

International Journal of Acarology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/taca20>

Revision of the family Carabodidae (Acari: Oribatida) II. Redescription of *Austrocarabodes ensifer* (Sellnick, 1931), *Aokiella florens* Balogh & Mahunka, 1967 and *Singabodes rarus* Mahunka, 1998

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Published online: 10 Apr 2013.

To cite this article: Nestor Fernandez, Pieter Theron, Christine Rollard & Sergio Leiva (2013): Revision of the family Carabodidae (Acari: Oribatida) II. Redescription of *Austrocarabodes ensifer* (Sellnick, 1931), *Aokiella florens* Balogh & Mahunka, 1967 and *Singabodes rarus* Mahunka, 1998, *International Journal of Acarology*, DOI:10.1080/01647954.2012.754493

To link to this article: <http://dx.doi.org/10.1080/01647954.2012.754493>

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Revision of the family Carabodidae (Acari: Oribatida) II. Redescription of *Austrocarabodes ensifer* (Sellnick, 1931), *Aokiella florens* Balogh & Mahunka, 1967 and *Singabodes rarus* Mahunka, 1998

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(Received 1 June 2012; accepted 26 November 2012)

Austrocarabodes ensifer (Sellnick, 1931) is redescribed and illustrated based on adult specimens using optical microscopy as well as scanning electron microscopy. *Aokiella florens* Balogh & Mahunka, 1967 and *Singabodes rarus* Mahunka, 1998 are redescribed and figured based on adult specimens using optical microscopy only. These three species are the type species of their respective genera, thus allowing us to redefine each. Although it is likely that *Singabodes* may be a synonym for *Aokiella*, further study is necessary to resolve the uncertainty.

Keywords: Acari; Oribatida; Carabodidae; redescrptions; *Austrocarabodes ensifer*; *Aokiella florens*; *Singabodes rarus*

Introduction

The genus *Austrocarabodes* was established by Hammer in 1966 with *Carabodes ensifer* Sellnick, 1931 as type species. Today, it is the second largest genus in the family Carabodidae with 82 species and 3 subspecies (Subias 2004, updated 2012). The genera *Baloghodes* Mahunka, 1986 and *Uluguroides* Mahunka, 1983 are considered subgenera within the genus *Austrocarabodes*. The latter has a worldwide distribution. The original description of the type species, *C. ensifer* Sellnick, 1931, contains many errors and this necessitated a review.

The genus *Aokiella* was established by Balogh and Mahunka in 1967 with *Aokiella florens* as type species. At present, this genus is considered a subgenus within the genus *Odontocephus* (Subias *op. cit.*), and the cited subgenus contains three species.

Lastly, the genus *Singabodes* was established by Mahunka (1998) with *Singabodes rarus* as type species. Since then, this genus has remained monotypic. In order to clarify the situation related to the genera and type species studied, we include a detailed corresponding redescription of each.

Materials and methods

Specimens studied with light 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 an Olympus BHC compound microscope (Olympus, Rungis, France) equipped with a drawing tube. To aid observations, some specimens were stained with chlorazol black E (Coineau 1974).

Specimens studied with the aid of scanning electron microscopy (SEM) were prepared as follows: specimens preserved in ethanol were carefully rinsed by sucking them several times into a Pasteur pipette, then transferring them for 2 hours to buffered glutaraldehyde (2.5%) in Sörensen phosphate buffer (pH 7.4; 0.1 M). After post-fixation for 2 hours in buffered 2% OsO₄ solution and rinsing in buffered solution, all specimens were dehydrated in a series of graded ethanols and dried in a critical point apparatus. Specimens were mounted on Al-stubs with double-sided sticky tape, after which they were gold-coated in a sputter apparatus.

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

The description of leg chaetotaxy (SEM, standard, polarized and phase contrast microscopes) of *Austrocarabodes ensifer* (Sellnick 1931) should be considered provisory owing to the limited number of previous studies and manifesting discrepancies in the existing literature; a future detailed study of chaetotaxy of legs during ontogenetic development in different genera is planned.

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

Morphological terminology

Morphological terms and abbreviations used are those developed by F. Grandjean (1928–1974) (cf. Travé and Vachon 1975), Norton and Pelletier (2009) and Fernandez et al. (2012).

Evans (1992) and Murley (1951) (*In: Evans op. cit.*) were followed for the setal types and ornamentation of cuticular surfaces, respectively.

Working through the relevant literature, it is striking how many synonymies occur with reference to terms applied to describe basic structures used as diagnostic criteria for genera and species within this family. Thus, in order to be able to complete a revisionary study, we had to investigate all existing synonymies in order to establish a standardized terminology for the family. In many works, terminologies were used interchangeably; however, we strove to use terms in the strict sense (as proposed by the original authors) in our endeavours to minimize confusion.

A number of specific morphological characters have never been described in detail before, and no terminology and/or abbreviations exist for these structures. The following have been included in the text and on the figures for the sake of clarity: humeral ridge (*h.r.*). Leg I: semicircular margin (*s.c.m.*) and depressed zone (*d.z.*). Many others related to the notogastral posterior depression (*n.p.d.*) as: anterior zone (*a.zo.*); external cuticular thickening (*e.thi.*); external zone (*e.z.*); fine, curved, line delimited anterior zone (*f.c.l.*); inner zone (*i.z.*); internal cuticular thickening (*i.thi.*); notogastral posterior depression hollow (*n.p.ho.*); posterior zone (*p.zo.*); thickening around setal insertion (*se.thi.*).

Genus *Austrocarabodes*

Hammer (1966, p. 59) established the genus, with the type species *Au. ensifer* (*C. ensifer* Selln, 1931, p. 117, Figures 20–21).

Redescription

Diagnosis

Prodorsum without elevated processes. Lamellae dorsolateral; dorsal part of lamella easily discernible by internal cuticular thickening and shallow cuticular lamellar furrow. Lamellar apex round, prolamellae present. Lamellar setae placed inside shallow lamellar furrow. Rostral margin round. Bothridial ring smooth, incomplete, with bothridial tooth. Notogaster oval, without anterior depression; dorsosejugal furrow narrow, well-delimited, easily discernible; circumgastric furrow present; humeral apophysis crossed obliquely by prominent cuticular ridge. Apical humeral apophysis zone overlaps posterior part of bothridia. Fourteen pairs of setae; *gla* and lyrifissures not discernible. Lateral inferior side of lamella concave, to permit concealment of leg I.

Tutorium is a strong, curved, cuticular thickening; supra tutorial depression deep. Pedotectum I prominent; pedotectum II small lamina, rounded apex. Sejugal depression deep. Lamellar antiaxial border, inferior part of bothridia and humeral apophysis extend laterally. Discidium is a triangular protuberance; epimera well-defined shallow furrows. Epimeral chaetotaxy 3-1-3-3. Deep anterior genital furrow. Four pairs of genital setae;

aggenital setae posterior to genital opening. Three pairs of adanal setae; anal plate sharply tipped. Two pairs of anal setae; lyrifissure *iad* not discernible. Structures involved in protection mechanism, present.

Type species

Austrocarabodes ensifer (Sellnick, 1931)

(Figures 1–40)

Diagnosis

Redescription

Elongate oval shape. Cerotegumental layer: prodorsum with irregular polygonous areas, upper surface with or without teeth; notogaster, irregular polygonous to amorphous areas. Central zone, laterally regular polygonous areas; humeral process, finger-like structures. Microsculpture prodorsum: irregular foveate patterns between dorsosejugal suture at rostral level. Pusticulate: dorsosejugal zone, notogaster and central, posterior and lateral zones. Smooth: lateral notogastral margin. Humeral apophysis irregularly tuberculate to smooth. Ventral: foveate. Setation: lanceolate-serrate prodorsum, notogaster, adanal, anal. Interlamellar setae largest; setae *ro* and *in* with two serrate veins; seta *le* with only one serrate vein. Notogastral setae with only one serrate vein; notogastral lateral setae (*p*₁, *p*₂, *p*₃, *h*₃) smaller. Genital, epimeric setae simple. Prodorsum convex without any processes; seta curving forward; size *in* > *le* > *ro*. Interlamellar setae far from shallow lamellar furrow. Sensillus spatulate, barbate, arching backward; internal medial eye present, anterior zone rostral setae. Notogastral humeral apophysis with prominent rod-like thickening. Notogastral seta lanceolate serrate; *p*₁, *p*₂, *p*₃, *h*₃, small. Cuticle of tutorial margin smooth with many cerotegumental teeth arranged on margin surface. Sejugal depression deep, clearly visible.

Apodematas 1, 2, *sj* and 3 clearly visible; *sj* across medial plan. Adanal setae: all lanceolate, serrate, *ad*₁, *ad*₂ broad; *ad*₃ thin. Tibia I and II with dorsal setae near solenidion; ungual setal pair I smooth, spur-shaped.

Material examined

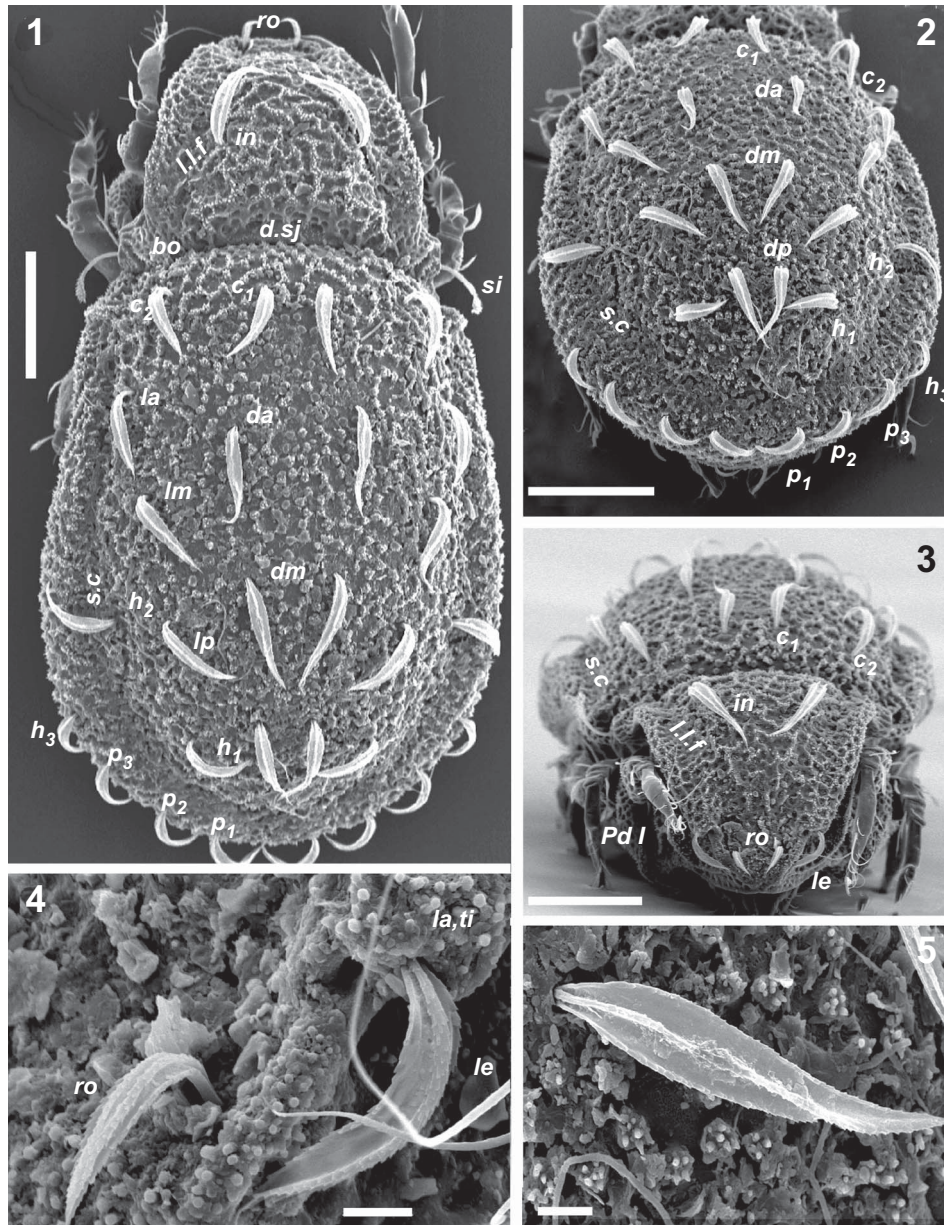
Austrocarabodes ensifer (Sellnick, 1931). Collected by B. Hauser and identified by S. Mahunka.

«Pel-74/16 Grèce: Leucade: Poros. Au pied des rochers au dessus du village, tamisage, 280 m. 11.V.1974; 27 exemplaires.» Material in collection of Muséum d'Histoire Naturelle, Genève.

