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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)

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ABSTRACT

Bovicarabodes jacquelinae **sp. nov**. is easily differentiated from other congeners by paired rounded to ovate prodorsal cavity with internal ovoid incision; presence of medial eye pillar; two cuticular ridges anterior to interlamellar setae; and incomplete bothridial ring with bothridial tooth. Notogastral anterior depression ovoid, with two posterior semicircular zones delimited by prominent furrow; notogastral anterior depression extending to beyond c_2 and *da* setae. Tutorium a strongly curving cuticular thickening; humeral apophysis elongate; small triangular discidium. Genital opening smaller than anal opening; aggenital and ad_3 setae in close proximity. *B. jacquelinae* is similar to *B. deharvengi*, differentiated principally by shape and position of elevated interlamellar process; position of interlamellar setal insertion; notogastral anterior depression; and shape of humeral process. *Tuberocepheus longus* (Balogh, 1962) is redescribed, with clarification being obtained by the use of optical and scanning electron microscopy. The genus is characterized by the combination of the following characters: Prodorsum divided into two ear-like processes; shallow lamellar furrow not clearly delimited; smooth narrow bothridial ring; bothridial tooth a finger-like projection; and conspicuous polyhedral posterior prodorsal depression. Notogaster 12 pairs of setae; seta *c* absent; medium-sized elevated zone situated between notogastral anterior depression and notogastral posterior depression; two pairs lateral paired elevations; three pairs central paired elevations; pedotectum I larger than tutorium. Epimeres poorly delimited; anterior genital furrow simple, lacking lateral depression; well-developed depression surrounding genital opening; depressions surrounding genital opening and anterior genital furrow connected by a narrow channel; anal opening larger than genital opening.

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Introduction

The genus *Bovicarabodes*, comprising three species, was established by Fernandez et al. (2013a) with *Bovicarabodes deharvenghi* as type. All species were collected in Madagascar. We have now included a fourth species, which was discovered while looking for *Tuberocepheus longus* (Balogh, 1962) in the collection of the MNHN (Museum National d'Histoire Naturelles, Paris). The new species presents all characteristics of the genus, but also includes a series of elements allowing easy differentiation from other members of the genus (*Bovicarabodes deharvenghi, Bovicarabodes levyi* and *Bovicarabodes fortdauphini*). After many decades of being preserved in 70% ethanol, specimens were difficult to study and too fragile to successfully support critical point drying in preparation for scanning electron microscopy (SEM). Studies were therefore carried out using optical microscopy only.

In a previous study (Fernandez et al. 2014), some of the problematic aspects of *T. longus* (Balogh, 1962) were briefly outlined. This species was initially described as *Machadocepheus longus* Balogh, 1962 and was subsequently designated type species of *Tuberocepheus* Balogh & Mahunka, 1969 (see "Discussion").

Over a period of time, several genera of the family Carabodidae (Fernandez et al. 2013a, 2013b, 2013c, 2013d, 2014) were reviewed, but *Tuberocepheus* material from the Hungarian Natural History Museum (HNHM) was unobtainable, delaying further work on this genus for several years. Over 1000 samples from the Betsch collection from Madagascar, deposited in the MNHN, Paris, France, were analysed over a period of 7 years, and recently significant quantities of *Tuberocepheus* specimens were obtained. We were therefore able to commence studies with SEM and optical microscopy.

Materials and methods

Specimens studied by optical microscopy were macerated in lactic acid and observed in the same medium using the open-mount technique (cavity slide and cover slip) described by Grandjean (1949) and Krantz and Walter (2009). Drawings were made using a Zeiss Axio Scope compound microscope (Carl Zeiss Microscopy GmbH, Jena, Germany) equipped with a drawing tube.

Specimens studied with SEM, preserved in ethanol, were carefully rinsed by sucking into a Pasteur pipette several times, and transferred to buffered glutaraldehyde (2.5%) in Sörensen phosphate buffer (pH 7.4; 0.1 m) for 2 hours. After 2 hours of postfixation in buffered 2% OsO_4 solution and being rinsed in buffer solution, specimens were dehydrated

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in a series of graded ethanol, dried in a critical point apparatus, and mounted on Al-stubs with double sided sticky tape, then gold coated in a sputter apparatus (Alberti and Fernandez 1988).

SEM observations were complicated by limited specimen numbers and anatomic particularities. Two different types of SEM were used in order to obtain observations of adequate quality: (1) Tescan Vega II LSU (Tescan Orsay Holdings, Kohoutovice, Czech Republic) (Direction of Collections-SEM-EDS-MNHN) and (2) Hitachi SU3500 (Hitachi High-Technologies Europe, Krefeld, Germany) (Plateau technique de Microscopie Electronique et de Microanalyse (PMEM) (MNHN) using accelerating voltage of 15 and 10 kV, respectively. The critical point apparatus used was an Emitech K 850 (Quorum Technologies Ltd., Ashford, Kent, UK) and the sputter a Jeol JFC-1200 (Jeol Ltd. Tokyo, Japan) (metalized 80″).

Measurements taken: total length (tip of rostrum to posterior edge of notogaster) and total width (widest part of notogaster) in micrometres (µm).

Leg chaetotaxy studies executed with the aid of standard, polarized and phase contrast microscopes are provisional, due to the fact that only adult specimens were available for study. Setal formulae of the legs include the number of solenidia (in parentheses); tarsal setal formulae include the famulus (ε).

New taxon description

Bovicarabodes jacquelinae sp. nov.

(Figures 1–5; Table 1)

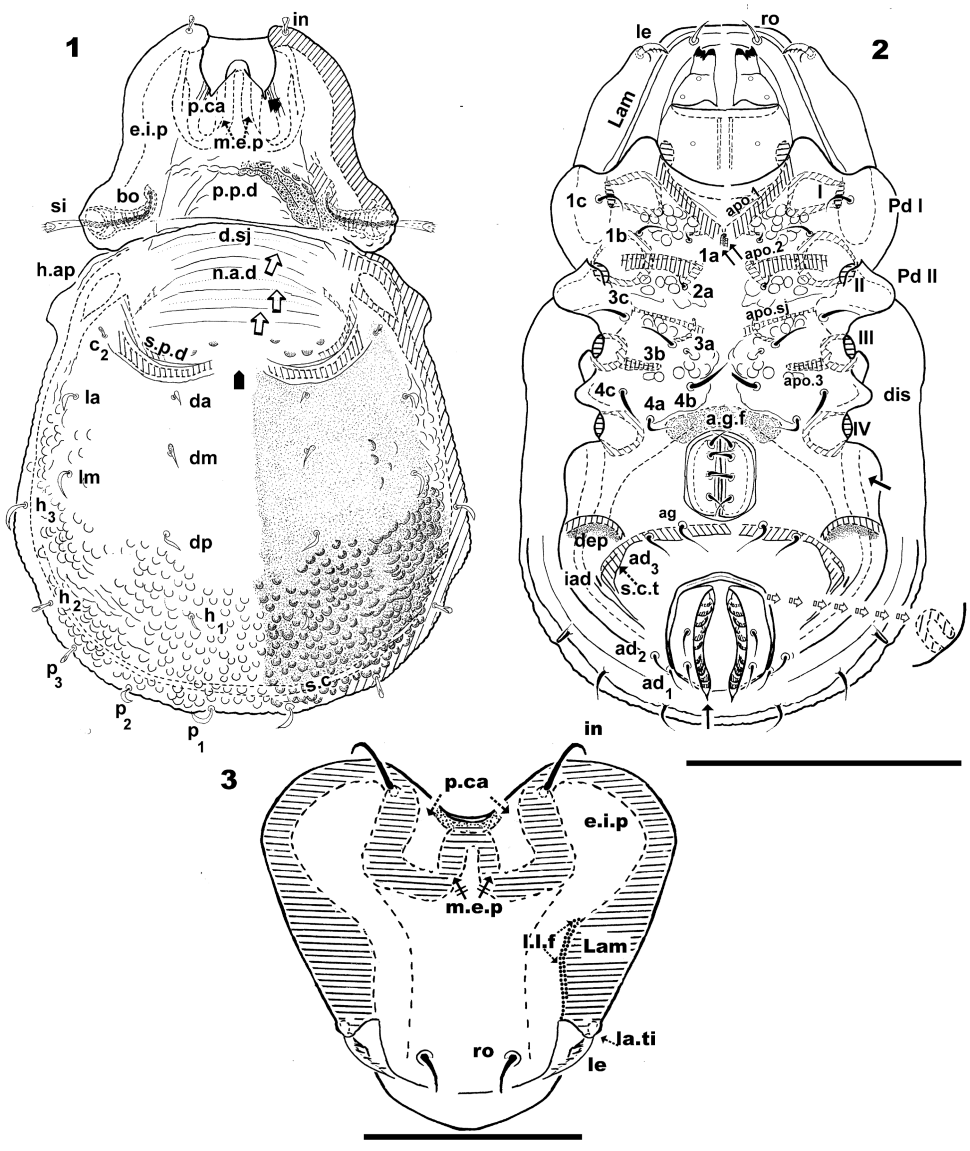
Morphology

Morphological terminology. Morphological terms and abbreviations used are those developed by Grandjean (1928–1974) in Travé and Vachon (1975) and Norton and Behan-Pelletier (2009).

Over the years, many different terms were used with reference to similar structures when describing genera and species in the family Carabodidae. We proposed generalized terminologies (Fernandez et al. 2013a, 2013b, 2013c, 2014) in order to be able to more easily compare genera and species within the family.

