_2$  central region;  $p_1$ ,  $p_2$ ,  $p_3$ ,  $h_1$ ,  $h_3$  marginally. Tutorium, pedotectum I; pedotectum II and discidium present, normal.

*Characters in common*: Elevated interlamellar process ending in a pair of elevated external elevations. Elevated central notogastral area.

We have to take into consideration that in 1962 Balogh found 10 pairs of notogastral setae, in 1969 Balogh and Mahunka described 10 pairs, and finally in 1986 Mahunka amended this to 12 pairs.

From our studies, it is evident that a small tilt in angle (Figures 22, 23, 53, 57) can completely change observation, and despite having used SEM and optical microscopy, dissection is vital in order to study and understand many structures. We still have doubts despite the use of all these, however we are confident that drawings and photos are accurate. The inaccuracy of the original description of *Tuberocephus* in terms of ambiguous illustrations, as well as enormous deviations produced by the same authors without displaying drawings or photos, make it necessary to consider the genus *Tuberocephus* hard to determine. Hopefully new research will change our opinion, we hope that we will be able to reveal our own errors and always remain open to critical opinion. We continue the search for *Tuberocephus* in the collection at the M.N.H.N.

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