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## Revision of the family Carabodidae (Acari: Oribatida) XIV. *Phyllocarabodes costaricensis* sp. nov. from Costa Rica and *Zimbabweae kenyaensis* sp. nov. from Kenya

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### ABSTRACT

*Phyllocarabodes costaricensis* sp. nov. and *Zimbabweae kenyaensis* sp. nov. are described using optical microscopy and scanning electron microscopy. For *Phyllocarabodes costaricensis* sp. nov., a detailed description is provided, along with a discussion on the position of *Phyllocarabodes* as subgenus within the genus *Carabodes*. We conclude that *Phyllocarabodes*, with a series of particular characteristics, is a distinct genus and not a subgenus of *Carabodes*. The genus *Phyllocarabodes* is redefined. *Zimbabweae kenyaensis* sp. nov. is closely related to *Zimbabweae pluosiae* Fernandez, Theron, Leiva 2016, exhibiting the following distinctive characters: shape of prodorsal zone promontories different; associated structures and trajectory of circumgastric depression dissimilar; pedotectum I, pedotectum II and discidium differ in shape; dissimilar disposition of promontories; differences in ventral and epimeral zones.

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### ARTICLE HISTORY

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### KEYWORDS

Carabodidae; systematics; *Phyllocarabodes*; *Carabodes*; problematic

### Introduction

The taxonomy of the family Carabodidae has historically been beset by many problems in the genera the authors have studied over the past few years (Fernandez et al. 2013a, 2013b, 2013c; Fernandez et al. 2014a, 2014b, 2016). The case of *Phyllocarabodes*, however, is a veritable imbroglia.

Important remarks: (1) type material was not available for study; (2) incomplete and controversial descriptions by the same authors; (3) taxonomic changes made without justification.

The description of the genus *Phyllocarabodes* by Balogh and Mahunka (1969b) was somewhat vague and incomplete. In 1986, Mahunka redefined the genus, with a contradictory description with several aspects opposite to the original description given by Balogh and Mahunka (1969b). In 1986, Balogh P. described a new species, *Phyllocarabodes ornatus* and made several comparisons with the type species, several of them contradictory.

Subías (2004, updated 2017) included the genus *Phyllocarabodes* as subgenus of *Carabodes* without providing an explanation for doing so.

We analysed the preceding papers and compared them to our results of the description of *Phyllocarabodes costaricensis* sp. nov. to clarify the taxonomic situation of *Phyllocarabodes* and determine if it is a subgenus of *Carabodes* or not.

The second species described in this article is *Zimbabweae kenyaensis* sp. nov., collected in Kenya.

### Materials and methods

Specimens studied by means of light microscopy followed the techniques described by Grandjean (1949) and Krantz and Walter (2009). Specimens studied with scanning electron microscope (SEM) followed the techniques of (Alberti and Fernandez 1988, 1990a, 1990b; Alberti et al. 1991, 1997, 2007; Fernandez et al. 1991). Equipment used is that of Fernandez et al. (2016).

For *Zimbabweae kenyaensis* sp. nov., the complexity of structures is evident in SEM micrographs (Figure 46–72). For ease of understanding and to facilitate observation, only the cuticular thickenings were indicated in drawings.

### Morphological terminology

Morphological terms and abbreviations used are those developed by Grandjean (1928–1974) (cf. Travé and Vachon 1975; Norton & Behan-Pelletier (in Krantz and Walter 2009; Fernandez et al. 2013a, 2013b, 2013c, 2014a, 2014b). For setal types Evans (1992) and for ornamentation of cuticular surfaces Murley (1951) (*In*: Evans *op.cit.*, 9) were used. The following are added: prodorsal longitudinal ridge (*p.l.r.*); promontories (*prm*), used as: *prm la*, *prm lm*, *prm lp*, *prm h<sub>1</sub>*, *prm h<sub>2</sub>*, *prm h<sub>3</sub>*, *prm p<sub>3</sub>*, *prm p<sub>2</sub>*, *prm p<sub>1</sub>* (promontories where the respective setae are inserted); transverse posterior prodorsal furrow (*t.p.p.f.*); transverse series of small aggenital promontories (*t.ag.p.*).