Institutions. MNHN Muséum National d'Histoire Naturelle, Paris, France; MHNG Muséum d'Histoire Naturelles, Genève.

Etymology. The specific epithet is dedicated in posthumous homage to Professor Dr Jacqueline Heurtault, Laboratoire des Arthropodes, Muséum National d'Histoire Naturelles, Paris, France.



Figures 1–3. *Bovicarabodes jacquelinae* **sp. nov.** Adult female. 1. dorsal view; 2. ventral view; 3. frontal view. Abbreviations: see "Materials and methods". Scale bars: 1–2 = 260 µm; 3 = 80 µm.

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 MNHN., preserved in 70% ethanol.

Diagnosis. **Integument**: Prodorsal microsculpture: *punticulate*: prodorsal posterior depression and near bothridium; *smooth*: lamellae, rostrum, horns paraxial borders, interlamellar teeth, medial eye pillar, bothridial ring. Notogastral microsculpture: *slightly tuberculate*: notogastral anterior depression; *tuberculate*: notogaster. Ventral zone: tuberculate. **Setation**: *simple*: rostral, interlamellar, subcapitular, epimeral, genital, aggenital, anal, adanal; *short lanceolate*: notogastral; *lanceolate barbate*: lamellar. **Prodorsum**: paired prodorsal cavity, rounded-ovate, with internal ovoid incision; medial eye pillar present; interlamellar setae directing posteriorly, situated on elevated interlamellar process; lamellae large; shallow lamellar furrow, hardly discernible; lamellar tip rounded; two cuticular ridges anterior to interlamellar setae; bothridia cup-shaped, smooth, incomplete bothridial ring with bothridial tooth. Sensillus uncinate. Prodorsal posterior depression clearly delimited laterally by cuticular thickenings. **Notogaster**: Posterior zone semicircular, anterior zone polyhedral; dorsosejugal furrow curving, clearly delimited; circumgastric depression present. **Lateral region**: Tutorium, strongly curving cuticular thickening; tutorial margin foveolate. Discidium: small triangular protuberance. **Ventral region:** Epimera slightly elevated; small depression at level of apodeme 1; *1a, 2a, 3a* setae small; anterior genital furrow present. Laterally to IV acetabulum extending to near anal opening, sigmoid cuticular thickening; genital plate smaller than anal plate; aggenital setae posterior to genital opening; aggenital and ad_3 setae close to *ag*; semicircular cuticular thickening situated posterior and close to genital opening; adanal setae ad_1, ad_2 immediately behind anal opening; ad_3 some distance away; anal plate: anterior lateral ovoid internal depression; posterior zone terminating in sharp tip.

Description

Measurements. Length 642 µm; width 312 µm. Female.

Shape: ovoid (Figure 1).

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

Cerotegument: Consistently thin layer, partially covering body and legs (removed for study).

Integument: Microsculpture complicated, varying according to body region.

Prodorsal microsculpture: *punticulate*: prodorsal posterior depression (*p.p.d*) zone, near bothridium (*bo*) (Figure 1); *smooth*: lamellae, rostrum, paraxial borders of horns, interlamellar teeth (Figure 1, indicated by ➧), surrounding prodorsal cavity (*p.ca*), medial eye pillar (*m.e.p*), bothridial ring (*bo.ri*) (Figure 4).

Notogastral microsculpture: *slightly tuberculate*: notogastral anterior depression (*n.a.d*), near furrow posterior notogastral anterior depression (*s.p.d*), rest of notogaster and epimeric zone, *tuberculate* (Figures 1, 2).

Setation. Simple: ***ro, in, subcapitular, epimeral, genital, aggenital, anal, adanal***; short lanceolate: ***notogastral***; lanceolate barbate: ***le***.

Prodorsum. Elevated interlamellar process (*e.i.p*) divided into two separate horn-shaped apically rounded processes, extending forward and upwards over rostral margin (Figure 1). In lateral view, large apically rounded protuberance (Figure 4). Paired *p.ca* situated on either side of medial eye pillar (*m.e.p); p.ca* rounded-ovate, clearly visible, separated by *m.e.p* (Figures 1, 3). Internal posterior edge of *p.ca* with ovoid incision (Figure 1, indicated by ➧). Setae *in* directed posteriorly, inserted apically and slightly recessed from tip of *e.i.p* (Figures 1, 3). Prodorsum descends obliquely to rostral margin; large laterodorsal lamellae with hardly discernible shallow lamellar furrow (*l.l.f.*), only visible when observed at an angle (Figures 3, indicated by dots); *la.ti* with apically rounded tip (Figure 3). Two cuticular ridges (Figure 4, indicated by ▼) on anterior zone of horn-shaped processes, anterior and close to *in* setae; rounded rostrum (Figure 3); *ro* setae curving anteriorly (Figure 3); *le* setae inserted on lamellar apex (Figure 3). Bothridia cup-shaped with smooth, incomplete *bo.ri* and bothridial tooth (*bo.to*) (Figure 4). Sensillus uncinate, arching upwards, tips usually pointed (Figure 1).

Posterior prodorsal zone: anterior to dorso-sejugal furrow (*d.sj*), prodorsal posterior depression (*p.p.d*) clearly laterally delimited by cuticular thickenings (Figure 1).

Notogaster. Shape: posterior zone semicircular; anterior zone polyhedral; well-delimited curving dorsosejugal furrow (Figure 1). Anterior notogastral depression (*n.a.d*) ovoid and conspicuous. Posterior area with two semicircular zones formed by cuticular thickening, delimited anteriorly by prominent furrow (*s.p.d*), situated on posterior zone of notogastral anterior depression; central area of *n.a.d* lacking semicircular structure (Figure 1, indicated by ➨)

Circumgastric depression (*s.c*) present (Figure 1), easily discernible on posterior part. Twelve pairs of setae (c_2, *da, dm, dp, la, lm,* h_1, h_2, h_3, p_1, p_2, p_3). Opisthonotal gland *gla* and lyrifissures (*im, ih, ips, ip*) in normal position (Figures 4, 5).

Lateral region. Tutorium (*Tu*) clearly visible as strongly curving cuticular thickening (Figure 4). Cuticle of tutorial margin foveolate. Deep cuticular depression (supra-tutorial depression) (*s.tu.d*) between *Lam* and *Tu*, parallel to both structures (Figure 4).

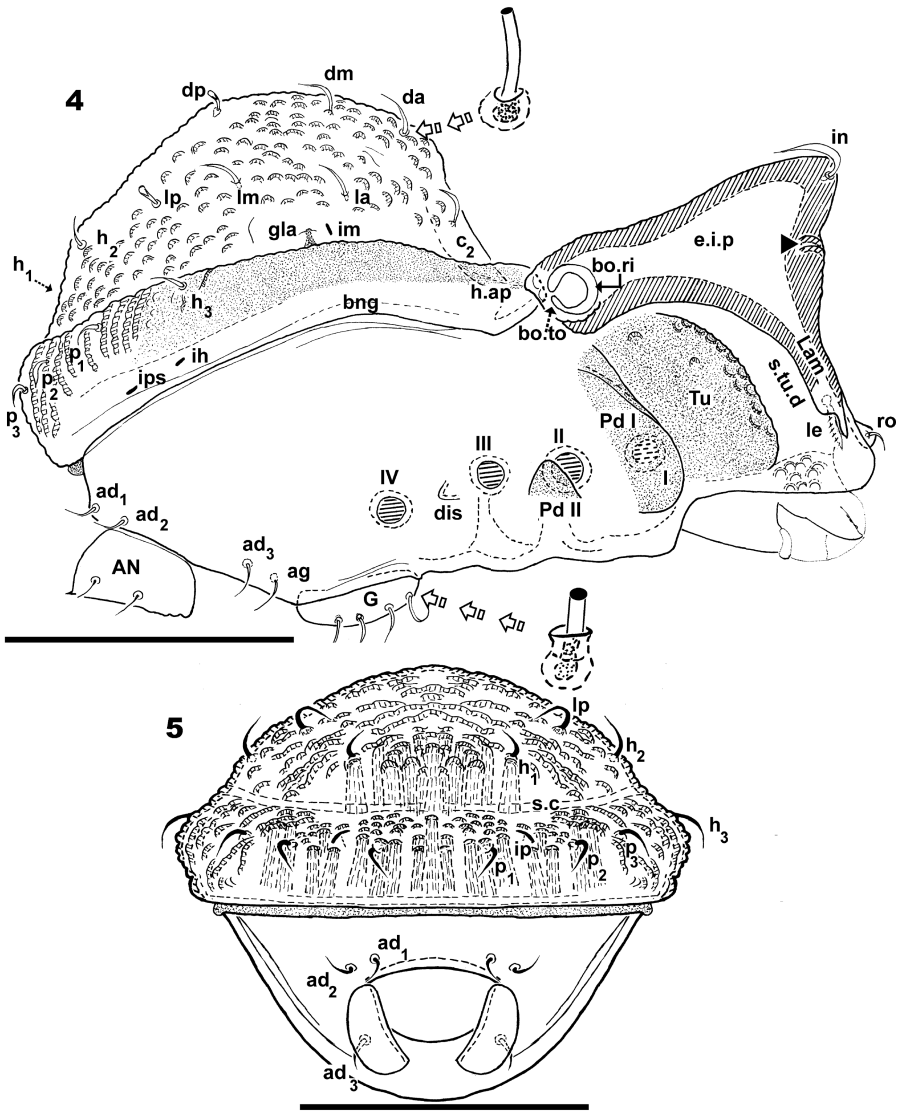
Pedotectum I (*Pd I*), prominent extended area, rounded end, covering first acetabulum (Figure 4); pedotectum II (*Pd II*), small rounded lamina (Figure 4). Three pairs of lyrifissures, *im, ih, ips*. Posterior to lyrifissures *im, gla* observed. Humeral apophysis (*h.ap*) elongate, tip extending to posterior bothridial zone (Figure 4); upper margin linear; inferior margin ovoid, both directing upwards. Discidium (*dis*) small, triangular protuberance. Polyhedral cavities hardly discernible.