Description

Measurements. SEM: 657 µm (645–670) × 355 µm (315–395) µm. Light microscopy: 532 µm (510–660) × 314 µm (310–327). Sex ratio in measured specimens 1:2 (male:female)

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



Figures 1–5. *Austrocarabodes ensifer* (Sellnick, 1931). Adult, (with cerotegument) scanning electron micrographs. 1. Dorsal aspect. 2. Dorsoposterior view. 3. Frontal view. 4. Rostral and lamellar setae. 5. Notogastral setae. Abbreviations: See Material and methods. Scale: 1–3 = 100 μ m; 4–5 = 10 μ m.

Cerotegument. Prominent complex thick layer, more or less uniformly covering almost the entire body and partially covering the legs.

The *cerotegumental layer* is composed of a basal layer (*c.b*), slightly porous (Figure 11, arrow), and a very complex structured layer elevated above it (Figures 1–11; 20–24).

Cerotegumental layer present.

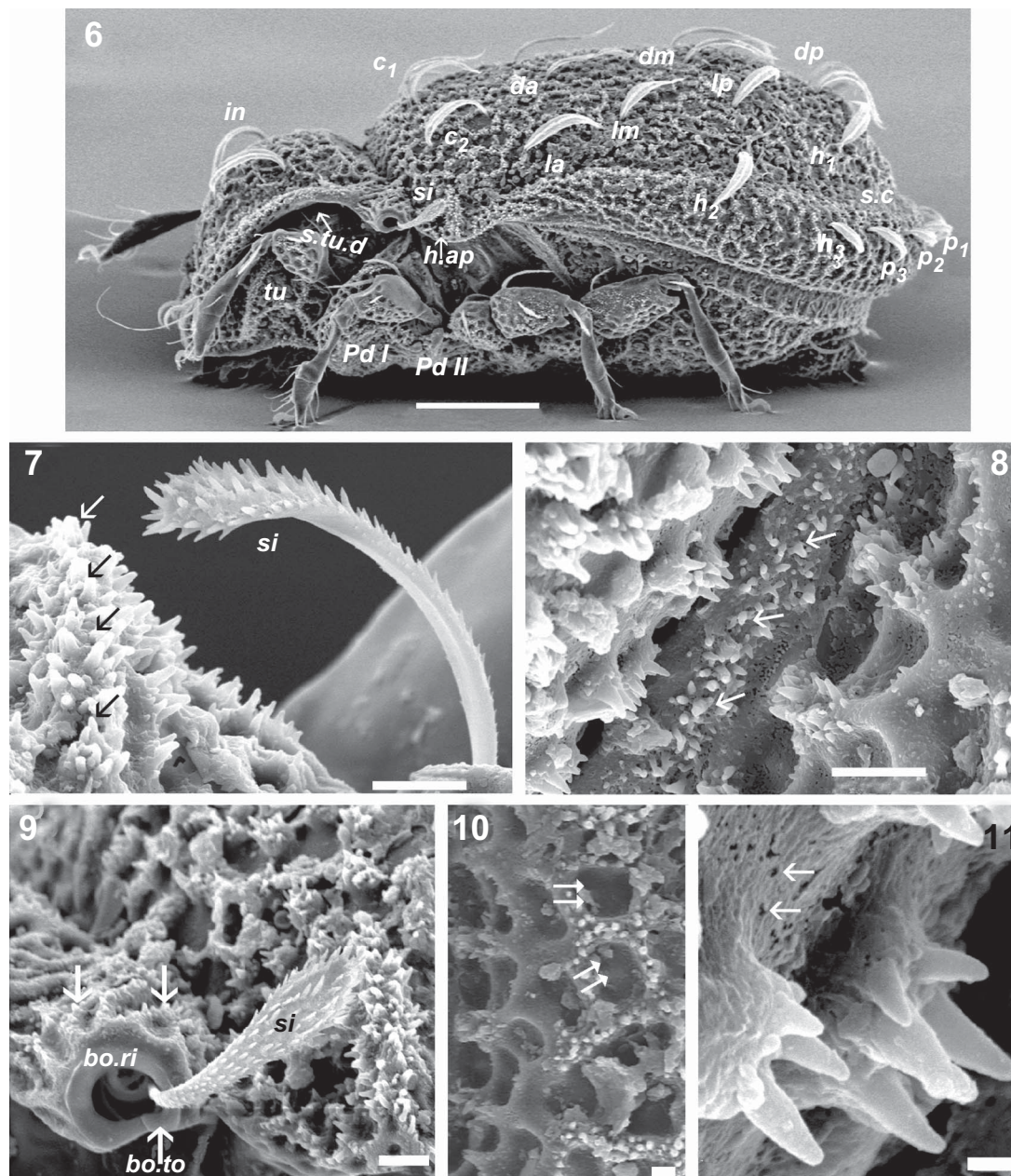
Prodorsum. Covered by thick cerotegumental layer (Figures 1, 3 and 6). *Irregular polygonous areas* with hollow bases and upper surface with irregular number of teeth (detail in Figure 10, double arrows); distribution: extending from central area, between shallow lamellar furrow (*l.l.f*),

backward, near the depressed area of dorsosejugal furrow (*dsj*), and forward to the level of *ro* insertion (Figures 1, 3 and 10). Polygonous area on bothridial surface shaped slightly differently (Figure 9 white arrow).

Regular polygonous areas with hollow bases and upper surface with: (a) *teeth*: lamellar area excluding lamellar margin (Figures 1 and 3); (b) *finger-like structures*: depressed zone around dorsosejugal furrow (Figures 8 and 11).

Small teeth, situated directly on surface of *c.b*, dorsosejugal furrow (Figure 8).

Notogaster. Polygonous areas (Figure 32). The *c.b* follows the cuticular irregularities. The small cerotegumental

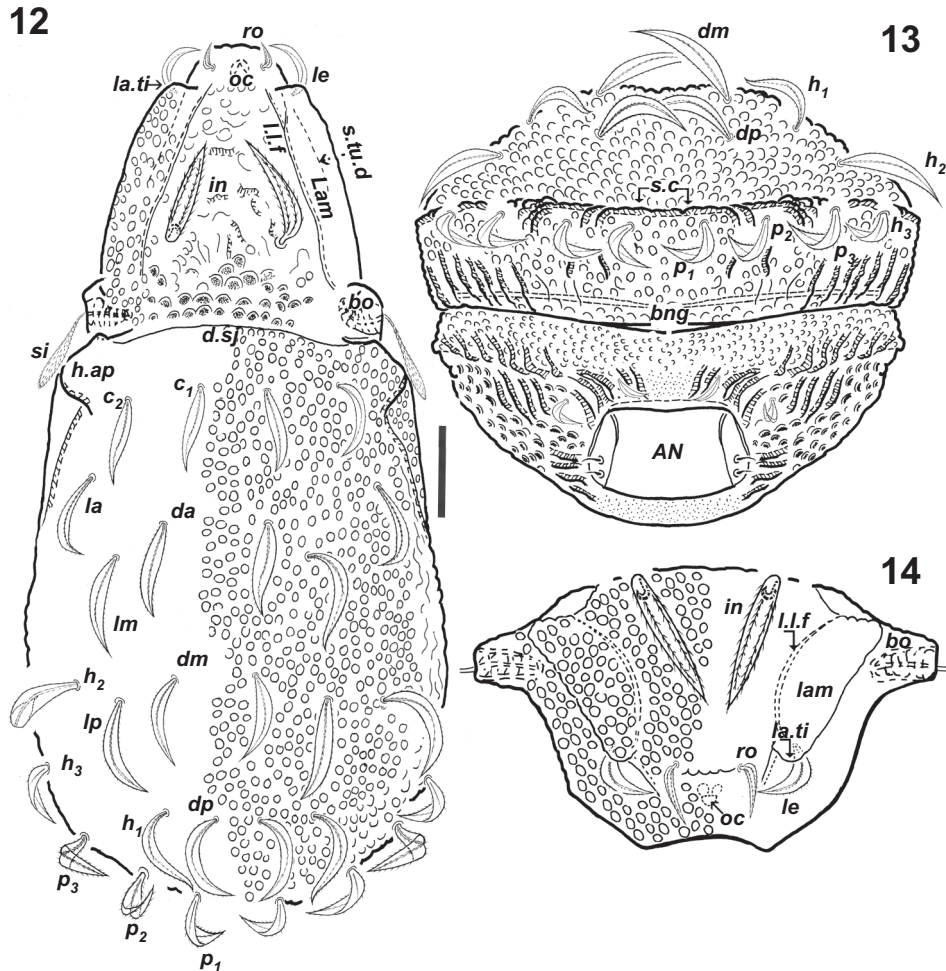


Figures 6–11. *Austrocarabodes ensifer* (Sellnick, 1931). Adult, scanning electron micrographs. 6. Lateral aspect. 7. Sensillus, lateral view and humeral apophysis; cerotegument, finger-like (arrow). 8. Cerotegument dorsosejugal area; small teeth situated on suture (indicated with arrow); right side prodorsum; left side notogaster. 9. Sensillus and humeral apophysis; bothridial cerotegument (white arrows); humeral apophysis cerotegument (white arrow). 10. Prodorsal cerotegumental layer, depressed area near *d.sj.* (double arrow indicates polygonal irregular areas), hollow bases, upper surface irregular number of teeth. 11. Cerotegumental finger-like structures; arrow indicates basal layer (*c.b*) slightly porous. Abbreviations: See Material and methods. Scale: 6 = 100 μm ; 7–10 = 10 μm ; 11 = 1 μm .

portions situated on the surface of *c.b* are irregularly distributed, following elevated cuticular zones. Each small portion has teeth on the upper surface (Figures 1, 2 and 32). Distribution: central notogastral area situated behind insertion of seta *c* and circumgastric depression (*s.c*). The polygonous areas between *s.c* and close to the notogastral margin (*n.g*) are more regular in shape (Figures 2, 6, 21 and 24). The number of teeth decreases towards *n.g*. In the dorsosejugal furrow zone (Figure 8), the upper surface of the small portions has finger-like structures. *Irregular small teeth*, notogastral margin (Figure 21). *Finger-like*

structures: cerotegumental structures following rod-shaped cuticular ridges (*h.t*), humeral apophysis (*h.ap*) (Figures 7 and 9).

Ventral region. Irregular amorphous layer with some irregularly distributed teeth: central zone epimeric area; around genital and anal opening; genital plate (Figures 20 and 24). *Irregular portions* anterior genital furrow (*a.g.f*) (Figure 20). *Polygonous to oval areas* with irregular distribution of teeth, all other areas of ventral region (Figures 20 and 21).



Figures 12–14. *Austrocarabodes ensifer* (Sellnick, 1931). Adult. 12. Dorsal aspect. 13. Posterior view. 14. Frontal view. Abbreviations: See Material and methods. Scale: 12–14 = 100 μ m.

Legs. Irregularly distributed teeth following cuticular microsculpture (Figures 27 and 28): trochanter and femurs of all legs (see legs).

Cerotegumental layer absent. lateral lamellar margin; bothridial ring; supra tutorial depression; sejugal zone and lateral cuticular depressions were the legs coapt; palp; legs: genu, tibia, tarsus (Figures 6, 29, 30 and 31).

Integument. Microsculpture complicated, varies according to body region and/or articulation zones of legs.

Prodorsal microsculpture. Irregularly foveate and irregularly ridged: dorsal zone near dorsosejugal zone and rostral setae level. Pusticulate: rostral setae zone and near dorsosejugal zone. Shallow lamellar furrow (l.l.f) clearly visible on animals with or without cerotegument (Figures 1, 3, 12 and 14). Lateral margin of lamellae and bothridial ring smooth; bothridia with ridges more or less aligned.

Notogastral microsculpture. Pusticulate: central, posterior and lateral zones (Figures 12 and 13). Smooth: near lateral margin. Irregularly tuberculate to smooth: h.ap.