### New taxon description

***Phyllocarabodes costaricensis* sp. nov.**  
(Figures 1–45)

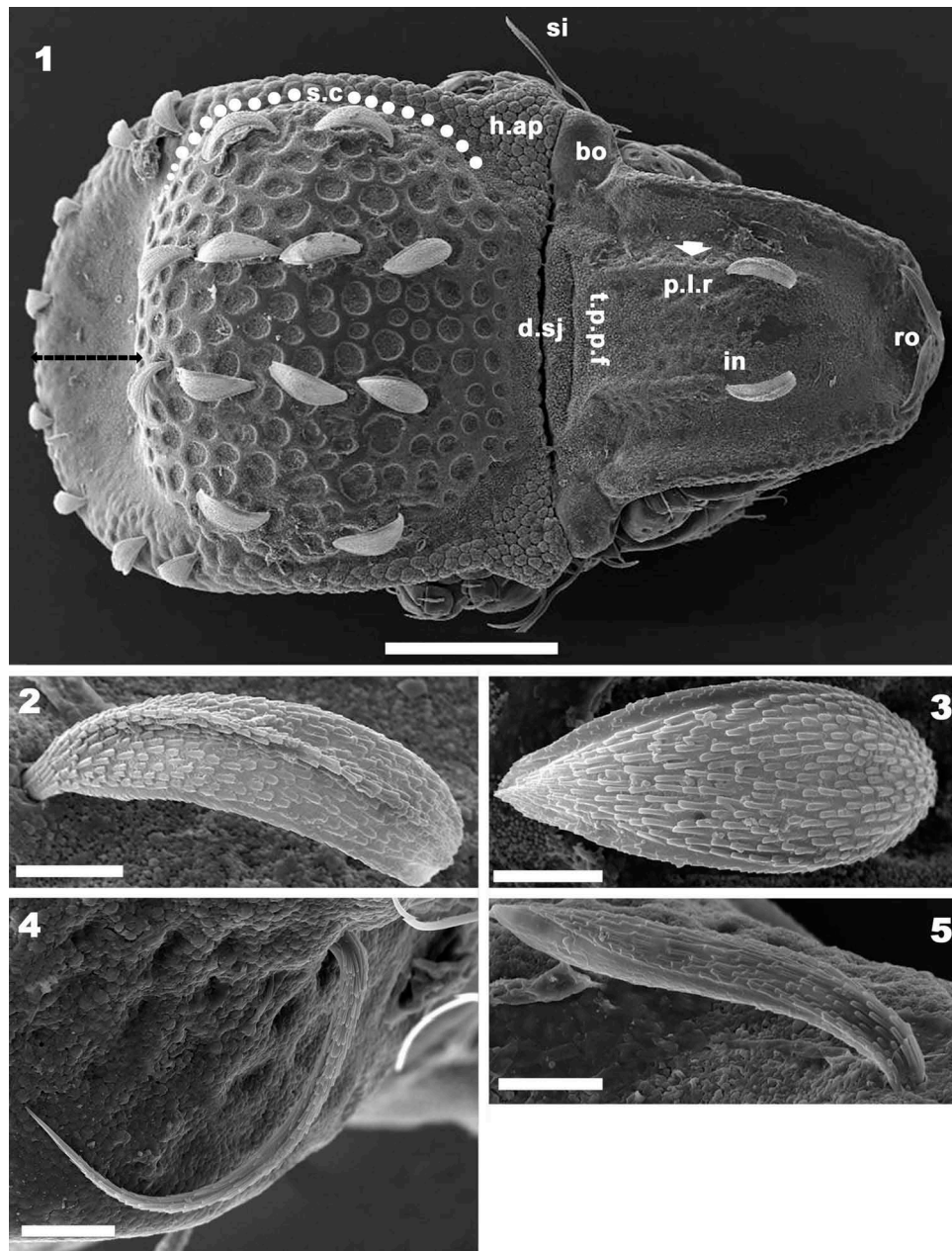
### Etymology

The specific epithet “*costaricensis*” is derived from Costa Rica, country of origin of the type material.