Ventral region (Figure 2). Epimera slightly elevated, delimited by shallow furrow (*bo.1, bo. 2, bo.sj*); epimere 4 fused; *apo.1, apo.2, apo.sj* and *apo.3* clearly discernible. Small depression (Figure 2, indicated by ⇈) on central zone at *apo.1* level.

Epimeral chaetotaxy 3-1-3-3; *1a, 2a, 3a* setae small relative to other epimeral setae. *Pd I, Pd II* and *dis* well discernible. Anterior genital furrow (*a.g.f*) present.

Sigmoid cuticular thickening originating laterally to acetabulum IV, extending to near anal opening (Figure 2, indicated by ↗).

Genital plate ovoid; small compared to anal plate; four pairs of genital setae; all setae more or less of equal size. Aggenital setae situated posteriorly to genital opening, close to medial zone; *ag* and ad_3 setae inserted close and ad_3 setae inserted slightly posterior to *ag* insertion level; semicircular cuticular thickening (*s.c.t*) situated posteriorly close to genital opening (Figure 2, indicated by ⇡). Rounded depression anterolaterally to *s.c.t*. Three pairs of adanal setae; ad_1, ad_2 close to each other, situated at level of posterior zone of anal plate; ad_3 distanced from other adanal setae. Anal plate: anterolateral zone with ovoid internal depression (detail indicated on Figure 2); posterior zone terminating in sharp tip (Figure 2, indicated by ↗). Two pairs of anal setae.



Figures 4–5. *Bovicarabodes jacquelinae* **sp. nov**. Adult female. 4. lateral view; 5. posterior view. Abbreviations: see "Materials and methods". Scale bars: 4 = 220 µm; 5 = 80 µm.

Table 1. *Bovicarabodes jacquelinae* **sp. nov.**, setae and solenidia.

Leg I	Femur	Genu	Tibia	Tarsus	Claw
Setae	*(l),v*	*(l),v*	*(l),v,d*	*(it),(tc),(ft),(u),(p),s,ε*	1
Solenidia		*σ*	φ_1, φ_2	ω_1, ω_2	
Leg II					
Setae	*(l),d,v*	*(l),v*	*d,l",v*	*(it),(tc),(ft),(p),(u)(a),s,(pv)*	1
Solenidia		*σ*	*φ*	ω_1 ω_2	
Leg III					
Setae	*l',v,d*	*l'*	*l",v*	*(it),(tc),ft",(p),(u)(a),s,(pv)*	1
Solenidia		*σ*	*φ*	*0*	
Leg IV					
Setae	*d,v*	*d,l'*	*l",v*	*(it),ft",(p),(u),(a),s,(pv)*	1
Solenidia		0	*φ*	0	

Lyrifissure *iad* easily discernible, situated posterolaterally to ad_3 setae and laterally to *s.c.t*.

Posterior aspect (Figure 5, Table 1). Circumgastric depression (*s.c*) clearly visible, located in front of p_1, p_2, p_3, h_3. Setal zone of h_1, p_1, p_2 with well-discernible muscular insertions. On posterior zone, tubercles and cuticular ridges are mixed; *ip*, lyrifissure situated between p_1 and p_2 setae.

Legs. Similar characteristics to *B. deharvengi* (Fernandez et al. 2013a).

Genus *Tuberocepheus* Balogh & Mahunka, 1969

In 1969 J. Balogh and S. Mahunka established the genus *Tuberocepheus* (Balogh and Mahunka 1969, p. 9), with *Machadocepheus longus* Balogh, 1962 designated as type species.

Redescription

Diagnosis: adult

Prodorsum. Elevated interlamellar process, divided in two ear-shaped structures by flat zone; posterior prodorsal depression well delimited, with interlamellar setae situated inside. Shallow lamellar furrow not clearly delimited; bothridial ring smooth, narrow; bothridial tooth, finger-like projection. *Notogaster*. Notogastral anterior depression conspicuous, polyhedral; posterior notogastral depression present, between depressions, elevated zone with lateral and central elevations. Lateral elevation with two pairs of promontories; central elevations with three pairs of promontories. Twelve pairs of setae; setae absent from notogastral anterior depression; four pairs situated on lateral elevations, two pairs on each promontory; three pairs on central elevations, a pair on each promontory; five pairs situated on postero-marginal zone. *Lateral region*. **Tutorium normal** (*Pd I* > *Tu*, see Table 3). Pedotectum I large blade; pedotectum larger than tutorium. *Ventral region*. Epimeric borders poorly delimited; central longitudinal zone depressed. Epimeric setae: 3-1-3-3.

Anterior genital furrow clearly visible, only one semicircular depression, without lateral depression; depression around genital opening well developed; communication between anterior genital furrow and lateral genital opening, by means of a narrow channel. Anal plate large in comparison to genital plate.

Type species: *Tuberocepheus longus* (Balogh, 1962), Madagascar.

Type species

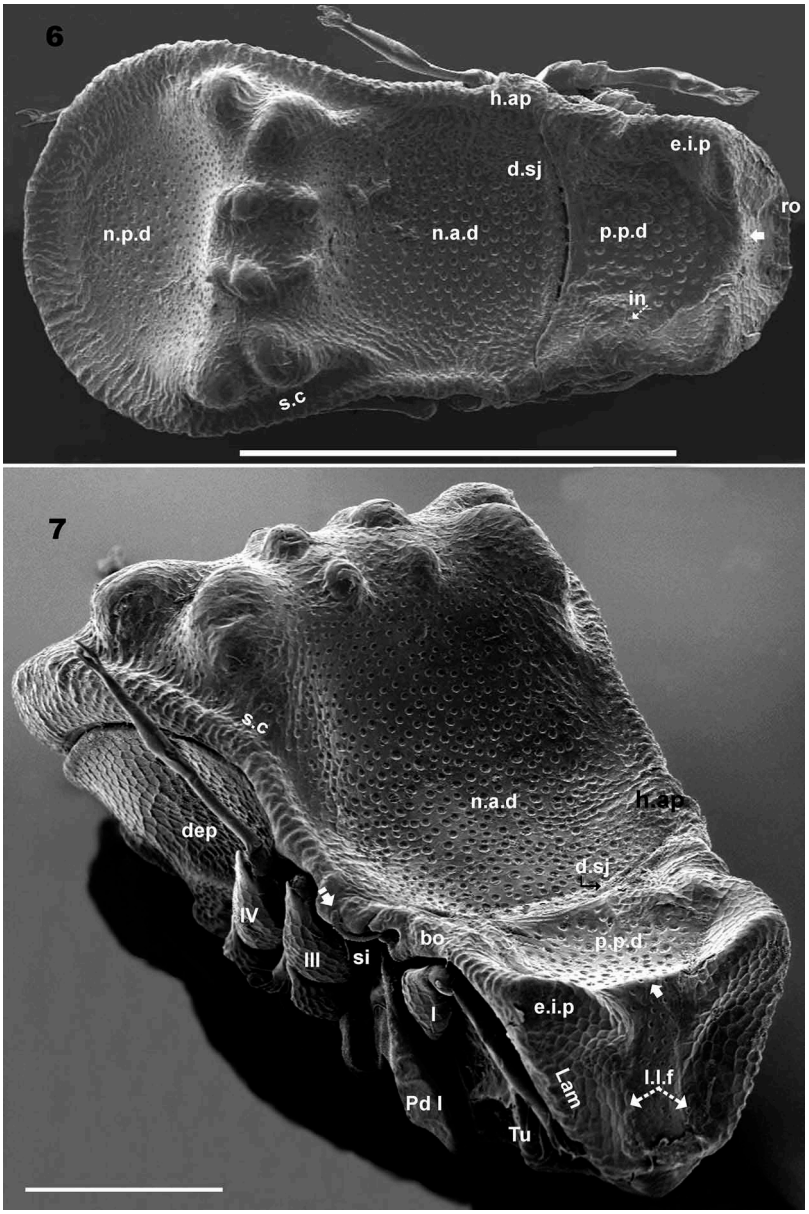
Tuberocepheus longus (Balogh, 1962)
(Figures 6–32; Table 2)

Table 2. *Tuberocepheus longus* (Balogh, 1962), setae and solenidia.