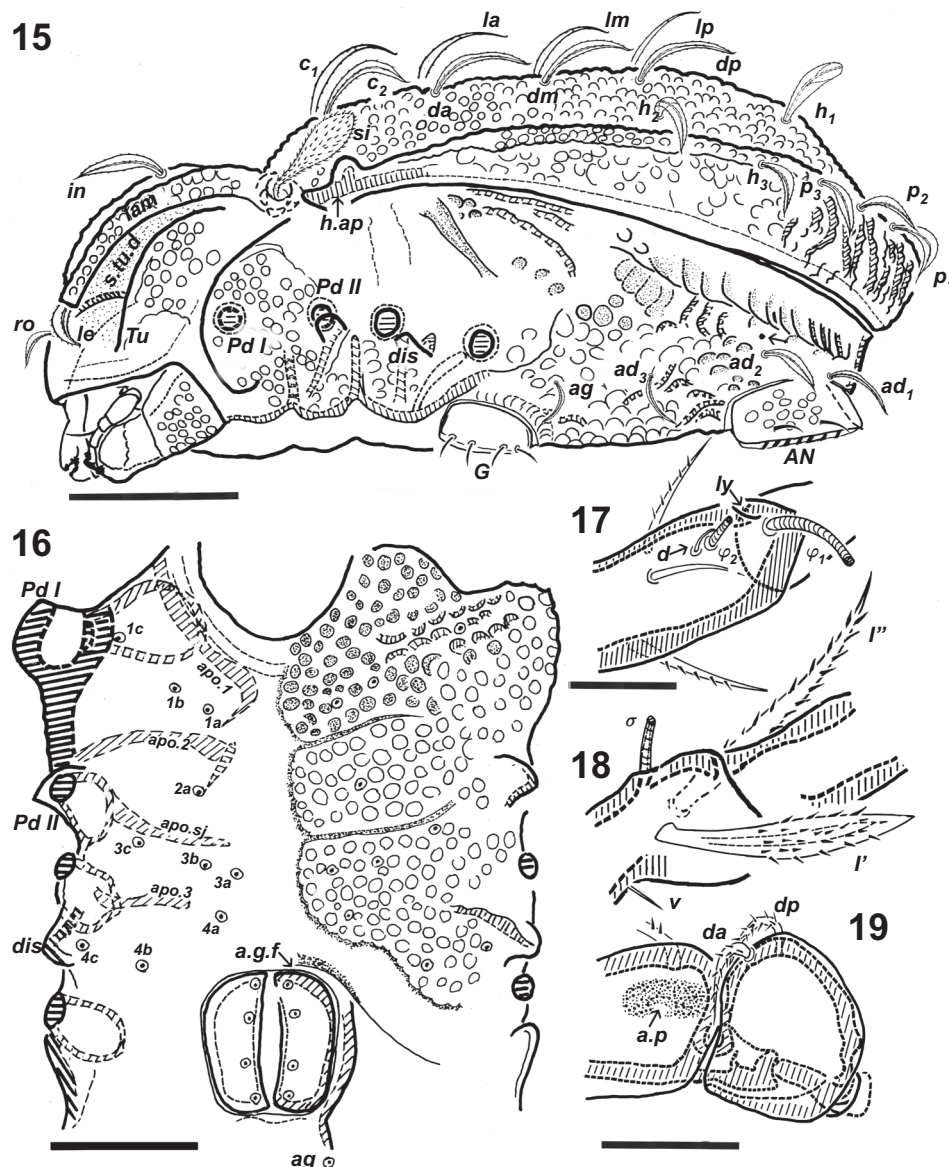
Ventral microsculpture. Foveate epimeral zone, discidium, zone around genital and anal opening (Figures 20 and 24).

Lateral zone. Behind legs and sejugal zone, smooth; across h.ap prominent ridge (h, r) (Figure 20).

Posterior zone. Many irregular thickenings near bng and around anal area. Foveate: ventral antiaxial; granulate near ventral shield margin (Figure 13).

Legs microsculpture. Reticulate-foveate patterns: trochanters III and IV, antiaxial; femur IV, antiaxial (not dorsal zone; femur III, antiaxial (not femoral groove); femur II, antiaxial (not dorsal zone); femur I, antiaxial anterior zone (not basal and dorsal) (Figures 6, 27 and 28). Smooth: tibiae and tarsi (I–IV); femurs I, II, IV, dorsal zone; femur III, femoral groove and surrounding area; femur I, basal and dorsal zone (Figures 27, 28, 29 and 30).

Setation. Prodorsal, notogastral, adanal and anal setae lanceolate-serrate, but ro and in with two medial longitudinal serrate veins; le, with only one vein (Figures 3, 4, 12 and 14); in largest (80–95 μ m length); le (40–52 μ m length),



Figures 15–19. *Austrocarabodes ensifer* (Sellnick, 1931). Adult. 15. Lateral aspect. 16. Ventral aspect, arrow indicating the position of anterior genital furrow. 17. Apical zone, tibia I, dorsal view, arrow indicating position of *d* seta and lyriffisure. 18. Genual I paraxial; solenidion σ not entire. 19. Trochanter and femur (partial) leg II, paraxial. Abbreviations: See Material and methods. Scale: 15 = 100 μm ; 16 = 50 μm ; 17, 18 = 10 μm ; 19 = 25 μm .

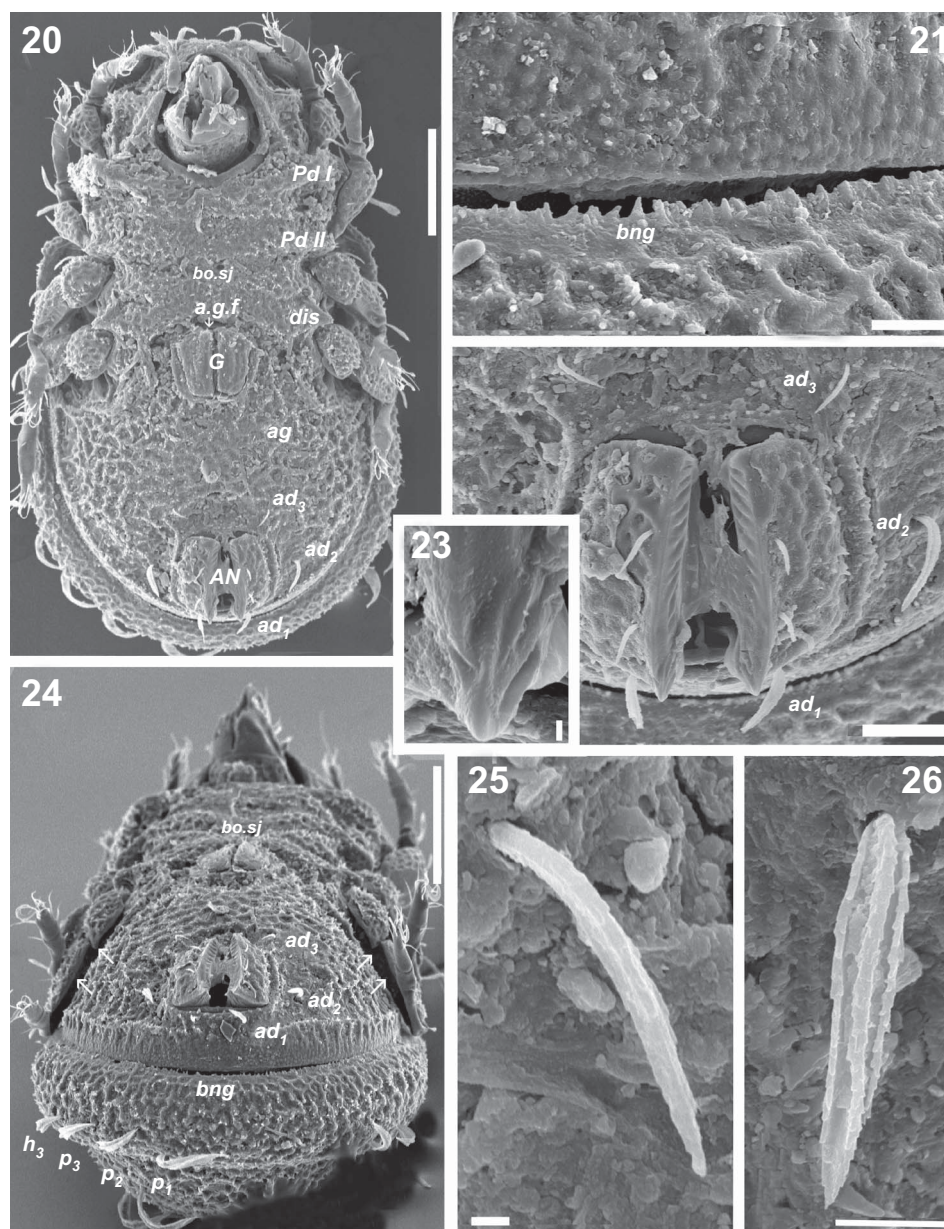
ro (28–32 μm length); notogastral setae all with only one medial serrate vein (Figures 1, 2, 5, 6, 12, 13 and 15). Setae *c₁*, *c₂*, *da*, *dm*, *dp*, *la*, *lm*, *lp*, *h₁* and *h₂*, largest (85–100 μm length); *p₁*, *p₂*, *p₃* and *h₃*, smaller (30–47 μm length); anal setae thin, only one vein (10–17 μm length) (Figure 22); adanal setae with only one vein but setae *ad₁* and *ad₂* broad (25–34 μm length) (Figure 26), setae *ad₃* thin (15–19 μm length) (Figure 25).

Genital and epimeric setae small, simple. For leg setae, see Legs.

Prodorsum. Convex shape (Figures 6 and 15) without any processes. Three pairs of anteriorly directed setae; size *in* > *le* > *ro*, all lanceolate-serrate (see Setation).

Lamellae dorsolateral; in dorsal view (animal with cerotegument) *l.l.f* is easily discernible with SEM

(Figure 1); in animals without cerotegument, an internal cuticular thickening is clearly visible, beginning near the bothridia and terminating on the internal side of the rounded apex of lamella (*la.ti*) (Figures 12 and 14); in frontal view, this internal cuticular thickening is visible on the cuticular surface as a shallow furrow. This internal cuticular thickening (internal part *la.ti*) extends towards the junction zone as prolamellae (*prl*) (Figures 12 and 14). Near the paraxial margin of lamella, the supra tutorial depression (*s.tu.d*) (Figure 12) is visible (by transparency). Lamellar setae laterally (Figures 14 and 15); seta *in* situated far from *l.l.f* (Figures 12 and 14). Rostral margin rounded (Figure 14). Bothridia cup-shaped with bothridial ring (*bo.ri*), smooth, does not extend to bothridial tooth (*bo.to*) (Figure 9).



Figures 20–26. *Austrocarabodes ensifer* (Sellnick, 1931). Adult, with cerotegument, scanning electron micrographs. 20. Ventral aspect. 21. Posterior view; above ventral zone, below notogastral zone; cerotegument detail. 22. Anal plate. 23. Detail anal plate, posterior teeth (acute process). 24. Posteroventral view; arrow indicates paraxial side of legs. 25. ad_3 seta. 26. ad_2 seta. Abbreviations: See Material and methods. Scale: 20, 24, = 100 μm ; 21, 22, 26 = 10 μm ; 23, 25 = 1 μm .

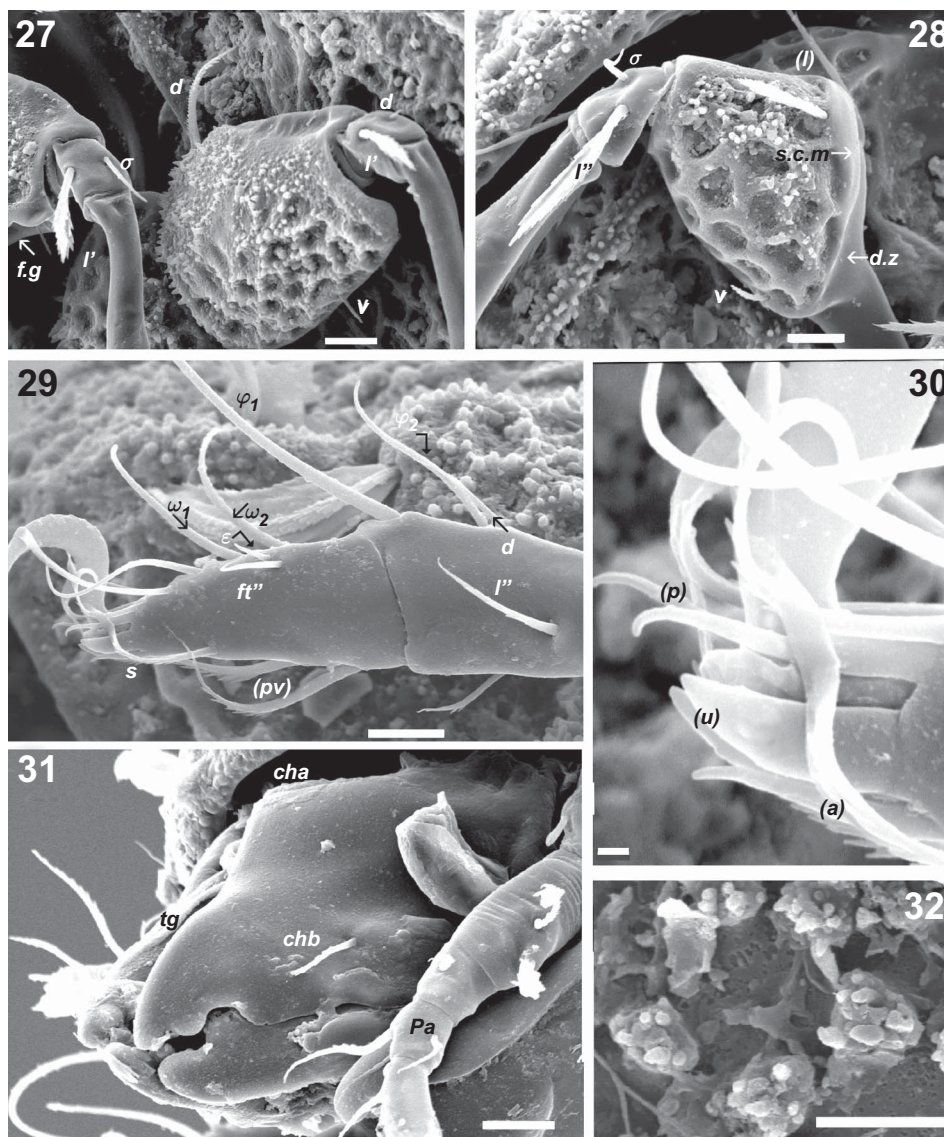
Sensillus spatulate, barbate (Figures 1, 6, 7, 9, 12 and 15) arching backward; in lateral position (Figure 7), small barbated dorsally; barboles increase in size from basal to apical (Figures 7 and 9). Forward to rostral setae, medial eye (*oc*) clearly visible (Figure 14).