### Material examined

**Holotype:** Female “CR 0978 Tu 11 Costa Rica Turrialba forêt naturelle du catie alt.560 m. Triage d’humus côté est surface nid d’Atta au pied de *Castilla elastica* 1.IX. 1978. LEG P. WERNER”, material deposited in the Collection of the Natural History Museum of Geneva (NHMG), Switzerland; preserved in 70% ethanol.

**Paratype:** Two adult females, same locality and date as Holotype; deposited in Collection of NHMG; preserved in 70% ethanol. Material studied using SEM: three specimens, not deposited.



**Figure 1–5.** *Phyllocarabodes costaricensis* sp. nov. Adult female, SEM observations. **1.** dorsal view; **2.** interlamellar setae; **3.** notogastral setae; **4.** lamellar setae; **5.** rostral setae. Abbreviations: see section on “Material and methods”. Scale bars: 1 = 100  $\mu$ m; 2–5 = 10  $\mu$ m.

#### Diagnosis (adult female)

**Setation:** *in* setae, *Salix* leaf-shaped; *ro* setae elongate leaf-shaped; *le* setae, long phylliform, small dentitions; notogastral, adanal setae ovoid leaf-shaped, rugous margin; genital setae (three first pairs), setiform with longitudinal ribs; genital setae (last three pairs) flagelliform; epimeric setae, elongate barbate; anal setae, spiniform. Prodorsum elongated; posterior prodorsal depression absent. Prodorsal longitudinal ridge bearing insertions of the interlamellar setae; bothridium rounded, with bothridial opening curling to resemble a mouse ear. Tutorium: large curving lamina, with aligned ventrally dentitions. Pedotectum II, small rectangular lamina. Notogaster, light bulb-shaped; 10 pairs of setae with particular disposition; circumgastric furrow incomplete. Epimeral setal formulae 1-1-3-3; setae *3b*, *3c* situated more or less parallel, close to each other. Six pairs of genital setae. Lyrifissure *iad* lateral of *ad*<sub>3</sub> setae.

#### Description

**Measurements.** SEM 460  $\mu$ m (455–466)  $\times$  183  $\mu$ m (177–194) ( $n = 3$ ). Light microscopy: 463  $\mu$ m (458–472)  $\times$  184  $\mu$ m (179–194) ( $n = 3$ ).