	Femur	Genu	Tibia	Tarsi	Claw
Leg I					
Seta	*da,dp,l",v*	*l",v*	*d,(l),v*	*(p),(it),(tc),(ft),(u),(a),s,(pv),ε*	1
Solenidia		σ	φ_1,φ_2	ω_1, ω_2	
Leg II					
Seta	*da,dp,l",v*	*l",v*	*d,l",v*	*(p),(it),(tc),(ft),(u),(a),s,(pv),pl"*	1
Solenidia		σ	φ	ω_1, ω_2	
Leg III					
Seta	*d,l',v*	*l'*	*l',v*	*(it),(tc),ft',(p),(u),(a),s,(pv)*	1
Solenidia		σ	φ	0	
Leg IV					
Seta	*d,v*	*d,l'*	*l",v*	*(p),(it),ft',(u),(a),s,(pv)*	1
Solenidia		0	φ	0	

Diagnosis

Redescription. **Microsculpture**. *Foveate*: posterior prodorsal depression; zone between shallow lamellar furrow; anterior notogastral depression; zone between central and lateral notogastral promontories; notogastral posterior depression. *Reticulate-foveate*: antiaxial prodorsal zone; bothridium posterior dorsal zone. *Polyhedral-foveate network*: prodorsum, elevated interlamellar process zone; between lamellar border and shallow lamellar furrow; tutorium; pedotectum I; femurs I, II; trochanter, femurs III, IV, ventral depressions. *Erased reticulate-foveate* (microsculpture flattened giving an impression of being partly erased): epimeric zone; subcapitulum near *h* setae. *Smooth*: bothridial ring; bothridial tooth; subcapitulum, zone *a, m* setae. *Smooth-rough* (flat microsculpture with appearance of a smoothed but poorly finished wall): elevated zones of notogastral promontories near *da, dm, dp, la, lm, lp,* h_1. *Reticulate-foveate with cuticular thickenings*



Figures 6–7. *Tuberocepheus longus* (Balogh, 1962). Adult female. 6. dorsal view; 7. anterolateral view. Abbreviations: see "Materials and methods". Scale bars: 6 = 400 µm; 7 = 200 µm.

(reticulate-foveate mixed with ribbon-like rectilinear or irregular cuticular thickenings): posterior notogastral margin; near circumgastric furrow on both sides. ***Setation*** (legs not included). *Simple*: rostral, interlamellar, notogastral, subcapitular *h*, epimeral, genital, aggenital, anal, adanal. *Lanceolate-pectinate*: lamellar. ***Prodorsum***. Complex elevated interlamellar process with depressed central area; *in* setae situated anterior to bothridial level and marginally to prodorsal posterior depression; rostral margin rounded; *ro* setae curving; relatively flat zone between shallow lamellar furrows. ***Notogaster***. Humeral apophysis polyhedral; dorsosejugal furrow convex; anterior notogastral depression ovoid, large, extending from dorsosejugal furrow to the starting point of elevations; first marginal notogastral seta (h_3) at level of *lp* and h_1 setae; two pairs of lyrifissures *ih, ips* visible: circumgastric furrow clearly discernible. ***Lateral region***. lamellar setae barbate, hardly discernible, concealed by lamellae. Supra tutorial depression deep, with posterior pocket depressions.

Bothridial opening incomplete, with conspicuous posterior indentations. Bothridial ring tilting towards bothridial opening; a series of fine parallel alignments near bothridial tooth; *Pd I* prominent extended lamina, rounded apex; *Pd II* medium-sized, more or less triangular, anterior part convex and posterior part concave. Lyrifissures *ih, ips*; ovoid projection posterior to IV acetabulum; aggenital setae posterior to genital opening; Large ovoid depressions behind legs IV, extending posteriorly between genital and anal opening; two other elongated ovoid depressions, parallel, slightly inclined to anal plate; anal plate terminating in sharp tip. ***Ventral region.*** Conspicuous longitudinal medial epimeral depression with central ovoid depressions. Apodemes: *apo.1, apo.2, apo.dj, apo.3* clearly visible, epimeral borders hardly discernible. Epimeral setae *1a* and *3a* small; *2a* medium-sized; genital opening surrounded by narrow elevated zone. Depressions: semicircular anterior genital furrow; polyhedral depressions laterally on either side of genital opening; spur (cuticular expansion) forming contact zone between polyhedral depression and anterior genital furrow, delineating a narrow channel; between genital and anal opening, large paired ovoid to polyhedral depressions. Lateral to anal opening, large paired ovoid depression. Genital plate: rectangular, rounded corners. Anal plate trapezoidal, terminating in short sharp tip. One pair of aggenital setae laterally to rounded depressions, far from ad_3 setae; three pairs adanal setae.

Material examined. **Holotype**: ♀ Female "Mad, 220. Madagascar. Forêt d'Ambalamarovandana – FDHMA (Forêt dense humide moyenne altitude). 1550 m altitude. 24,1,1971. Litiere et Berlese. Coll. J.M. Betsch" deposited in the Collection of the Muséum National d'Histoire Naturelle, Paris, France, preserved in 70% ethanol. **Paratypes**: four females. Same data as Holotype; two deposited in MNHN; two in MNHG. Two other specimens, female, observed under SEM, not deposited; all specimens preserved in 70% ethanol.

Type locality: Forêt d'Ambalamarovandana. Material used for SEM observations not deposited.

Description

Measurements. SEM: 695 µm (693–831) × 421 µm (375–460). Light microscopy: 714 µm (709–842) × 442 µm (386–472), measurements of specimens deposited in MNHN and MHNG; all specimens female.

Shape. Elongate oval (e.g. Figure 6).

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

Cerotegument. Consistently thick layer (3–5 µm), covering body and legs, following cuticular irregularities. Observation not impeded (Figure 28, indicated by ⇧).

Integument

Microsculpture complicated, varying according to body region. *Foveate*: very clearly delimited round-ovoid fovea, internally pocket-shaped (Figures 13, 18): posterior prodorsal depression (*p.p.d*) (Figures 10, 11, 20), zone between shallow lamellar furrow (*l.l.f*) (Figures 6, 7, 14, 15), anterior notogastral depression (*n.a.d*) (Figures 6, 7, 10, 11, 17), zone between central and lateral notogastral promontories (Figures 6, 7, 11, 17, 18, 20, 21), notogastral posterior depression (*n.p.d*) (Figures 6, 7, 10, 11, 17, 18, 19, 20, 21). *Reticulate-foveate*: fovea not clearly delimited, polyhedral, surrounded by cuticular thickening (Figures 7, 11, 12, 14, 24): antiaxial prodorsal zone, bothridium (*bo*) posterior dorsal zone, notogaster near *s.c. Polyhedral-foveate network* (Figures 14, 15, indicated by ⇪): prodorsum, elevated interlamellar process (*e.i.p*) zone, between lamellar border and *l.l.f* (Figures 6, 7, 14, 15), tutorium (*Tu*), pedotectum I (*Pd I*), femurs I, II, trochanter, femurs III, IV, ventral depressions (*dep*) (Figures 8, 11, 14, 16). *Erased reticulate-foveate*: microsculpture is flattened giving an impression of being partly erased: epimeric zone, subcapitulum near zone *h* setae (Figure 25). *Smooth*: bothridial ring, bothridial tooth, subcapitulum, zone *a, m* setae (Figures 12, 24, 28). *Smooth-rough*: flat microsculpture with appearance of a smoothed but poorly finished wall: elevated zones of notogastral promontories near setal insertions *da, dm, dp, la, lm, lp,* h_1 (Figures 11, 17, 18, 20, 21, 25). *Reticulate-foveate with cuticular thickenings*, reticulate-foveate mixed with ribbon-like rectilinear or irregular cuticular thickenings: posterior notogastral margin posterior to *h.ap*, from near circumgastric furrow (*s.c)* (both sides) up to notogastral margin (*b.ng*) (Figures 7, 8, 11, 16, 17, 19, 20).