Notogaster. Shape oval; *dsj* narrow, well-delimited (Figures 1 and 12), *s.c.* present, easily discernible (Figures 1, 2 and 3); from *s.c.* to upper concave shape, humeral apophysis (*h.ap*) prominent (Figures 6, 9 and 15), with large rod-like ridge, clearly discernible in lateral view (*h.r*).

Fourteen pairs of setae all lanceolate serrate; *gla* and lyrifissures not discernible, cuticular microsculpture and cerotegumental layer obscures observation.

Lateral region. Apical zone *h.ap* overlapping posterior part of *bo* (Figure 6). Across *h.ap*, bearing rod-like cuticular ridge (*h.r*) (Figures 7, 9 and 15); on *h.r*, cerotegumental finger-like structures aligned to each other (Figures 7 and 9).

Lamellar margin clearly visible; seta *le* in apical position; inner zone of lamella concave, to allow complete withdrawal (concealment) of leg I (similar to *Bovicarabodes deharvengi*); *tu* well visible as strongly curved cuticular thickening (Figures 6 and 15). The cuticle of the tutorial margin is smooth, but many cerotegumental teeth set on border surface (Figure 6). Between *lam* and *tu*, parallel to both structures, runs a deep *s.tu.d*; (Figures 6 and 15). In the zone extending forward from bothridia and terminating at



Figures 27–32. *Austrocarabodes ensifer* (Sellnick, 1931). Adult, with cerotegument; scanning electron micrographs. 27. Legs III and IV, femora, genua, tibiae (partial) antiaxial. 28. Leg I, femur, genu and tibia (partial) antiaxial. 29. Leg I, tarsus, tibia (partial), antiaxial. 30. Seta (u), (p), (a) tarsus I, antiaxial. 31. Chelicera, palps, antiaxial. 32. Cerotegumental notogastral polygonate areas. Abbreviations: See Material and methods. Scale: 27, 28, 29, 31, 32 = 10 μm ; 30 = 1 μm .

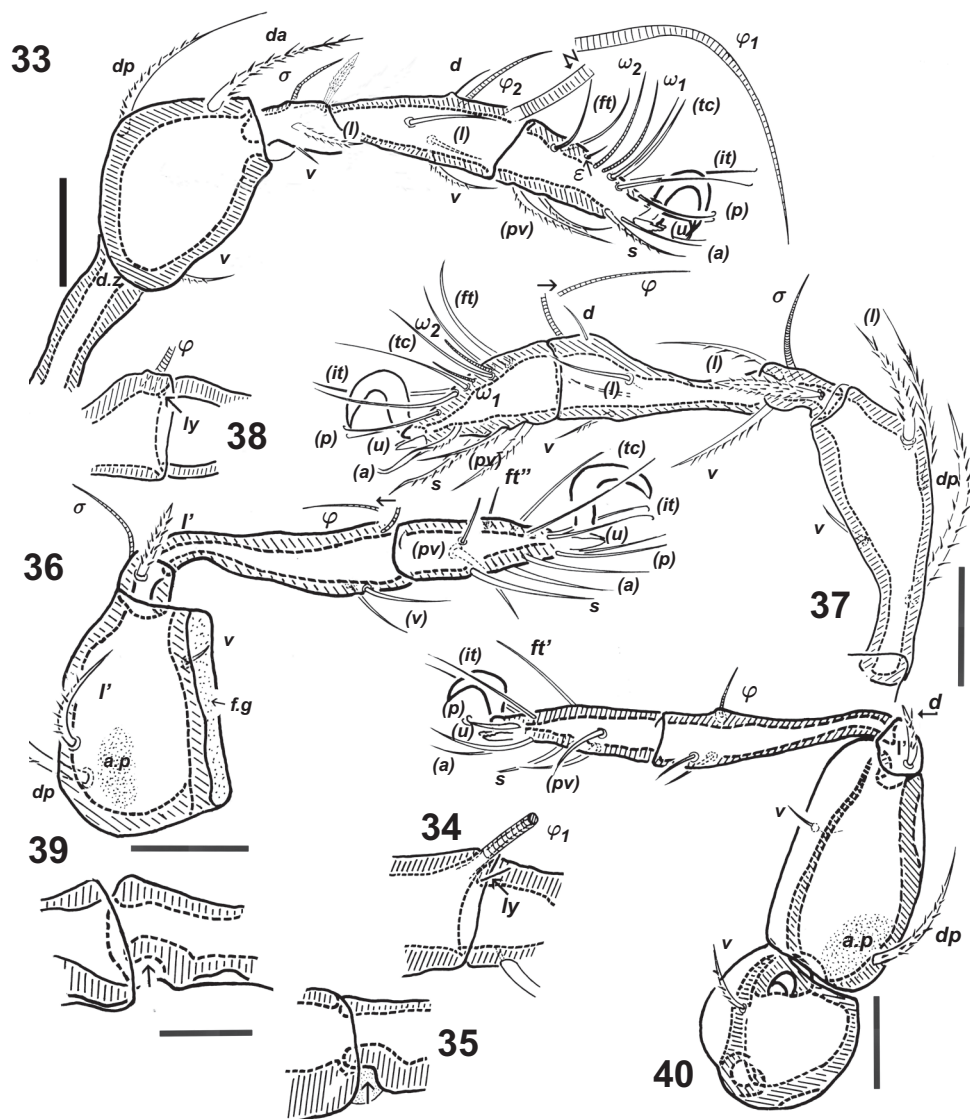
s.tu.d, cuticle is smooth. Pedotectum I, prominent extended lamina, rounded, covering the first acetabulum. Pedotectum II, small lamina, rounded apex. Sejugal depression (*sj*), deep, clearly visible (Figures 6 and 15).

The *lam* border, the inferior part of *bo*, and inferior part of *h.ap* are extended, forming a concave lateral expansion which plays an important role in the protection mechanism of this species.

Discidium. triangular protuberance, between acetabula III and IV (Figures 6, 15, 16, and 20). Above and underneath coxa IV many cuticular thickenings and irregular shallow polyhedral to ovoid depressions occur (Figures 6 and 15). Above *ad*₂, at level of insertion of setae a round point (indicated by arrow in Figure 15), probably a pore!

Ventral region. Epimera defined by shallow furrows, easily discernible in animals with cerotegumental layer (Figures 20 and 24). Epimeral chaetotaxy 3-1-3-3, most of setae were broken; in many cases, only insertion points visible (Figures 16 and 20). Apodemes 1, 2, *sj* and 3 clearly visible; *sj* across medial plan (Figure 4B). Immediately anterior to the genital plate a deep furrow (*a.g.f*) clearly visible by scanning electron microscope (SEM) (Figures 20 and 24); in optical observation, cuticular thickening which delimits *a.g.f* clearly visible (Figure 16). Four pairs of genital setae in unique line (Figure 16). Aggenital setae posterior to genital opening (Figure 16).

Three pairs of adanal setae, all setae lanceolate serrate but *ad*₁ and *ad*₂ broad (Figure 26) and *ad*₃ slender (Figure 25). Anal plate sharply tapered towards posterior



Figures 33–40. *Austrocarabodes ensifer* (Sellnick, 1931). Adult. Legs. 33. Leg I, antiaxial. 34. Tibiotarsus detail, solenidion φ_1 and tarsal lyrifissure indicated by arrow. 35. Genu–tibia detail of articulation, indicated by arrow. 36. Leg III antiaxial. 37. Leg II, antiaxial. 38. Tibiotarsus articulation lyrifissure indicated by arrow. 39. Genu–tibia articulation, arrow indicates particularity, see text. 40. Leg IV, antiaxial. The porose area indicated is situated paraxially. Abbreviations: See Material and methods. Scale: 33, 36, 37, 40 = 50 μm ; 34, 35, 38, 39 = 10 μm .

(Figures 22–24). Two pairs of anal setae: lanceolate, serrate, slender, similar to *ad*₃; lyrifissure *iad*, not discernible. Cuticular depressions clearly visible but only behind legs.

Posterior aspect. Notogaster round; *s.c* conspicuous, well-delimited furrow (Figures 2 and 13); many more or less parallel thickened cuticular ridges (Figure 13). Lyrifissures not discernible.

Gnathosoma. Infracapitulum diarthric, three pairs infracapitular setae, chelicera with *cha* and *chb* barbeled; Trågardh's organ clearly visible (Figure 31).

Legs. The legs were studied directly on intact animals. It is possible to study the legs undissected; however, certain imprecisions are possible, principally related to the position of setae of the trochanters, femora and genua. Many

detailed drawings were made to enable us to interpret the detail correctly.

The shape of the legs can best be studied from a posterior ventral view (Figure 24); in all legs, the paraxial zone is very flat and coapted to the cuticular surface. This enables the instantaneous deployment of leg folding as protection mechanism (see Fernandez et al. 2012). Legs monodactyle, with claws bearing small internal teeth.

Leg I (Figures 17, 18, 28–30 and 33–35). Femur with two well-delimited zones: basal zone narrow, smooth cuticle and middle to anterior zone polygonal in shape, cuticle reticulate-foveate; all setae barbate (Figures 28 and 33).

These two zones are clearly demarcated by a semi-circular margin (*s.c.m*). Following the *s.c.m*, a depressed area (*d.z*) exists (Figure 28), as well as between *s.c.m*

and *d.z.*, in order to permit placement of tibia II between femur I and the internal part of pedotectum I during leg folding (see *B. deharvengi*, Fernandez et al. *op. cit.*). In Figure 33, the drawing of the femur is slightly rotated and not exactly antiaxial; for this reason, the setae of this segment appear to be more dorsally placed than in reality. Genu typically very small (Figures 18 and 28) with prominent barbeled antiaxial setae; solenidion σ setiform, small. Tibia with two solenidions, φ_1 very long, tactile, situated on small apophyses (Figure 29), which are easily discernible in dorsal position (Figure 17); φ_2 setiform, small; small seta *d* inserted slightly away from solenidion insertion, but in many cases closely associated with the solenidion (Figures 17, 29 and 33). The ventral genu-tibia articulation is particular (Figure 35, arrow), neither a socket nor the standard articulation; the dorsal tibiotarsus articulation is overlapped by the small apophysis and conceal the tarsal lyrifissure (Figures 17 and 34). Tarsus with two small baculiform solenidia ω_1 and ω_2 ; ε small but clearly visible. The unguital seta (*u*) smooth and spur-shaped (Figure 30).

Leg II (Figures 37–39). Femora elongate with barbeled setae, paraxially prominent porose area; antiaxially foveate to reticulate-foveate integumental pattern; dorsal margin with integument and posterior area smooth. Genu small; large antiaxial barbeled setae; ventral articulation genu-tibia particular (Figure 39, indicated by arrow) similar to that of genu-tibia I. Solenidion φ tactile, medium length; seta *d* small, close to solenidion insertion. Tibiotarsus articulation by small synarthrodial membrane permitting limited movement. Lyrifissure concealed by articulation zone (Figure 38, arrow).

Leg III (Figures 18, 27 and 36). Trochanter rectangular, dorsally rounded; two dorsal barbeled setae. (Figure 19). Femur roughly rectangular; femoral groove (*f.g.*) with small inner seta (Figures 27 and Figure 36), antiaxially foveate to reticulate integumental pattern; paraxially, large porose area (Figure 19).

Leg IV (Figures 27 and 40). Basal antiaxial integument of femur with foveate to reticulate-foveate pattern and smooth dorsally (Figure 27). Smooth dorsal cuticular zone with longitudinal depression which permits insertion of this part into *f.g.*; basally concave paraxial blade (Figure 27) enables partial concealment of tibia; both structures used during leg folding process (see *B. deharvengi*, Fernandez et al., 2012).

Setal formulae (trochanter to tarsus): I (1-3-3-4-16-1) (1-2-2); II (1-4-3-4-15-1) (1-1-2); III (2-3-1-2-14-1) (1-1-0); IV (1-2-2-2-13-1) (0-1-0).

Genus *Aokiella*

The genus was established by Balogh and Mahunka in 1967.

Only two figures exist, one dorsal and one ventral: Figures 11 and 12, p. 64.

In 1986, in his revision of the family Carabodidae, Mahunka (*op. cit.*, p. 82), redescribed the genus.