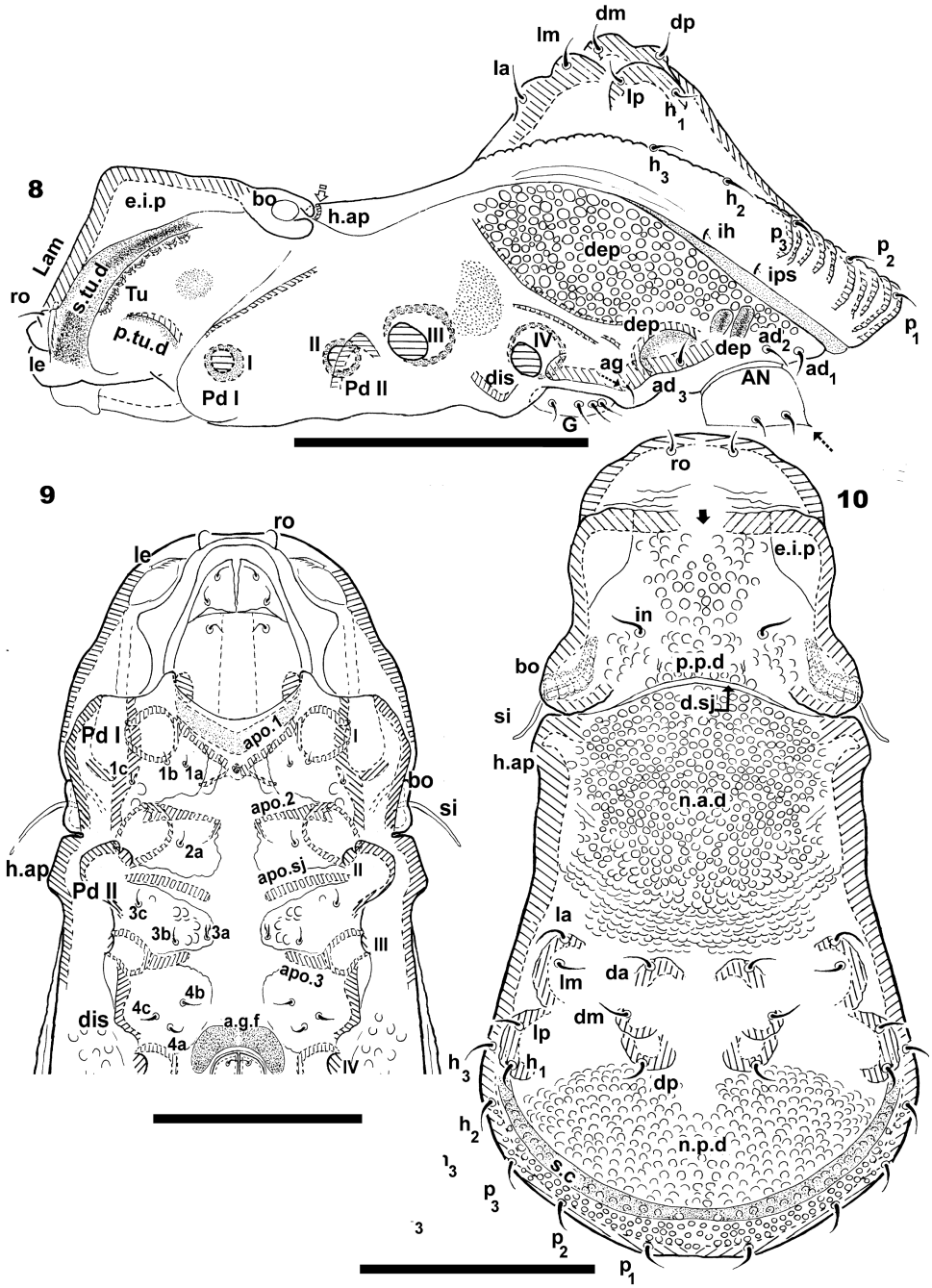
Setation (legs not included). *Simple*: rostral, interlamellar, notogastral, subcapitular *h*, epimeral, genital, aggenital, anal, adanal; length: (measurements taken on six specimens under SEM) *ro* = 10 µm (8–12); *in* = 30.5 µm (23–34); *da, dm, dp, la, lm, lp,* h_1 = 12 µm (10–17); h_2, h_3, p_1, p_2,p_3 = 6 µm (8–14); subcapitular *h* = 21 µm (18–23); *a* = 9 µm (7–13), *m* = 4 µm (3–8); *g* 17(19–22); *epimeral* = 10 µm (9–14) (except *1a, 2a, 3a* tiny); *ag* = 20 µm (18–21); *an* = 9 µm (8–11); ad_1, ad_2 = 17 µm (15–18), ad_3 = 20 µm (17–21). *Lanceolate-pectinate*: lamellar; length *le* = 35 µm (34–38) Measurements of setae are to be considered provisional as, though preservation was good, these mites were preserved in alcohol for over 35 years and possible damage to setal tips cannot be easily ascertained (though optical observations can assist in assessment).

Prodorsum

Posterior to elevated interlamellar processes (*e.i.p*) and between them and dorsosejugal furrow (*d.sj*), conspicuous polyhedral prodorsal posterior depression (*p.p.d*) (Figures 6, 7, 10, 11, 14, 15, 20); *e.i.p* complex, with depressed central area (Figures 6, 7, 10 and 20 indicated by ⬑, Figures 11, 14, 15) defining two ear-like structures. Observations from various angles aid understanding of this structure. Setae *in* situated anteriorly to bothridial level (Figures 6, 10, 11) and marginally to *p.p.d*. Rostral margin rounded (Figures 14, 15); *ro* setae curving (Figures 14, 15). Lamellae (*Lam*) developed dorsolaterally; two shallow furrows on prodorsum (*l.l.f*) (Figures 14, 15), between them a well-defined, more or less flat zone with different cuticular microsculpture (Figures 14, 15).

Notogaster

Shape: zone behind *h.ap* and starting point of promontories, rectangular; posterior to starting point of promontories ovoid; *h. ap*. polyhedral. Semicircular depression (Figure 8, indicated by ⇪). Dorsosejugal furrow (*d.sj*) well delimited by large convex line.



Figures 8–10. *Tuberocepheus longus* (Balogh, 1962). Adult female. 8. lateral view; 9. ventral view; 10. dorsal view. Abbreviations: see "Materials and methods". Scale bars: 8 = 240 µm; 9 = 100 µm; 10 = 80 µm.

Anterior notogastral depression (*n.a.d*) ovoid, large, extending from *d.sj* posteriorly to more or less half the total notogastral length, to starting point of elevations.

Posterior notogastral depression (*n.p.d*) large, conspicuous crescent shape (Figures 6, 10, 11, 19, 20).

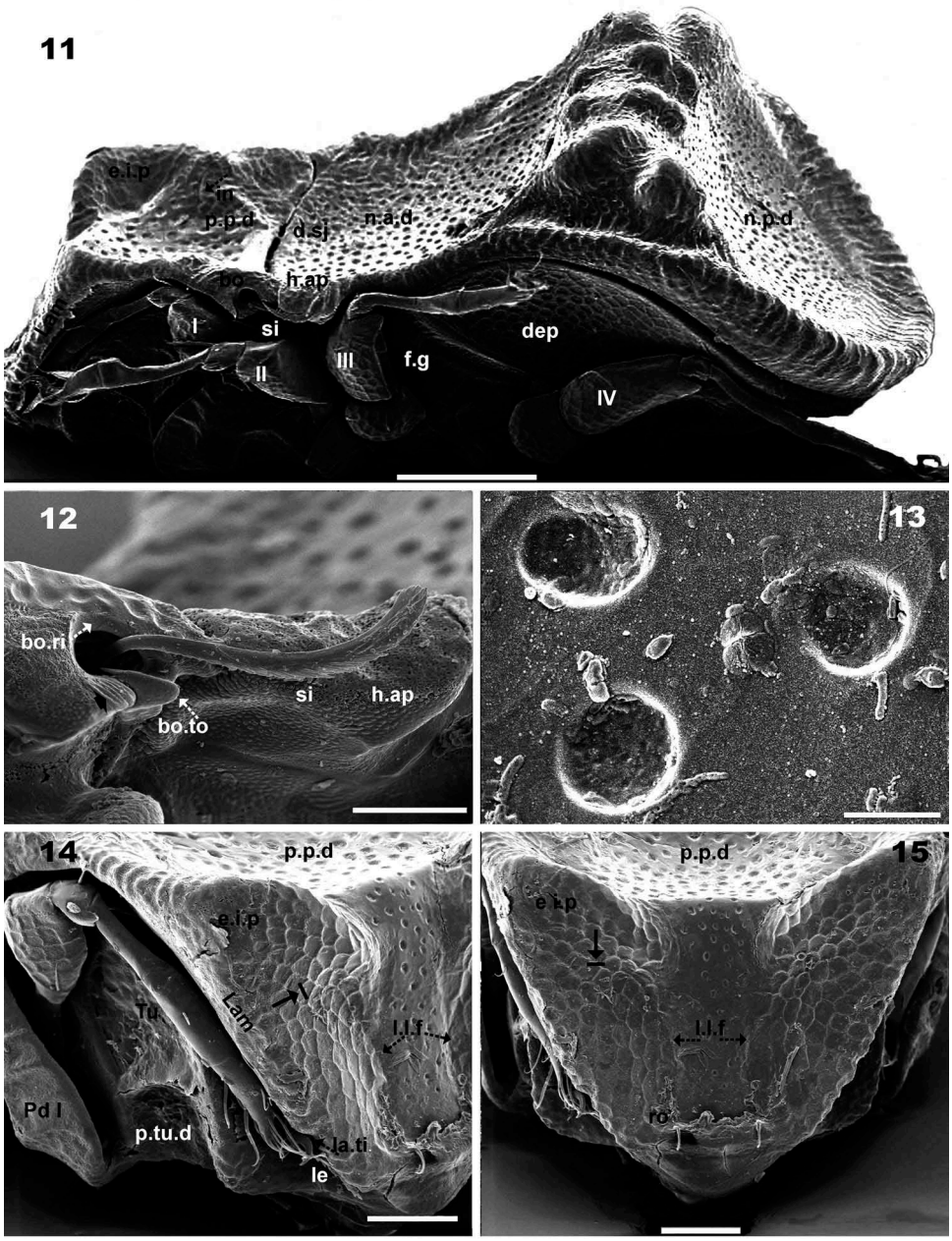
Elevated zone between *n.a.d* and *n.p.d* with both lateral and central paired elevations. Central paired elevations (Figures 6, 7, indicated by white arrows, Figures 17, 20); with three dorsal promontories containing *da, dm, dp* setae; a setae on each. Lateral paired elevations with two dorsal promontories (Figures 6, 7, indicated by black arrows, Figures 11, 17, 20), bearing *la, lm, lp, h_1* setae, two setae per promontory (*la, lm* on the first and *lp, h_1* on the second) (Figures 10, 17). In all cases, setae are not situated on the top of promontories (Figures 17, 21). Twelve pairs of notogastral setae, 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 10). No setae in *n.a.d*. The first marginal notogastral seta (h_3) occurs between the level of *lp* and h_1 setae (Figure 10). Two pairs of lyrifissures visible, *ih* and *ips* (Figure 8). The *s.c* is easily discernible from the vicinity of *h.ap* as a conspicuous furrow (Figures 6, 7, 11, 19, 20).

Lateral region

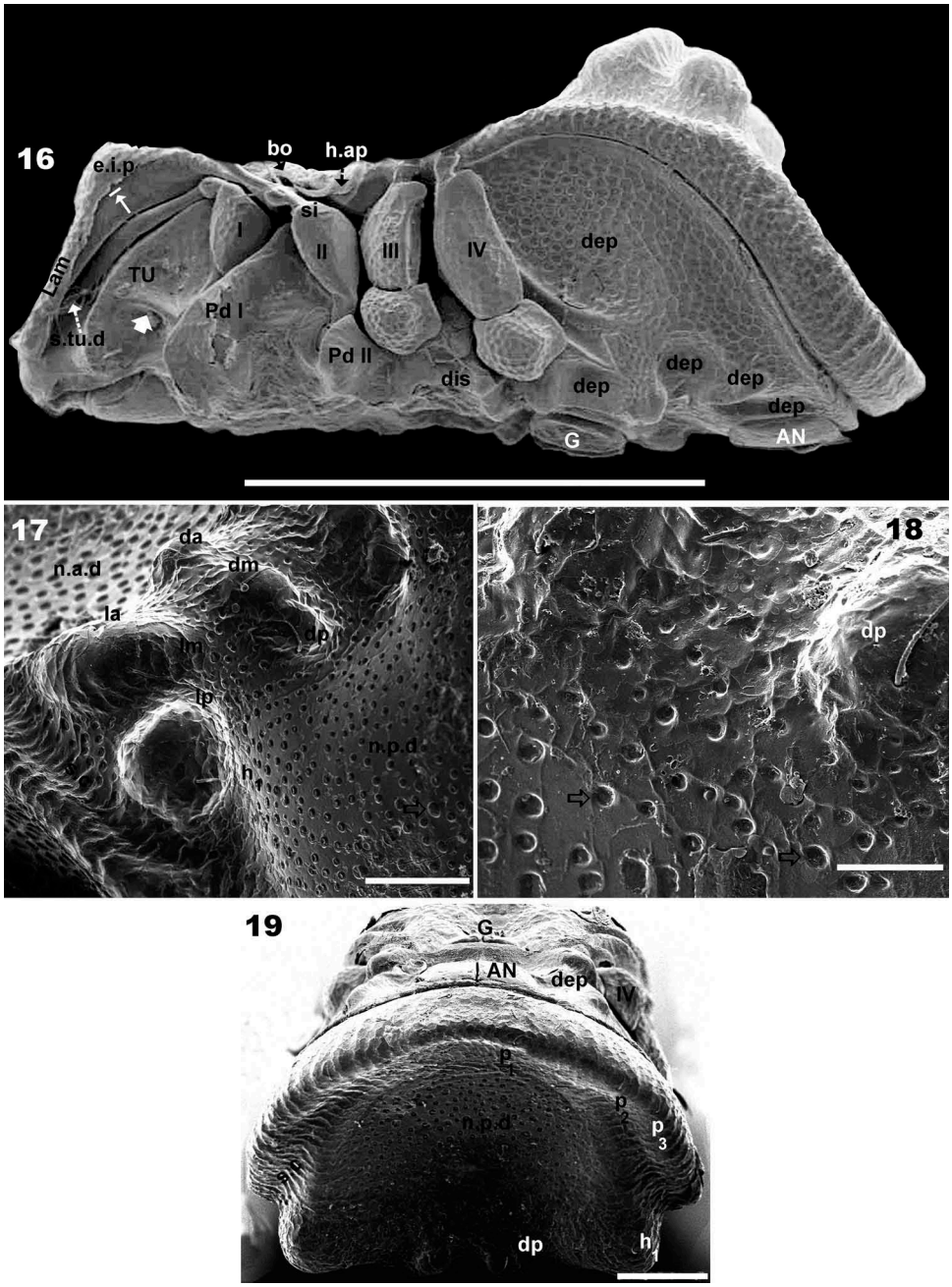
Observation in lateral view is crucial to understanding several structures, and various observation angles are necessary (Figures 7, 8, 11, 14). *Lam* (Figures 7, 8, 11, 14) and interior convex zone clearly observed (Figure 8), along with longitudinal slot which partially conceals leg I during deployment of protection mechanism (Figures 7, 11, 14); *le* setae barbate, hardly discernible, concealed by *Lam* (Figure 14, indicated by ⇢). Tutorium (*Tu*) normal (see Table 3), without particularities (Figures 7, 8, 11, 14). Pedotectum (*Pd I*) large blade, rounded apex (Figures 7, 8, 11, 14). Supratutorial depression (*s.tu.d*) deep (Figures 8, 11) with posterior pocket depressions (*p.tu.d*) (Figures 8, 11, 14, indicated by ⇨).

Table 3. Comparison between genera *Antongilibodes, Mangabebodes* and *Tuberocepheus*.

	Antongilibodes	*Mangabebodes*	*Tuberocepheus*
Prodorsum			
Elevated interlamellar process	Divided in two ear-like processes	Ear-like process absent	Divided in two ear-like processes
Insertion of setae	On *p.p.d*	On *p.p.d*	On *p.p.d*
Shallow lamellar furrow	Well delimited	Well delimited	Not delimited
Bothridial ring	Smooth, large	Smooth, large	Smooth, narrow
Bothridial tooth	Teeth	Large	Finger-like projection
Posterior prodorsal depression	Not discernible	Poorly developed	Conspicuous, polyhedral
Notogaster			
Notogastral setae pairs	Fifteen	Twelve	Twelve
Distribution notogastral setae	*c1, c2, c3* inner *n.a.d*	Setae *c* absent	Setae *c* absent
Elevated zone between *n.a.d* and *n.p.d*	Narrow	Large	Medium-sized
Lateral paired elevations	Two pairs	Two pairs, well developed	Two pairs
Central paired elevations	Unpaired	Two pairs, poorly developed	Three pairs
Ventral region			
Tutorium	Normal shape	Spoon-shaped	Normal shape
Relation pedotectum I–tutorium	*Pd I ≥ Tu*	*Tu > Pd I*	*Pd I > Tu*
Epimeres	Poorly delimited	Well delimited	Poorly delimited
Anterior genital furrow	With lateral depression	Lateral depression absent	Lateral depression absent
Depression surrounding genital opening	Poorly developed	Well developed	Well developed
Connection between depressions	Not connected	Connected by narrow channel	Connected by narrow channel
Relative size anal/genital opening	Anal > genital	Anal ⋙ genital	Anal ≫ genital



Figures 11–15. *Tuberocepheus longus* (Balogh, 1962). Adult female. 11. lateral inclined view; 12. bothridial zone, lateral view; 13. prodorsal ornamentation, zone *p.p.d.*; 14. anterolateral view; 15. prodorsum, frontal view. Abbreviations: see "Materials and methods". Scale bars: 11 = 100 µm; 12 = 10 µm; 13 = 5 µm; 14–15 = 50 µm.



Figures 16–19. *Tuberocepheus longus* (Balogh, 1962). Adult female. 16. lateral view; 17. notogastral promontories, lateral inclined view; 18. notogaster, posteroventral view; 19. ornamentation, zone between promontories and *n.p.d*. Abbreviations: see "Materials and methods". Scale bars: 16 = 400 µm; 17 = 50 µm; 18 = 10 µm; 19 = 80 µm.

Bothridial opening incomplete, with conspicuous posterior indentation (Figure 12). Bothridial ring (*bo.ri*) smooth, narrow, rotated to bothridial opening; a series of fine parallel alignments near bothridial tooth (*bo.to*) (Figures 11, 12, indicated by m); *bo.to* particular as a smooth finger-like projection (Figure 12). Humeral apophysis (*h.ap*) with a semicircular depression lodging posterior part of bothridium (Figure 8, indicated by ⇧), and an elongated depression receiving sensillus (*si*) (Figure 12, indicated by ➧), when protection mechanism is activated (see Fernandez et al. (2013a)). *Pd I* prominent extended lamina, rounded apex; *Pd II* medium size, more or less triangular with anterior part convex and posterior part concave, apical zone directing upwards (Figures 8, 16). Lyrifissures *ih, ips* clearly discernible (Figure 8). Clearly visible ovoid projection (Figure 8, and in 16, indicated by ↘) posterior to acetabulum IV. Aggenital setae (*ag*) situated posterior to genital opening.

Many conspicuous depressions (*dep*): large structure polyhedral-foveate network, situated behind legs IV, extending posteriorly (Figures 8, 16); others ovoid, situated between genital and anal openings, and two others, elongated ovoid, directing parallel, slightly inclined to anal plate (Figures 8,16). Anal plate terminating in sharp tip (Figures 8, 16, indicated by arrow).

Ventral region

Tutorium (*Tu*) hardly discernible, without particularities in shape and size (Figures 9, 25). *Pd I, Pd II* and *dis* well visible. *Pd I* expanded, *Pd II* ovoid to polyhedral, *dis* more or less triangular. Rounded lateral expansion (Figure 25, indicated by ⇧) posterior to acetabulum IV. Epimeric zone: erased reticulate-foveate microsculpture, alternating elevations and small epimeric setae. Conspicuous longitudinal medial epimeric depression (Figure 25) with central ovoid depressions (Figure 25, indicated by ➧). Apodemes *apo.1, apo.2, apo.dj, apo.3* clearly visible, epimeric borders hardly discernible (Figures 9, 25).

Epimeral chaetotaxy 3-1-3-3; setae *1a* and *3a* small (Figure 9); *2a* medium-sized; other epimeral setae relatively large, of similar length. Genito-anal zone complex. Several structures can only be

adequately observed in SEM. In Figure 25 observation was made with posterior–anterior inclination and slight lateral rotation.