Subias (*op. cit.*) considered the genus established by Balogh and Mahunka (1967) as a subgenus of *Odontocephus* with three species: *Odontocephus (Aokiella) florens* Balogh & Mahunka, 1967, *Odontocephus (Aokiella) latiseta* (Mahunka, 2008) and *Odontocephus (Aokiella) rotundus* (Hammer, 1979).

Redescription

Diagnosis

Prodorsum slightly convex, without elevated processes. Lamellae dorsolateral; dorsal part easily discernible by paraxial lamellar margin and internal cuticular thickening. Prelamellae exceed beyond insertion level of rostral setae. Seta *in* situated on internal lamellar margin; *le* lateral to apical lamellae. Rostral margin rounded. Bothridial ring present. Dorsosejugal furrow narrow, slightly arched. Notogaster with posterior dorsal depression. Fifteen pairs of setae; *dm*, *dp*, *lm*, *lp*, *h*₁, *h*₂, situated around posterior dorsal notogastral depression, directed towards centre of depression; circumgastric furrow shallow. Anterior of humeral apophysis overlaps posterior bothridial part. Tutorium strong cuticular thickening. Supratutorial depression deep. Pedotectum I, extended lamina, rounded apex; pedotectum II small, triangular lamina. Lateral margin of lamellae, inferior part bothridia, inferior part humeral process extend laterally. Epimera less defined; apodemata 1, 2, *sj* and 3 easily discernible. Epimeral chaetotaxy 3-1-3-3. Discidium well developed, triangular. Four pairs of genital setae. Anterior genital furrow clearly visible. Aggenital setae posterolateral. Three pairs of adanal setae. Anal plate sharp elongated tip. Two pairs of anal setae. Lyrifissure *iad*, situated posteriorly and external to *ad*₃ seta. Femur III, furrow present. Legs structurally adapted to execute protection mechanism.

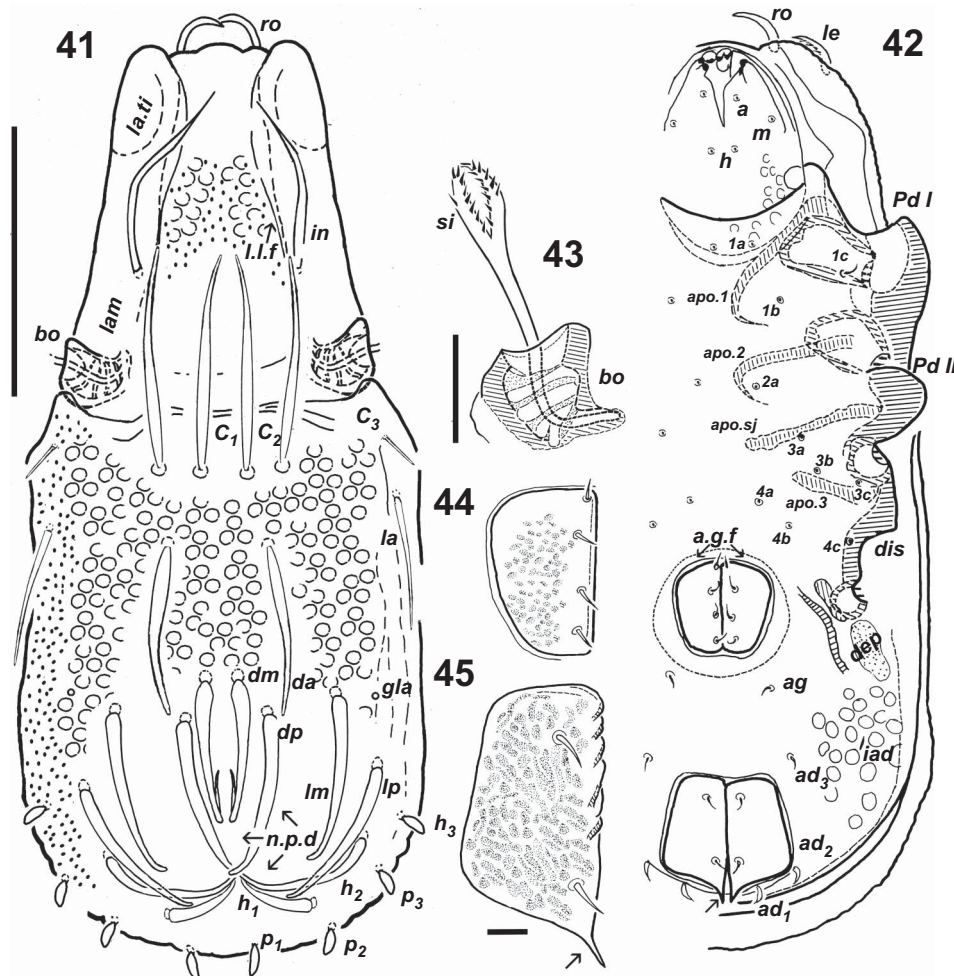
Type species

Aokiella florens Balogh & Mahunka, 1967
(Figures 41–49)

Redescription

Diagnosis

Prodorsum: setae: *in* simple, long, situated antiaxial internal lamellar margin; *ro* spiniform, curved directed paraxially; *le* barbeled, curved and situated laterally on lamellar apex. Setae, size *in* > *le* > *ro*. Sensillus apically rounded, with medial furrow, barbeled. Notogastral posterior depression simple, round; Notogastral setae: *c*₁, *c*₂, *c*₃ and *la*, simple; *c*₁, *c*₂, middle zone broad, directed forward, exceeding dorsosejugal suture; *c*₃, directed laterally on humeral apophysis near apex; length *c*₁ = *c*₂ > *la* > *c*₃. Setae *la* and *da* directed backward. Seta *dm* basally broad and apically rounded; setae *dm*, *dp*, *lm*, *lp*, *h*₁ and *h*₂, rounded apices. Circumgastric furrow originating near seta *la*. Setae *p*₁, *p*₂, *p*₃, *h*₃, *ad*₁, *ad*₂ and *ad*₃, lanceolate, barbeled. Setae *an*₁, *an*₂, *ag*, *g*₁, *g*₂, *g*₃ and *g*₄, epimeres simple.



Figures 41–45. *Aokiella florens* Balogh & Mahunka, 1967. Adult. 41. Dorsal aspect, arrow indicates the *n.p.d.* area. 42. Ventral aspect. 43. Sensillus and bothridium, lateral. 44. Genital plate. 45. Anal plate. Arrow indicates acute process. Abbreviations: See Material and methods. Scale: 41–43 = 50 μm ; 44, 45 = 10 μm .

Subcapitular setae barbeled. Humeral apophysis apex triangular. Lyrifissure *ia* between *c*₃ and *la*; *ips* between *h*₃ and *p*₃, others not discernible. Conspicuous cuticular depression between setae *ad*₂ and *ad*₃.

Material examined

Aokiella florens Holotype 0-50-67/as/Vietnam, 1966. Leg.Pocs. 1963.IX.17 Cu-Phoung, material in HNHM.

We studied the holotype material (the only existing specimen) but the details observed on the exemplar do not exactly correspond with the original description. The material is in rather poor condition, and the notations indicating locality, date, etc. are hardly visible.

Description

Measurements. Light microscopy: 374.3 μm \times 164 μm (310–327).

Colour. impossible to determine, the material is very transparent.

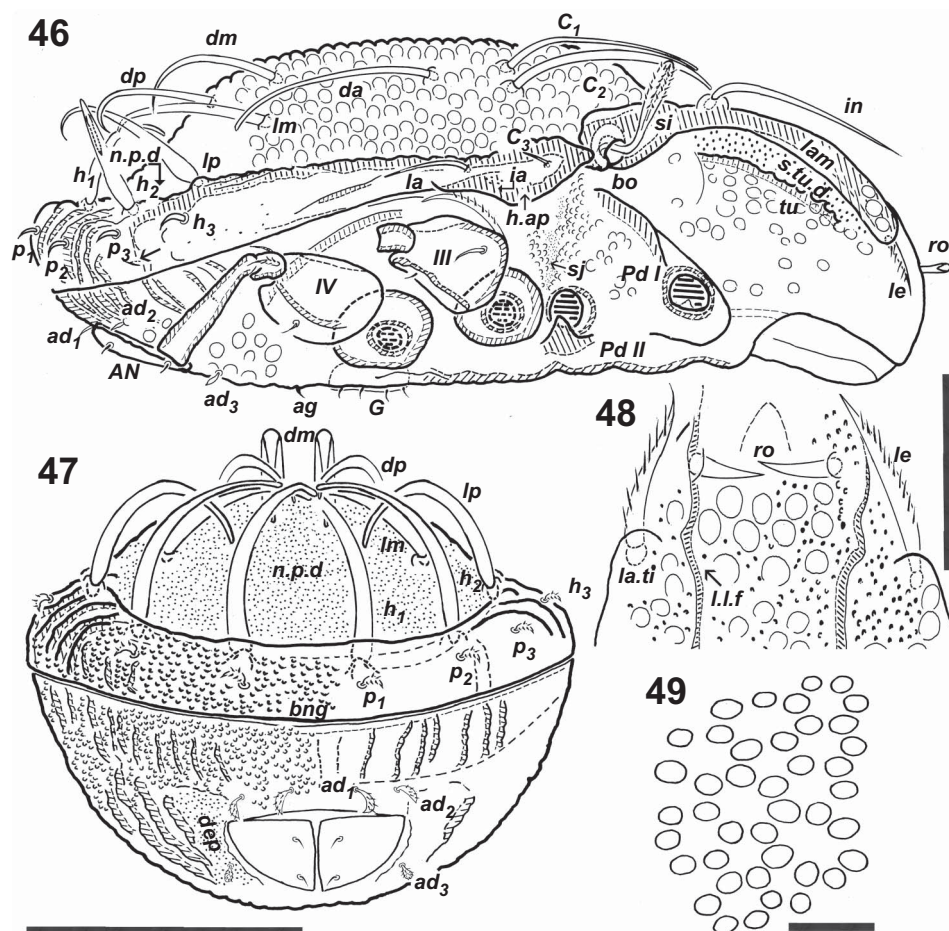
Cerotegument. Only remnant visible on the lateral side behind legs.

Integument. Prodorsum with foveate to falsifoveate pattern (Evans *op. cit.*), punctuate between the foveas (Figures 41 and 48). Lateral (Figure 46) foveate.

Notogaster foveate, but the foveae are arranged in circles of 5–7 (Figure 49) (impossible to make a more exact observation, owing to poor condition of material). The foveae are possibly distributed around a slightly elevated cuticular area. Between *s.c* and *bng* granulate (Figure 41). Posteriorly granulate (Figure 47) with many parallel cuticular thickenings (Figure 47). Posterior notogastral depression zone, rest of cerotegument or dirt obscured observation, but appears more or less smooth.

Lateral foveate at level of *Pd I*. Sejugal zone: punctate and in the depression zone: smooth to punctulate (Figure 46, arrow).

Ventral foveate (Figure 42); epimeric zone hardly discernible. Genital plate (Figure 44) irregular depressed areas and small tubercles. Anal plate: (Figure 45) irregular elevated areas (round to extended), irregularly distributed. Posteriorly and laterally to anal opening: granulate to punctate, with many more or less parallel cuticular crests (Figure 47).



Figures 46–49. *Aokiella florens* Balogh & Mahunka, 1967. Adult. 46. Lateral aspect. 47. Posterior aspect. 48. Rostrum frontal view. 49. Notogastral microsculpture. Abbreviations: See Material and methods. Scale: 46, 47 = 100 μm; 48 = 50 μm, 49 = 20 μm.

Setation. Prodorsal: seta *in* simple, long (Figure 41); seta *ro* spiniform, curved (Figures 41 and 48), directed paraxially; *le* barbeled, curved (Figures 46 and 48). Notogastral setae: *c1*, *c2*, *c3* and *la*, simple; *c1*, *c2* and *c3*, middle zone broad; *c3* and *la*, normal; length $c_1 = c_2 > la > c_3$. Seta *dm* slightly different, basally broad and apically rounded; setae *dp*, *lm*, *lp*, *h1* and *h2*, similar shape, apically rounded, these six pairs of setae are situated around notogastral posterior depression (*n.p.d*) zone and all are directed towards the centre of this depression (easily visible in posterior (Figure 47) and lateral (Figure 46) views (see Notogaster and Discussion).

Setae *p1*, *p2*, *p3*, *h3*, *ad1*, *ad2* and *ad3*, lanceolate, barbed; *an1*, *an2*, *ag*, *g1*, *g2*, *g3* and *g4*, epimeres simple (only two complete epimeral setae found, others broken); subcapitular setae *a*, *m* and *h*, barbellate.