Genital opening situated in elevated zone, with narrow surrounding zone (Figure 25), externally to this area the following can be observed: semicircular depression (*a.g.f*) anterior to and in contact with epimeric zone; lateral polyhedral depression can be observed (Figure 25, indicated by 1)); a spur (cuticular expansion) in the zone of contact between lateral polyhedral depression and *a.g.f*, reducing the zone of contact, delineating a narrow channel (Figure 25, indicated by ↑↑); large paired ovoid to polyhedral depressions (Figure 25, indicated by 2) behind and between the genital and anal zones, each depression with a small rounded to polyhedral depression (Figure 25, indicated by 3). Lateral to anal opening and separated by cuticular ribbon from large paired ovoid depressions (Figure 25, indicated by 2), a paired polygonal depression visible (Figure 25, indicated by 4), this depression is deep anteriorly in the zone near the paired ovoid depressions (Figure 25, indicated by 2) and shallow posteriorly. Anterior to depressions indicated by number 4, and between them and the depression indicated by number 3, a medium-sized polyhedral depression (Figure 25, indicated by 5) is observed, deep in lateral and anterior zones and shallow posteriorly (Figure 25). Laterally, extending anteriorly and posteriorly, large shallow depression (Figure 25, indicated by 6), with polyhedral-foveate network cuticular microsculpture is observed.

Genital plate smaller than anal plate (Figure 25). Genital plate (Figure 26): rectangular with rounded corners, four pairs of genital setae. Anal plate (Figure 27) trapezoidal; two pairs of aligned anal setae situated in central posterior zone. Plate terminating in short sharp tip. One pair of aggenital setae situated laterally to rounded depressions (indicated by 2), far from ad_3 setae; three pairs of adanal setae.

Gnathosoma and palp (Figures 22, 28). Conspicuous diarthric subcapitulum; subcapitular setae *h, m, a* clearly visible. Zone of *h* and *m, a* with different microsculpture (see integument). Palp, *sul*, (*ul), acm* eupathidium; solenidion ω long, easily discernible.

Posterior aspect. (Figures 19, 20)

Due to the very complicated shape, two SEMs Figures (19, 20) are included with alternate angles and information. Figure 19: posterior promontories with *dp* setae on central paired elevations, appearing to be at similar level as posterior promontories, with setae h_1 on lateral paired elevation; *n.p.d* semicircular. Microsculpture on *n.p.d* extending to central and lateral elevation zones. The *s.c* is clearly discernible as a conspicuous furrow, situated externally to the zone of posterior promontories of the lateral paired elevation, where h_1 setae are situated, this furrow follows along notogastral margin, situated posterior to p_1, p_2, p_3 setae.

Figure 20: lateral and central paired elevations clearly visible; *n.p.d* semicircular. Foveate microsculpture easily discernible on *n.p.d* and on promontory zone. Posterior promontories of lateral elevations bearing setae h_1, situated posterior to level of posterior promontories of central elevations with setae *dp*. The *s.c* is well discernible at level of lateral promontories with h_1 setae; however, around the notogastral margin it appears as a shallow groove. Notogastral marginal posterior zone between p_1 and p_2 setae showing shallow depression interrupting continuity of *s.c* groove. This shallow depression is hardly discernible on Figures 6, 11 (indicated by *). Clearly visible *p.p.d; e.i.p* representing an ear-like shape, and flat depressed central area (indicated by black arrow), microsculpture clearly discernible.

Legs (Figures 23, 24, 31–34)

Claws, lacking teeth, with fine longitudinal furrows (Figure 23); legs I, II, III more or less equal length, IV longer (Figure 11). Femurs of each leg different (Figures 29, 30–32), legs III and IV playing an important role in leg folding process (see Fernandez et al. (2013a)); genu III small, hinge-like articulation with femur (Figure 34); tibia I, IV long; II medium length and III short; tarsi I, II similar in shape and length (short and robust) and III and IV similar in shape and length (long and thin). Setal formulae (trochanter to tarsus) and solendia: 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) (see Table 2). Setal formulae to be considered provisional until such time as immature stases have been studied to resolve doubts.

Discussion

Bovicarabodes jacquelinae **sp. nov**. is quite different from *B. levyi* and *B. fortdauphini* but presents some characters in common with *B. deharvengi*, such as shape and position of *e.i.p*. and *in* setal insertion on prodorsum; *n.a.d* anterior zone and *h.p*. shape on notogaster.

Problems related to Tuberocepheus longus (Balogh, 1962)

Due to an inability to obtain the deposited material of *Tuberocepheus longus* (Balogh, 1962) (see "Introduction" and Fernandez et al. 2014, p. 317–318) we searched amongst samples in the Betsch Collection of the MNHN. The task proved difficult due to the superficial original description (text and figures, Balogh 1962), but after an exhaustive search, we were able to locate specimens. To highlight problems original transcriptions are provided in chronological order.

Machadocepheus longus Balogh, 1962

Balogh (1962, p. 139–141). Figures 29–31 established: "*Machadocepehus longus* **sp**. **nov**. (Figure 29–31) 675–810 X 345–452µ. Sensillus exteriora, sursum et anteriora versus directus, non incrassatus, setulis brevibus armatus.Setae in parvæ et tenues; setæ la in declivitate antica propodosomatis dispositæ, interiora versus directæ, non longæ. Setae *ro* parvæ, anteriora versus directæ.

Lamella desuper adspetæ marginales, paulo convergentes, anteriora versus dilatatæ, línea brevi transversali, translamellam imitanti conjunctæ. Pars media interlamellaris prodoposomats feveolid dispersi, non bene limitatis ornata.

Hysterosoma desuper adspectum multo longius, quan latum, posteriora versus paulo dilatatum; antice ad humeros lamina dorsi tuberculi sint 10 in area transversale dispositi. Tuberculi laterales utrinque 3 magni; tuberculi mediales utrim 3 multo minores. Tuberculi laterales antici setas duas, tuberculi reliqui setam unicam gerentes.

Setæ postero-marginales utrinque 5. Dorsum irregulariter foveolatum. Foveolæ ante tubercula optime expressæ; post tubercula obscure limitate.

Corpus a latere aspectum valde, insigne. Propodosoma fere horizontale, anteriora versus subitodeclive, fere perpendiculare. Pars antica hysteromomatis humillina, excavata, tantum 230 alta; pars media valde elevata, 366µ alta, tuberculis supra dictis rotundatis ornata; pars postica declivis, paulo excavata. Margo hysterosomatis elevatus, lineis perpendicularibus dense ornatus.

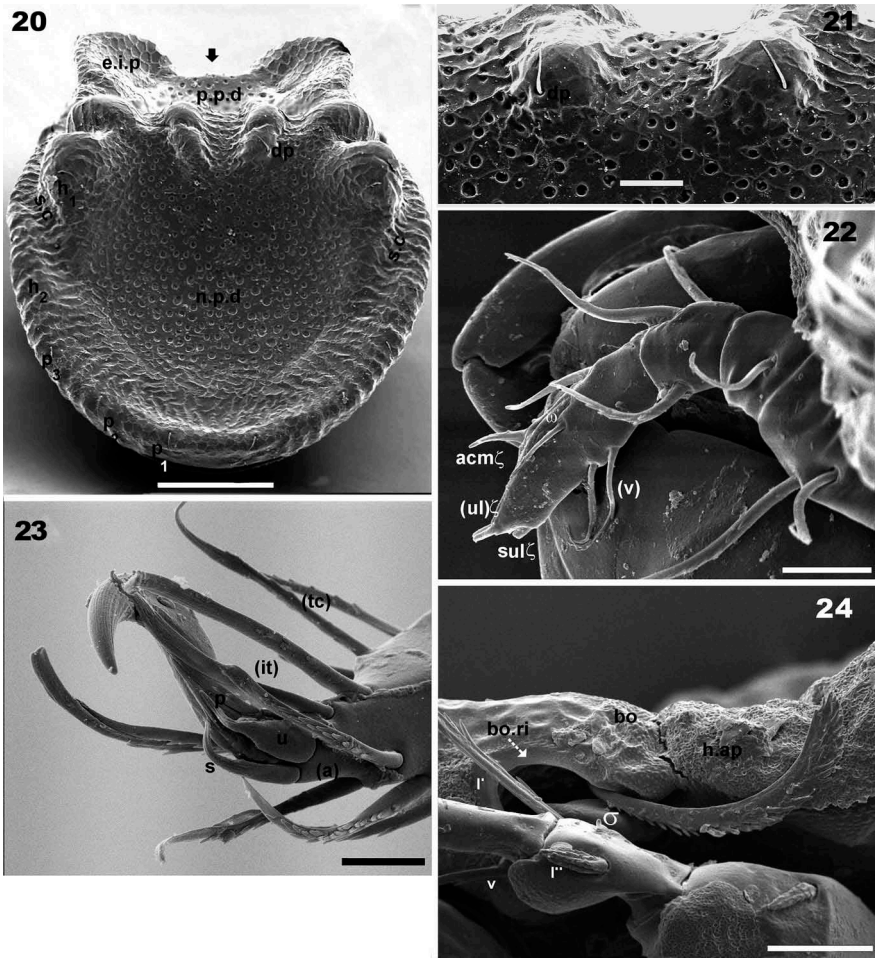
Setæ genitales utrinque 4, setae anales utrinque 2.Setæ ad_1 et ad_2 post anum, setæ ad_3, multo anterius dispositae. Pori iad ano valde separate

Venter costis chitineis paullo complicate sculptus (vide, Figure 31).

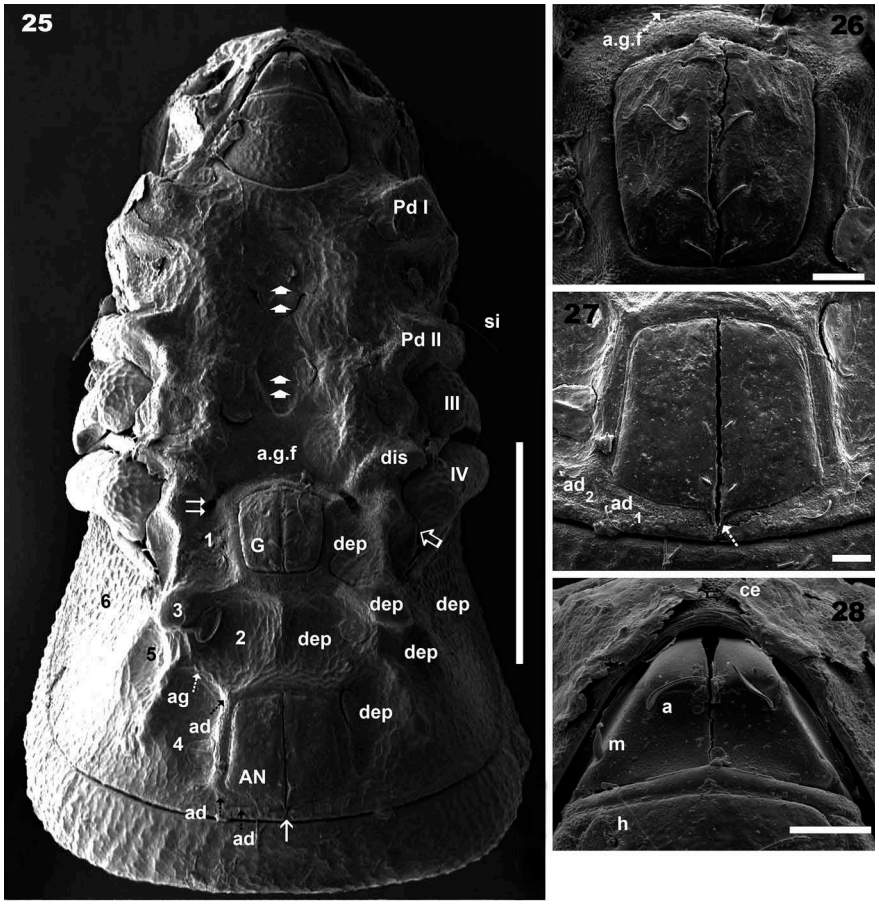
Species hæcnova speciei nota (*M. excavatus* Bal.1958) statura multo mahjore, sculptura dorsi diversa.

Madagascar-Centre: Manjakandriana, Ambatolaona .IX.1958 Leg:A.Robinson

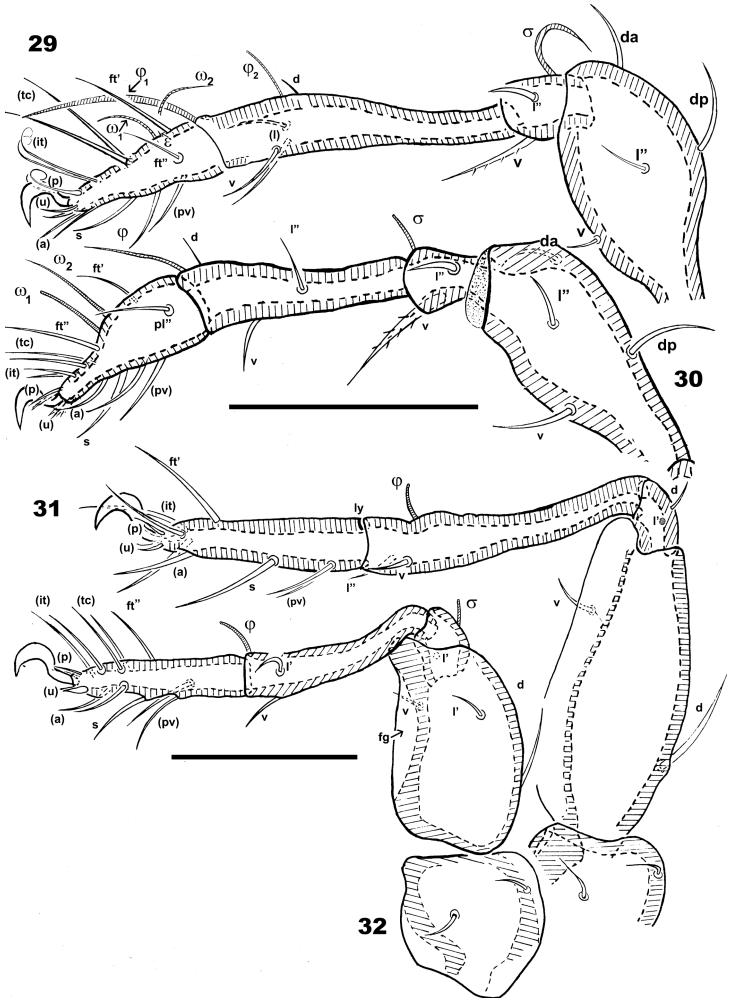
Holotypus: 1 ex., paratypi: 3 ex."



Figures 20–24. *Tuberocepheus longus* (Balogh, 1962). Adult female. 20. anteroposterior view; 21. central notogastral promontories, detail; 22. palp, lateral view; 23. Tarsus I, apical zone; 24. sensillus, lateral view. Abbreviations: see "Materials and methods". Scale bars: 20 = 100 µm; 21 = 20 µm; 22–24 = 10 µm.



Figures 25–28. *Tuberocepheus longus* (Balogh 1962). Adult female. 25. ventral view, with anteroposterior inclination and slight lateral tilt; 26. genital plate; 27. anal plate; 28. subcapitulum. Abbreviations: see "Materials and methods". Scale bars: 25 = 200 µm; 26 = 20 µm; 27 = 20 µm; 28 = 50 µm.



Figures 29–32. *Tuberocepheus longus* (Balogh, 1962). Adult female. Legs. 29. leg I, antiaxial view; 30. leg II, antiaxial view; 31. leg IV, antiaxial view; 32. leg III, antiaxial view. Abbreviations: see "Materials and methods". Scale bar: 29–31 = 40 µm; 32 = 30 µm.

Tuberocepheus *Balogh & Mahunka, 1969*

Balogh and Mahunka (1969, p. 9) included the following one and a half lines of text describing the new genus as a footnote in a paper on South American Oribatid mites:

> Following a comparison of the Carabodid species described hitherto, the species *Machadocepehus longus* Bal. 1962 (Madagascar) is to be excluded from this genus and a new genus established for it, as follows:
>
> Tuberocepheus gen. n
>
> Ten pairs of notogastral and 4 pairs of genital hairs. Six pairs of minute and simple hairs arising on 5 pairs of tubercles on notogaster.
>
> Remarks: The new genus rather resembles Spatulocepheus gen. n., described above but the number of genital and adanal hairs as well as the epimeral setal formula clearly distinghuish it.

Mahunka (1986, p. 107):

> *Tuberocepheus* Balogh & Mahunka, 1969 (Figs.72–73, 107).
>
> Balogh et Mahunka, 1969, p. 9.
>
> Prodorsum: A pair of strong transversal apophyses present. Lamellae with sharp apex, lamellar setae phylliform, arising on the lateral surface of lamellae. Rostral and interlamellar setae thin, simple, originating in interlamellar region. Sensillus long, its head dilate, laminate. Tutorium strongly developed.
>
> Notogaster: dososejugal suture well visible, but behind it a deep hollow present. Median part of notogaster highly elevated, with some crests. Twelve fine notogastral setae, 7 pairs arising in the elevated region, five pairs in the posteromarginal position.
>
> Coxisternal region: Epimeral borders well separating the epimeral fields from each other, median longitudinal field very broad. Epimeral setal formula: 3-1-3-3.
>
> Anogenital region: a pair of strong longitudinal crista running parallel with the genital and anal apertures posteriorly. Anogenital setal formula: 4-1-2-3. Two pairs of adanal setae originating in postanal, one pair in preanal position. Lyrifissure iad well visible.
>
> Type species: *Machadocepheus longus* Balogh, 1962, Madagascar.

Mahunka (1986) completely altered the description of Balogh and Mahunka (1969) in describing the new genus *Tuberocepheus*, changing from a species with 10 pairs of notogastral setae to one with 12 pairs (7 in the central zone and 5 marginally); however, it is not clear from the text if Mahunka studied the type material.

With regard to *T. longus*, however, nothing is mentioned. Was this redescription prepared without studying type material? Further unknown aspects are related to drawings. For example, in Balogh's original description (1962), illustrations are small and of poor quality, in 1969 the description by Balogh and Mahunka is only in text, and in 1986, Mahunka's drawings are very similar to original illustrations by Balogh in 1962, only with more setae. The original lateral drawing by Balogh in 1962 is unpresentable, and Mahunka (1986) included only dorsal and ventral illustrations. Clearly this group with its prominent morphological characteristics and very complicated topography is virtually impossible to study using only optical microscopy, and a scarcity of specimens and being given general dorsal and ventral views compounds the problem. The number of setae is one, but not the only distinguishing character.

Comparison

A preliminary comparison between *Tuberocepheus, Mangabebodes*, and *Antongilibodes* was given in Fernandez et al. (2014), and

resulting from the present study, it was deemed necessary to provide a final comparison (see Table 3, which shows the comparison of characters considered to be significant). It should be noted a series of specimens from different world regions, possibly belonging to *Machadocepheus*, have been studied. A study of *Machadocepheus excavatus* Balogh, 1958 (type material) allowed us to compare these genera.

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