Prodorsum. Slightly convex without any processes (Figures 41 and 46). Three pairs of setae; size $in > le > ro$ (Figures 41, 46 and 48) (see Setation). Lamellae dorsolateral; in dorsal view, easily discernible internal margin of lamella and internal cuticular thickening originating near the bothridia and ending internal to *la.ti* (Figure 41); this internal cuticular thickening extends as prolamellae (*prl*) (Figure 9C) that exceed the rostral level insertion. Seta *in*

situated antiaxially to internal lamellar margin (Figure 41), seta *le* situated laterally (Figures 46 and 48). Rostral margin rounded (Figure 41). Bothridia cup-shaped, bothridial ring exists but hardly discernible (Figure 46). Sensillus apically rounded, with medial furrow, barbeled (Figures 43 and 46) and directed slightly forward (Figure 46). Rostral setae directed to sagittal plane (Figure 48).

Notogaster. Oval shape; *dsj* narrow, well delimited, slightly arched (Figure 41).

Notogastral anterior depression absent but with a notogastral posterior depression (*n.p.d*) (see below); *h.ap* prominent, anterior part overlaps posterior part *bo* (see lateral) (Figures 41 and 46).

The *s.c* is hardly discernible as a tiny furrow originating near *la* seta and terminating near *gla*; close to this gland, the *n.p.d* exists and the *s.c* disappears (Figure 41).

Setal disposition particularly *c1* and *c2* directed forward, exceeding *dsj*; *c3* directed laterally; *la* and *da* directed backwards; *dm*, *dp*, *lm*, *lp*, *h1* and *h2*, converging towards central zone *n.p.d*; these six pairs of setae are situated around *n.p.d* and their apical tips converge to the central zone of this depression (clearly visible in lateral and in posterior views – see below). The *gla* situated on border of *n.p.d*.

(Figure 41). Setae p_1 , p_2 , p_3 and h_3 , marginal. Lyrifissures not discernible

Lateral region (Figure 46). Tutorium (*tu*) easily discernible as a strong cuticular thickening, margin undulated owing to cuticular microsculpture; *s.tu.d* deep. Lateral lamellar margin curved and internal side of lamellae concave (seen by transparency), easily discernible. All prodorsal setae clearly discernible; *la.ti* round; *le* seta inserted apically; sejugal region deep. *Pd I* extended lamina, rounded apex; dorsal margin with cuticular thickening; *Pd II* small, triangular lamina.

Humeral apophysis (*h.ap*) apically triangular, basally more or less rectangular, anterior apex overlaps posterior bothridial margin; c_3 seta on *h.ap* near apex, and *la* seta on *h.ap*, but near notogastral margin; the *s.c* exists in this zone. Between setae c_3 and *la*, a structure exists on internal margin of *h.ap* with all characteristics of lyrifissure *ia*; between setae h_3 and p_3 , lyrifissure *ips*, others not discernible. Large depression behind femora III and IV.

The lamellar border, inferior part of bothridia and inferior part of *h.ap* are extended laterally as a concave expansion and play an important role in protection mechanism.

The *n.p.d* easily discernible and setae h_1 , h_2 , *lp*, *lm* and *dp*, installed on periphery of depression, directed towards the centre. Behind leg IV, many cuticular thickenings (ridges) occur.

Ventral region (Figure 42). Epimera less defined (material very transparent). Apodemata 1, 2, *sj* and 3 well discernible. Epimeral chaetotaxy 3-1-3-3; seta insertion points clearly visible, setae small and broken.

To the front of the genital plate a furrow (*a.g.f*) exists, but to enable proper observation, it is necessary to rotate the specimen in order to allow observation from different angles.

Discidium clearly visible; between acetabulum leg IV and genital plate, cuticular thickening, and behind opening leg IV, large depressed area (*dep*).

Four pairs of genital setae situated in a unique line (Figure 44). Aggenital setae posterolateral. Three pairs of adanal setae; ad_3 , posterior and slightly external to *ag* seta level; ad_1 , ad_2 and ad_3 , similar shape, but ad_3 thin.

Anal plate internal margin with cuticular thickening and posterior margin with long and acute process (Figure 45); two pairs of anal setae; lyrifissure *iad* situated posterior and external to ad_3 setae.

Posterior aspect (Figure 47). Clearly visible *n.p.d* and position of setae *dm*, *dp*, *lm*, *lp*, h_1 and h_2 . Many ridges to p_2 . Between ad_2 and ad_3 , a prominent *dep* delimited by cuticular thickening exists. External to this *dep*, many cuticular thickenings; zone with microsculpture granulate to punctuate.

Legs. In bad condition, study of setae is problematic. Many setae are broken, and the segments are too much transparent to study. Only some characteristics are visible; femur III with *f.g* and small setae inside the groove, dorsal part of

femur adapted to be concealed under *h.ap* lateral expansion (Figure 46); femur IV with dorsal zone adapted to be placed into *f.g* during leg folding process.

Genus *Singabodes*

Diagnosis

The genus was established by Mahunka in 1998.

Redescription

Diagnosis

Prodorsum convex without elevated process. Lamellae dorsolateral; paraxial margin and shallow lamellar furrow easily discernible. Lateral lamellar margin curved, internal edge concave. Seta *in* situated on dorsal lamellar margin; seta *le* laterally situated on rounded part of lamellar apex. Rostral margin rounded. Bothridial ring smooth. Notogaster oval with complex posterior depression process; dorsosejugal furrow narrow rectilinear. Circumgastric furrow shallow. Notogastral setae, 15 pairs. Notogastral setae: posterior notogastral depression bearing h_1 , h_2 , *lp*, *lm*, *dp*, *dm* (vestigial) and *gla*; setae p_1 , p_2 , p_3 and h_3 situated marginal notogaster. Only one lyrifissure discernible, *im*. Humeral apophysis extended, overlaps posterior bothridial margin. Tutorium strong cuticular thickening. Supratutorial depression deep. *Pd I* extended lamina with rounded apex; *Pd II* small, triangular lamina, apically rounded. Discidium triangular protuberance. Behind IV acetabulum, genital and anal plates, many depressions. Lateral margins: lamellae, bothridia, humeral process, extended laterally, partially concealing legs; femur III with femoral groove. Apodemes 1, 2, *sj* and 3 easily discernible. Epimeral chaetotaxy 3-1-3-3; anterior genital furrow clearly visible. Four pairs of genital setae. Aggenital setae situated posterior to genital opening. Three pairs of adanal setae. Two pairs of anal setae; lyrifissure *iad* situated posterior and external to ad_3 .

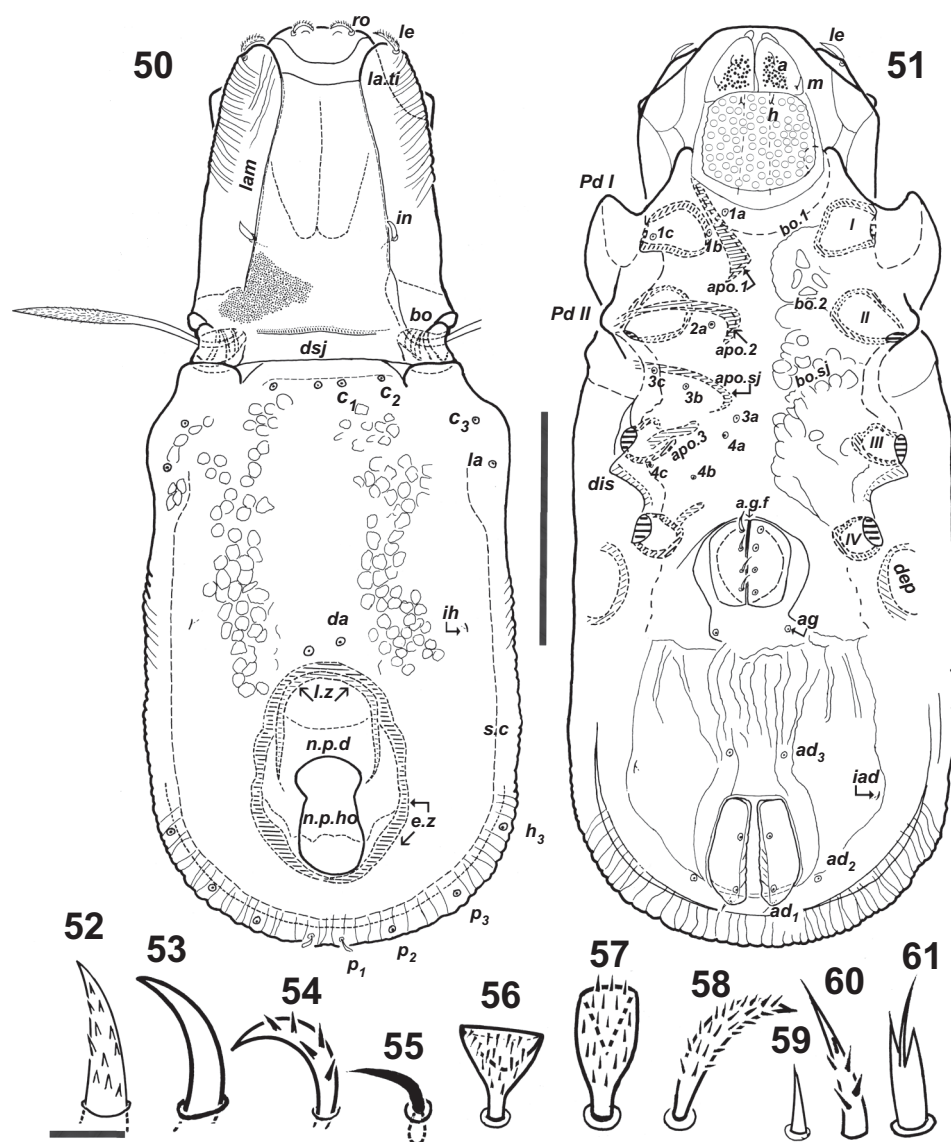
Type species

Singabodes rarus Mahunka, 1998
(Figures 50–69)

Redescription

Diagnosis

Prodorsum. Lamellar apex antiaxially rounded, paraxially concave, ending in triangular structure, not elevated and attached to cuticular surface. Prolamellae exceed rostral setal insertion level, ending near rostral margin; *in* spiniform, smooth, curved; *ro* spiniform, curved, barbellate; *le* situated behind acute lamellar tip, spiniform, faintly curved, barbellate. Setal size: $le > in = ro$. Notogaster oval shape. Posterior notogastral depression complex: round pocket shape, only superior dorsal part open, in irregular cavity. Inner part divided into external and internal zones; external zone ovoid, contains setae h_1 , h_2 and *lp* and cuticular thickening situated around setal insertion. Ovoid internal zone



Figures 50–61. *Singabodes rarus* Mahunka, 1998 Adult. 50. Dorsal aspect. 51. Ventral aspect. 52. *le* seta. 53. *in* seta. 54. *ro* seta. 55. Epimeric seta. 56, 57, 58. Notogastral seta (not seta of inner notogastral posterior depression), and adanal seta, different position. 59. Subcapitular setae. 60. *ag* and *g*₂, *g*₃, *g*₄ setae. 61. *g*₁ seta. Abbreviations: See Material and methods. Scale: A, B = 100 μ m; C–L = 10 μ m.

contains anterior and posterior zones. Posterior zone carrying setae *dp*, *lm* and *gla*. Anterior zone bearing *dm* vestigial setal insertion. Setae *h*₁, *h*₂, *lp*, *dp* and *lm* situated in notogastral posterior depression; triangular concave shape, large barbules apically, directed outwards via the opening on top. Lanceolate barbeled setae: *c*₁, *c*₂, *c*₃, *la*, *p*₁, *p*₂, *p*₃, *h*₃. Epimera well defined. Epimeric setae simple, small. Setae *g*₁, *g*₂, *g*₃, *g*₄ and *ag*, barbeled but *g*₁, slightly different, similar barbs, in apical zone. Adanal small, lanceolate, barbeled. Subcapitular setae spiniform. Only one lyrifissure discernible, probably *im*. Many depressions behind acetabulum IV near genital and anal plates.

Material examined

Singabodes rarus Mahunka, 1998. Holotype Singapore Bukit Imah.

Collector. D.H. Murphy. 9-VII-1969.D-12-7. Muséum d'Histoire Naturelles, Genève

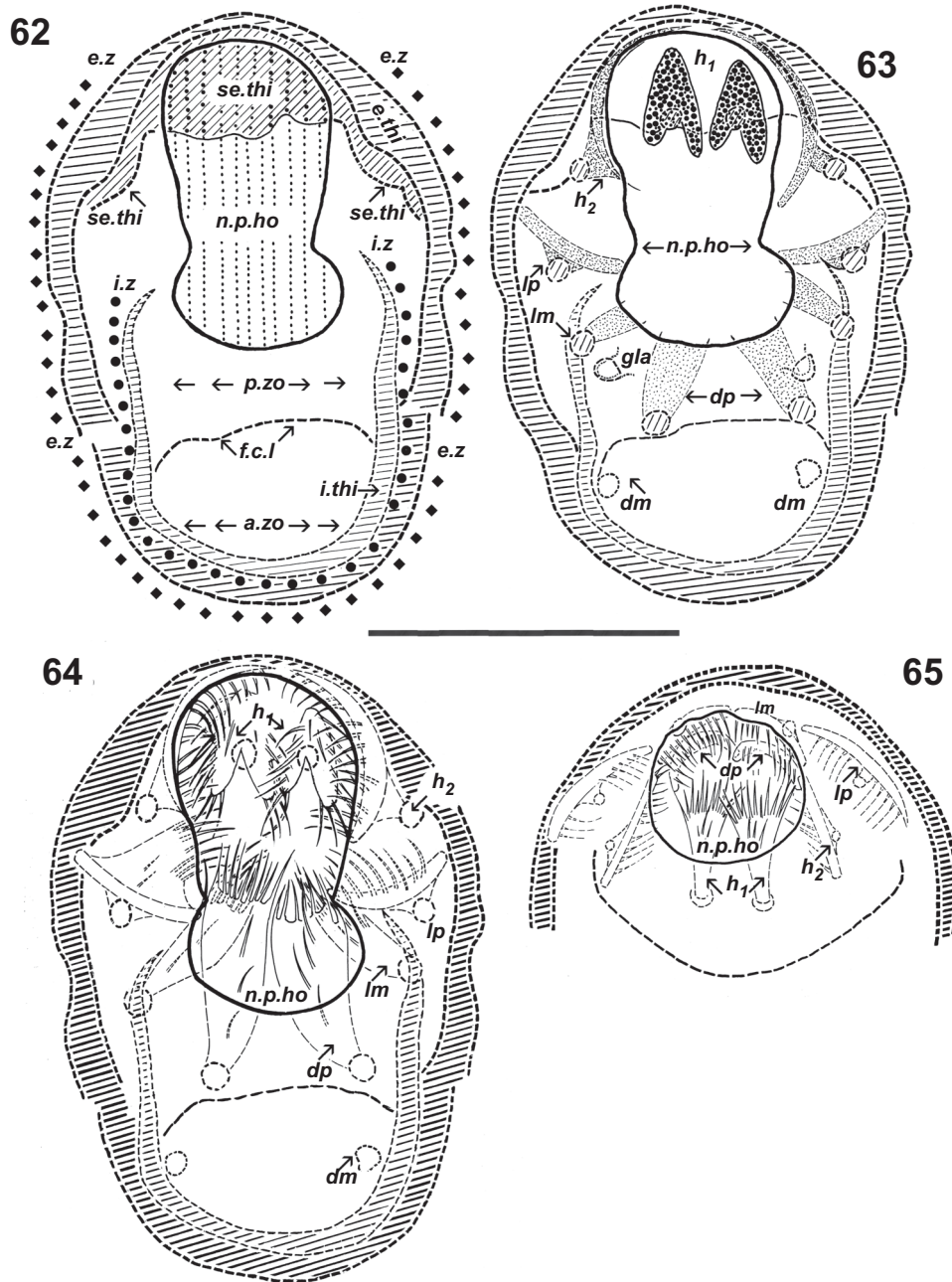
Description

Measurements. Light microscopy only: 352 μ m \times 138 μ m. (Figures 50, 51 and 62).

Colour. specimens without cerotegument: brown clear to yellow.

Cerotegument. Impossible to describe; mostly damaged.

Integument. Prodorsum punctuate to puncticulate (*sensu* Evans *op. cit.*); anterior antiaxial part of lamellae many parallel crests (Figure 50), in frontal view, the parallel thickening extends to internal margin of lamellae (Figure 69). From the level of seta *in* forward, between the



Figures 62–65. *Singabodes rarus* Mahunka, 1998 Adult. Notogastral posterior depression. 62. Dorsal view, without setae. 63. Dorsal view, schematic setae position. 64. Dorsal view, setae, integrated drawing. 65. Posteriodorsal view, setae integrated drawing. Abbreviations: See Material and methods. Scale: 62–65 = 75 μ m; with small diamond-shaped marks indicating the extension of external zone (*e.z*) and with small black circles indicating extension of internal zone (*i.z*).

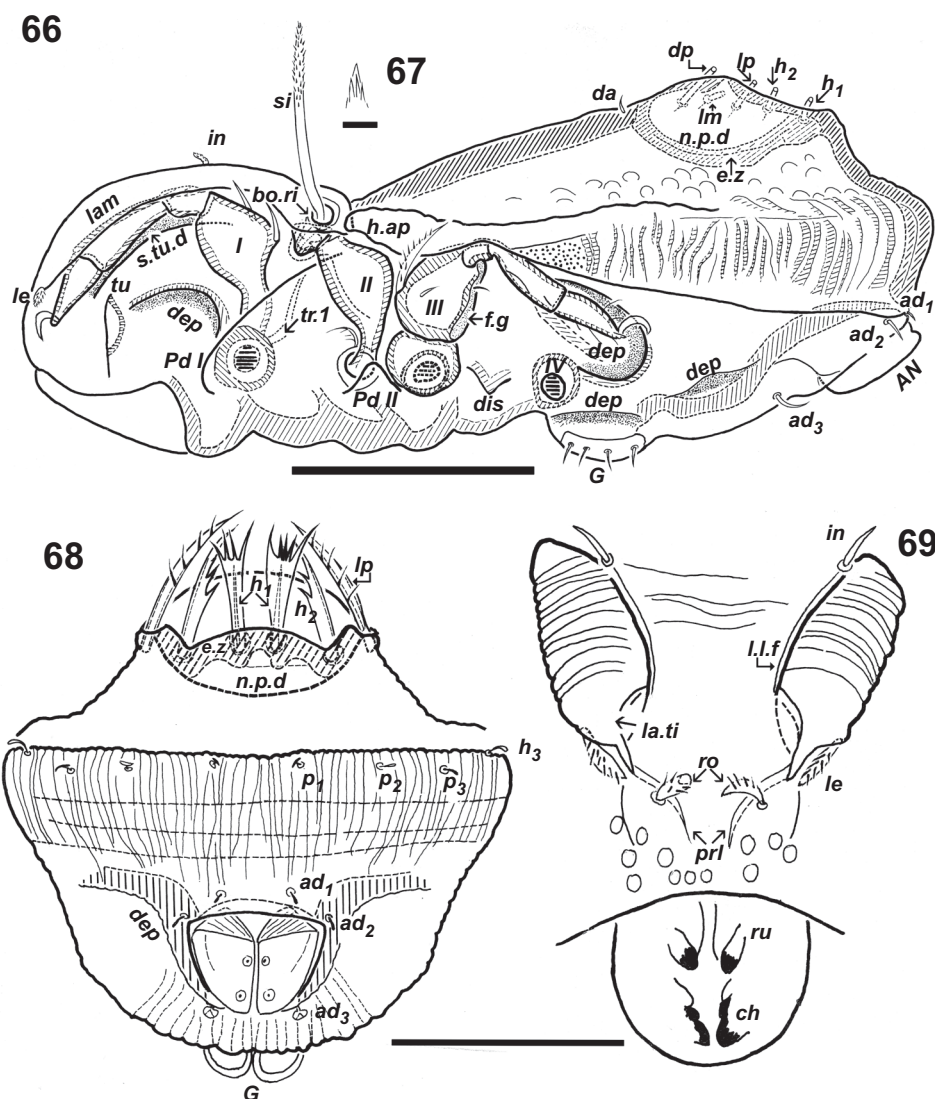
internal lamellar margin; many ridges occur. Near rostrum punctulate (Figure 64).

Notogaster tuberculate (*sensu* Evans *op. cit.*); central area less visible, the tubercles seem less pronounced (Figure 50). Lateral at level of lyrifissure *lm*, many oblique parallel thickenings. Posteriorly many parallel cuticular thickenings (Figures 50, 51 and 63). Lateral, posterior to *h.ap* near *bng* (punctuate to punctulate) (Figure 62), following this zone, many thickenings perpendicular to *bng*.

Ventrally tuberculate (Figure 51). Behind legs IV prominent depressed areas. Behind *ag* seta many irregular thickenings and depressed areas (Figure 51. Infracapitulum

around seta *h* foveate and (arrow) seta *m* granulate to punctate (Figure 51).

Setation. Prodorsal setae: *in* spiniform, smooth, curved (Figure 53); *ro* spiniform, curved, barbeled (Figure 54); *le* spiniform, slightly curved, barbeled (Figure 52). Notogastral setae: *c₁*, *c₂*, *c₃*, *la*, *p₁*, *p₂*, *p₃*, *h₃*, lanceolate barbeled (Figures 56–58; setae *dm*, *dp*, *lm*, *lp*, *h₁*, *h₂*) situated in the notogastral posterior depression (*n.p.d*) (=hollow, Mahunka 1998), structurally very different from other notogastral setae; *h₁* more or less triangular shape, concave, triangular section barbeled, apical zone long



Figures 66–69. *Singabodes rarus* Mahunka, 1998 Adult. 66. Lateral aspect, simplified drawing, only setae into the notogastral posterior depression and setae *da* are indicated. 67. Sensillus apical area, lateral view. 68. Posterior view. 69. Frontal view. Abbreviations: See Material and methods. Scale: 66 = 100 μm , 67 = 15 μm ; 68, 69 = 75 μm .

barbs (Figures 63–65); h_2 , lp , triangular, slightly concave; apically long barbs (Figures 63–65); lm , dp , triangular, apically long barbs (Figures 64 and 65); dm , only insertion visible, internally $n.p.d$ (Figures 63 and 64). Epimeric setae simple, small (Figure 55); g_2 , g_3 , g_4 , ag , barbeled (Figure 60); g_1 different to others, only barbs similar, in apical zone (Figure 61). Adanal setae small, lanceolate barbeled (Figures 56–58). Subcapitular setae spiniform (Figure 59).

Prodorsum. Slightly convex shape without any processes (Figures 50 and 66). Three pairs of setae; size $le > in = ro$ (Figure 50). Lamellae dorsolateral; dorsal and frontal views easily discernible internal margin and $l.l.f$, beginning slightly in front of in seta and ending on the internal side of the apical tip of lamella ($la.ti$) (Figure 69). The $la.ti$ antiaxially rounded and paraxially concave; a prolamella (prl), curved to paraxial, exceeds the rostral setal level insertion, ending near the sagittal plane not far from

the rostral margin (Figure 69). Seta le situated laterally on the antiaxial rounded part of $la.ti$ (Figure 69).

Seta in situated on dorsal lamellar margin (slightly paraxial) (Figure 69); le seta lateral side lamellar apex (Figures 50 and 69). Rostral margin rounded (Figure 50), this structure visible situated between the lamellae in dorsal view but is not detectable in frontal view. Bothridia cup-shaped, $bo.ri$ smooth (Figure 66).

Sensillus setiform; apex acute, with large barbs (Figures 66 and 67); median zone to apex many tiny barbs.

Notogaster. Shape oval; dsj narrow, well-delimited, rectilinear (Figure 50). Lacking anterior notogastral depression but with a particular notogastral posterior depression ($n.p.d$) (Figure 66). Fifteen pairs of setae: c_1 , c_2 , c_3 , da , dm , dp , la , lm , lp , h_1 , h_2 , h_3 , p_1 , p_2 , p_3 ; dm vestigial, only insertion discernible. Prominent $h.ap$, extended anterior rounded part, overlaps posterior bothridial part (see lateral) (Figures 50 and 66). The $s.c$ a shallow furrow originating near la seta.

The *n.p.d* deep, ovoid with an “oven” shape; superior dorsal part with irregular, ovoid hollow *n.p.ho* connecting the inner part with exterior (Figures 62–65, 66 and 68). The *n.p.ho* irregularly shaped, with anterior and posterior margins rounded (Figure 62). Internally the *n.p.d* bears six pairs of setae as well as *gla*. Inner part of *n.p.d* structurally complex with two well delimited zones: external (*e.z*) and internal (*i.z*) (Figure 62).

External zone (*e.z*) ovoid delimited by cuticular thickening (*e.thi*); *e.z* contains three pairs of setae (*h₁*, *h₂*, *lp*); with a prominent ridge, extending around the insertion zone of setae (*se.thi*) (Figure 62).

The internal zone (*i.z*), ovoid, delimited by an internal cuticular thickening (*i.thi*). The *i.z* contains two zones: posterior (*p.zo*) and anterior (*a.zo*). The *p.zo*, is a structure with an open posterior end, near level of *n.p.ho* (Figures 62 and 63), and bears two pairs of setae (*dp*, *lm*) and the *gla*. The *a.zo*, delimited by closed anterior end of *i.thi* and posteriorly by a finely curved line (*f.c.l*), situated behind *dp* insertion; between the *a.zo* and the *f.c.l* is an ovoid area. Inner *a.zo* exists as a small rounded structure, possibly the vestigial basal attachment of *dm* seta (Figures 62 and 63).

The shape, position and situation of the six pairs of setae are particularly unique and very interesting; the long apical barbules of five of these pairs extend out of the *n.p.ho* (Figures 63–65), only the *dp* vestigial setal insertion is not related to the *n.p.ho*. Seta *h₁* situated in the posterior part of *n.p.ho* and some body setae and apical barbules extend outward (Figures 63 and 64). The insertion of *h₂* seta a small distance from the *n.p.ho* margin, but the semicircular seta body is positioned near the *n.p.ho* margin and the apical barbules are extended to the exterior through the *n.p.ho* (Figures 63 and 64). The *lp* setae are situated far from the *n.p.ho* and only a few apical barbules extend outward from the *n.p.ho* (Figures 63 and 64). The *lm* and *lp* setae insertions are closer to *n.p.ho* with part of the body setae and many apical barbules extending from the *n.p.ho*. Finally the vestigial *dm* setal insertion is some distance from the *n.p.ho* (Figures 63 and 64).

Setae *p₁*, *p₂*, *p₃*, *h₃* are situated on the notogastral margin and are not related to the *n.p.d* (Figure 50). Only one lyrifissure, probably *im*, discernible.

Lateral region. Tutorium (*tu*) clearly discernible as a prominent cuticular thickening; *s.tu.d* deep (Figure 66 portrays leg I partially situated in the *s.tu.d*). Lateral lamellar margin curved and internal side of lamellae concave, showing legs partially concealed under the interior part of lamella (Figure 66); *la.ti* basally rounded, terminating in an acute tip (Figure 69); seta *le* inserted near apex of lamella but situated laterally (acute lamellar tip, situated dorsally) and on the rounded anterior zone of apex (Figures 66 and 69). Towards the front of acetabulum I, under *tu*, a conspicuous semicircular depression occurs (Figure 66). Bothridial opening with *bo.ri*; *do.to* exists but not clearly visible (Figure 66). *Pd I* an extended lamina with rounded apex; *Pd II* small, triangular lamina, rounded apically (Figure 66); *n.p.d* easily discernible; setae *h₁*, *h₂*, *lm*, *dp*, *dm* clearly

discernible inside the depression; seta *da* situated anterior zone *n.p.d*; discidium easily discernible between legs III and IV (Figure 66). Behind leg IV, near genital and anal plates, many depressions and cuticular thickenings occur (Figure 66). The lamellar lateral margin, bothridial lateral margin, and margin of humeral apophysis extend laterally and partially conceal the legs (Figure 66) (in the cited figure, leg IV is removed and tibia, tarsus II eliminated, to permit observation of the position of leg I related to the discidium and the posterior depression areas). The *f.g* femur clearly visible (Figure 66).

Ventral region (Figure 51). Epimera well defined. Apodemes 1, 2, *sj* and 3 easily discernible. Epimeral chaetotaxy 3-1-3-3; setal insertion clearly visible, setae small (Figures 51 and 55).

Immediately anterior to the genital plate *a.g.f* exists, but for best observation the specimen has to be rotated and orientated in different positions. It can best be observed in a lateral view (Figure 66).

Discidium clearly visible between acetabulum III and IV. Behind acetabulum IV, prominent depressed area (*dep*) as well as other smaller depressed areas.

Four pairs of genital setae in a unique line (Figure 50). Aggenital setae posterior to genital opening. Three pairs of adanal setae; *ad₃*, to the front of anal plate, same longitudinal level as aggenital setae. Anal plate internal margin with cuticular thickening; two pairs of anal setae; lyrifissure *iad* situated further laterally, between *ad₃* and *ad₂* setae (Figure 51).

Posterior aspect (Figure 68). Notogastral posterior depression (*n.p.d*) and setae *h₁*, *h₂*, *lp*, *p₁*, *p₂*, *p₃*, *h₃* clearly visible. A very prominent cuticular thickening lateral to anal plate, many cuticular furrows behind anal plate. In notogastral zone of *p₁* to *h₃* many parallel cuticular thickenings occur.

Legs (Figure 66). The legs are only partially illustrated, the fourth pair lost. The general features/characteristics of legs are very similar to that of *B. deharvengi* (Fernandez et al., 2012) and clearly fulfill the same function during the protection mechanism display as was described for the latter genus.

Remarks

The cerotegument is a unique and interesting element, and although it is formed by secretions from the epidermis, it provides useful diagnostic characteristics on the species level. However, it is mostly neglected. Evidently, for proper study of the cerotegument, SEM observations should be complemented by light microscopy.

Austrocarabodes ensifer (Sellnick, 1931) presents all structures associated with the protection mechanism process as found in many other genera. However, in *A. ensifer*, many of the protection mechanisms and related structures are less developed than in *B. deharvengi*. This is specifically true for the depressed areas on lateral part of body, the femoral groove and the dorsal part of femur IV (this zone inserts into *f.g*). The trochanter and femur of leg IV

is paraxially flattened, and this facilitates the coaptation process of the leg with cuticular surface. The presence of a well-developed cerotegument with unique features in different areas may play an important role.

The sensillus and its relation to the cuticular thickening situated on the humeral process are very interesting. During deployment of the protection mechanism, the barbeled sensillus is withdrawn behind the cuticular thickening and cerotegumental layer with finger-like projections.

The presence of the shallow lamellar furrow and the internal cuticular thickening (clearly discernible in specimens with or without cerotegument) and the small *d* seta, associated with φ on tibia I and II, are very interesting characteristics which need to be studied in more detail. We consider the *d* seta incorrectly referred to in *Austrocarabodes hendriksi* Hugo, 2008 as *l'*, legs I and II, (Figure 2, p.28); *Austrocarabodes vernoncrookensis* Hugo, 2008 as *l'*, leg I (Figure 5, p.32); in *Austrocarabodes lucienensis*, Hugo, 2008 as *l'*, leg I (Figure 7, p.34); *Austrocarabodes lineasetosa* Hugo, 2010, (Figure 6) as integrated pair (*l*) and *Austrocarabodes mahunkai* Hugo, 2010 as *l'* (Figure 2).

Aokiella florens. We have already explained the need for detailed observations and not only from a dorsal and ventral view. *Aokiella florens* serves as a good example. Observations in lateral and posterior views are fundamental towards interpreting the existence of the notogastral posterior depression and the situation related to the notogastral setae. This insight assists us in relating *Ao. florens* to *S. rarus*.

In the present work, we reported nothing regarding the cerotegument and integumental characteristics of *Ao. florens* and *S. rarus* because of the poor condition of the material. It will thus necessitate observations on fresh material by light microscopy as well as scanning electron microscopy to add to our knowledge of these two species.

Discussion

Austrocarabodes ensifer Sellnick, 1931.

Better understanding of many different morphological aspects was gained due to the opportunity to study specimens with the use of optical and SEM microscopy. Also, the opportunity to study a larger number of specimens enabled us to study the legs in detail.

Many descriptions and redescrptions of the genus and type species were found in literature: the genus was described by Hammer (1966), redescrined by Mahunka (1986), Pérez-Iñigo (1971) and Murvanidze and Weigmann (2007); Hugo (2008) made a diagnosis of the genus, partially combining Hammer (1966) and Mahunka (1986) and added comments regarding the number of epimeral setae which was changed by Mahunka (3-1-3-3) in relation to Hammer's description (3-1-3-4). Hugo (2008) also reported three cases in which the setal number established

by Hammer was observed: *A. costulatus* Balogh, 1958, *A. nodosus* Hammer, 1966 and *A. maculatus* Hammer, 1966. The 14 notogastral pairs of setae were also mentioned.

In our redescription, with reference to the foregoing, we were able to add many characters and eliminate others which may be considered specific characters. As an initial step, the redescription of the genus was based only on the type species. All species included in the genus need to be reviewed and descriptions adapted to actual observations.

Conditions for the study of *Ao. florens* and *S. rarus* were very different to that of *Au. ensifer*. In the case of *Ao. florens*, only a single type specimen exists, while for *S. rarus*, two specimens exist (of which we could obtain only one). The condition of the material of *Ao. florens* is very poor and a study of this specimen required enormous effort; the material was very transparent and needed staining. *Aokiella florens* presented a major example of oversights and mistakes. In the original description by Balogh and Mahunka (1967), 15 pairs of notogastral setae were reported; but in the redescription by Mahunka (1986), the author indicated 14 pairs in text; he, however, drew 15 pairs. The arrangement of the notogastral setae *dm*, *dp*, *lm*, *lp*, *h*₁, *h*₂ is very particular; in the original species description only two figures exist, one dorsal and another ventral. In dorsal position the cited setae with their apices converging can be observed. In lateral view, a posterior notogastral depression can be observed, and observations from several different angles allow better understanding of the real situation. The setae are situated around or even slightly into the depression, and the tips of setae are orientated towards the central part of it. The latero-abdominal gland is found externally but near the antiaxial depression margin.

For *S. rarus*, we found many differences to the original description relating to number, length and shape of setae, prolamellae (named as prelamellae), shape of sensillus and many other errors related to the posterior notogastral depression (named "hollow"), its internal structure and setal arrangement; also the chaetotaxy of leg III was omitted in the text. The illustrations of the body were very schematic and with many undefined aspects; those of the legs contained mistakes and were not clearly labelled; for example, in Figure 9, tibia and tarsus of leg I and the *d* seta were associated with solenidion φ_2 , and in Figure 10, genu of leg I and seta *d* were provisionally placed near the solenidion. The figures of leg II were even more complicated; in Figure 13, leg II, and Figure 11, tibia and genu, leg II, the tibia had three setae and one setiform solenidion, and genu with three setae and one solenidion, but in Figure 13, the tibia had one seta and one solenidion (with particular shape) and genu with one solenidion and only one seta. Seta *d* existed only in tibia I and not in tibia II; genu I had a seta *d*.

Study of the posterior notogastral zone of *S. rarus* quickly leads to an understanding that the "hole" (*sensu* Mahunka 1998) is a specialized posterior notogastral depression, where the margins are close and delimit an ovoid structure containing six pairs of setae and the *gla*,

with an irregular opening through which the large barbeled apical zone of setae protrude. We noted six pairs of setae (*dm*, *dp*, *lm*, *lp*, *h*₁, *h*₂), five modified setae (*dp*, *lm*, *lp*, *h*₁, *h*₂) and one vestigial (*dm*). We observed that *S. rarus* has 15 pairs of setae and one vestigial (*dm* only insertion visible), with the following distribution: *c*₁, *c*₂, *c*₃, *la*, *da*, *h*₃, *p*₁, *p*₂, *p*₃ resembling that of *Ao. florens*. The setae *dm*, *dp*, *lp*, *lm*, *h*₁ and *h*₂ and the *gla*, which are situated around the posterior depression in *Ao. florens*, are found in the same posterior structure, with particular characteristics in *S. rarus*.

Mahunka in 1998 stated: "The characteristic notogastral structure, combined with the shape of setae and sensillus, makes it impossible to place this new species in any of the so far known genera of Carabodidae (Mahunka 1986)".

Subías (*op. cit.*) regards *Aokiella* as a subgenus of *Odontocephus*. We consider *Aokiella* as a genus in own right, but need to further study the genera *Odontocephus* and *Indotocephus* (also considered a subgenus of *Odontocephus*) for clarity.

Many important questions arise: Are the characteristics established by Mahunka really at generic level or do they represent specialization of one species only? Are differences pertaining to the shapes of the sensilli and setae (extensive differences exist between Mahunka's observation and ours) sufficient reason to establish a genus? For example, in other genera such as *Austrocarabodes*, many different sensillus types exist.

In the diagnoses of the genera *Aokiella* and *Singabodes* other small differences occur, but are these specific or generic? Only two other species occur in the genus *Aokiella* and only one in *Singabodes*, probably too small a number to obtain definitive conclusions! Without doubt, the two genera are closely related, and possibly should be considered congeneric. *Singabodes* may be a synonym of *Aokiella*, but further study is necessary. This is complicated by the lack of immatures for study, and the fact that the only particularity of *S. rarus* as species seems to be the "hole" (specialized posterior notogastral depression), but there seems to be other species with this particularity. Is this characteristic alone enough to establish *Singabodes* as a separate genus?

Acknowledgements

During our revision of the family Carabodidae, we encountered many difficulties in obtaining type materials but we were also fortunate to encounter some researchers who kindly assisted us.

Peter J. Schwendinger (Dr. Sc.), Curator of the Department of Arthropodology and Entomology at the Muséum d'Histoire Naturelles, Geneva, is especially thanked for his support in facilitating our research. Well preserved specimens of *Au. ensifer* Sellnick, 1931 and *S. rarus*, Mahunka, 1998, were obtained. Without his assistance it would have been an impossible task.

We are also grateful to Dr. László Dányi, HNHM, for assisting us in obtaining type specimens of *Ao. florens*.

The paratype of *S. rarus*, deposited in the Hungarian Natural History Museum, Budapest, was impossible to obtain.

We acknowledge the valuable comments made by each of the reviewers, which without doubt contributed to the quality of this paper.

This work is based partly upon research supported by the National Research Foundation (NRF), South Africa. Any opinion, findings and conclusions or recommendations expressed in the material are those of the authors and therefore the NRF does not accept any liability in regard thereto.

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