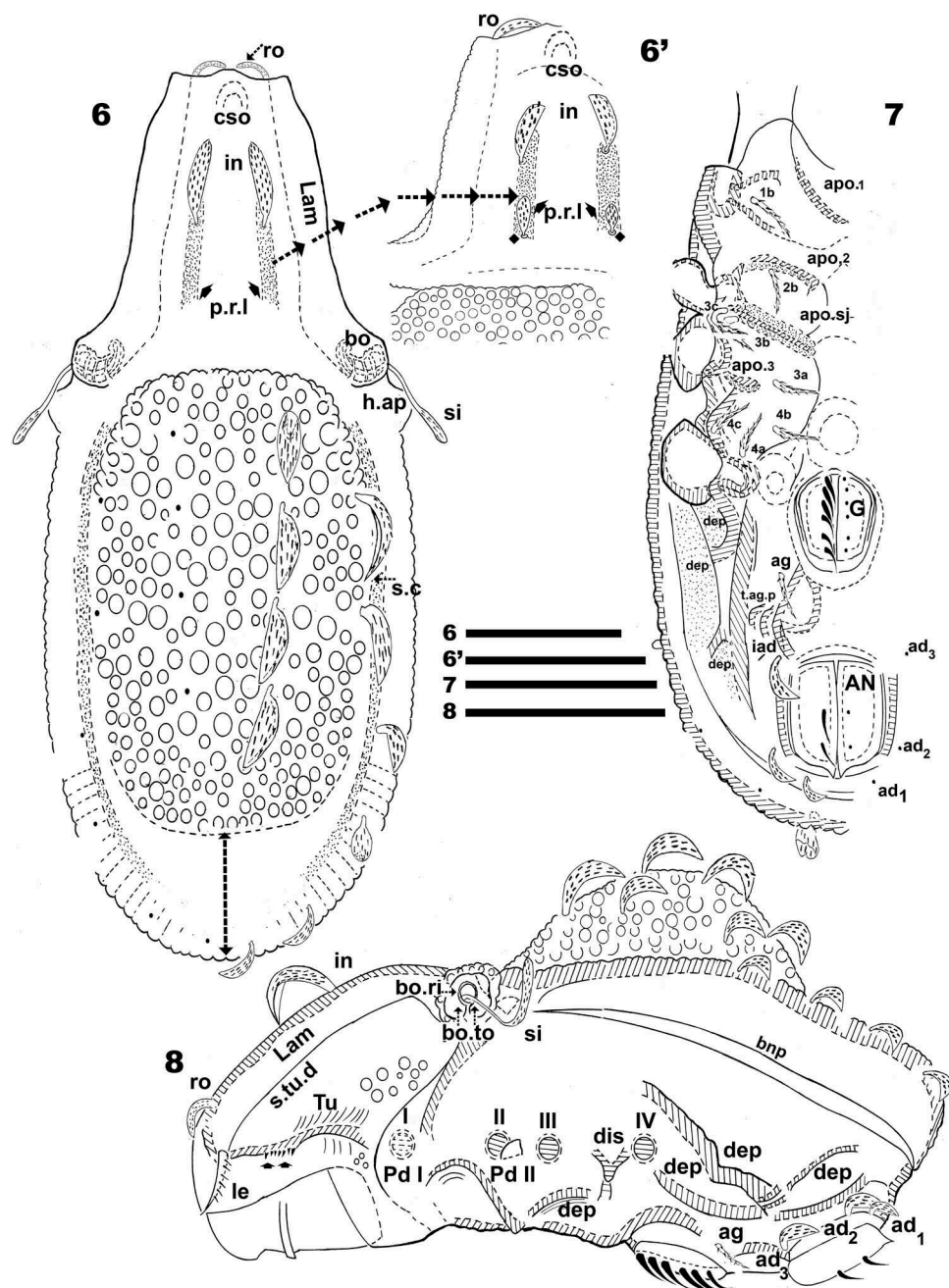
**Shape.** Elongate oval (Figures 1 and 6).

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

**Cerotegument.** Present: prodorsum, notogaster and ventral region. *Slightly granulated layer:* prodorsal region near *in* setae, notogaster marginal zone, subcapitulum, bothridial zone (Figures 15, 16, 25, 35 and 36); *layer of fine pustules:* central notogastral zone, genital plate, aggenital zone, prodorsum posterior zone, humeral apophysis, epimeral zone (Figures 12, 13, 19, 20, 27, 30 and 31).

**Integument.** Microsculpture. *Foveate:* notogastral elevated zone (Figures 1, 9, 19 and 20); *colliculate:* marginal zone, extending from *h.ap* to posterior marginal zone where notogastral lateral setae are situated (Figures 1, 10, 12, 13, 18 and 27); *granulate:* zone of *s.c* (Figures 9, 10, 12 and 16), bothridial zone (Figures 12 and 13); anterior and posterior zones of *d.sj* (Figures 1 and 12); *small foveate* (Figures 9 and 22): lateral prodorsal margin, in front insertions of *ro* setal, prodorsal zone between prodorsal longitudinal ridge





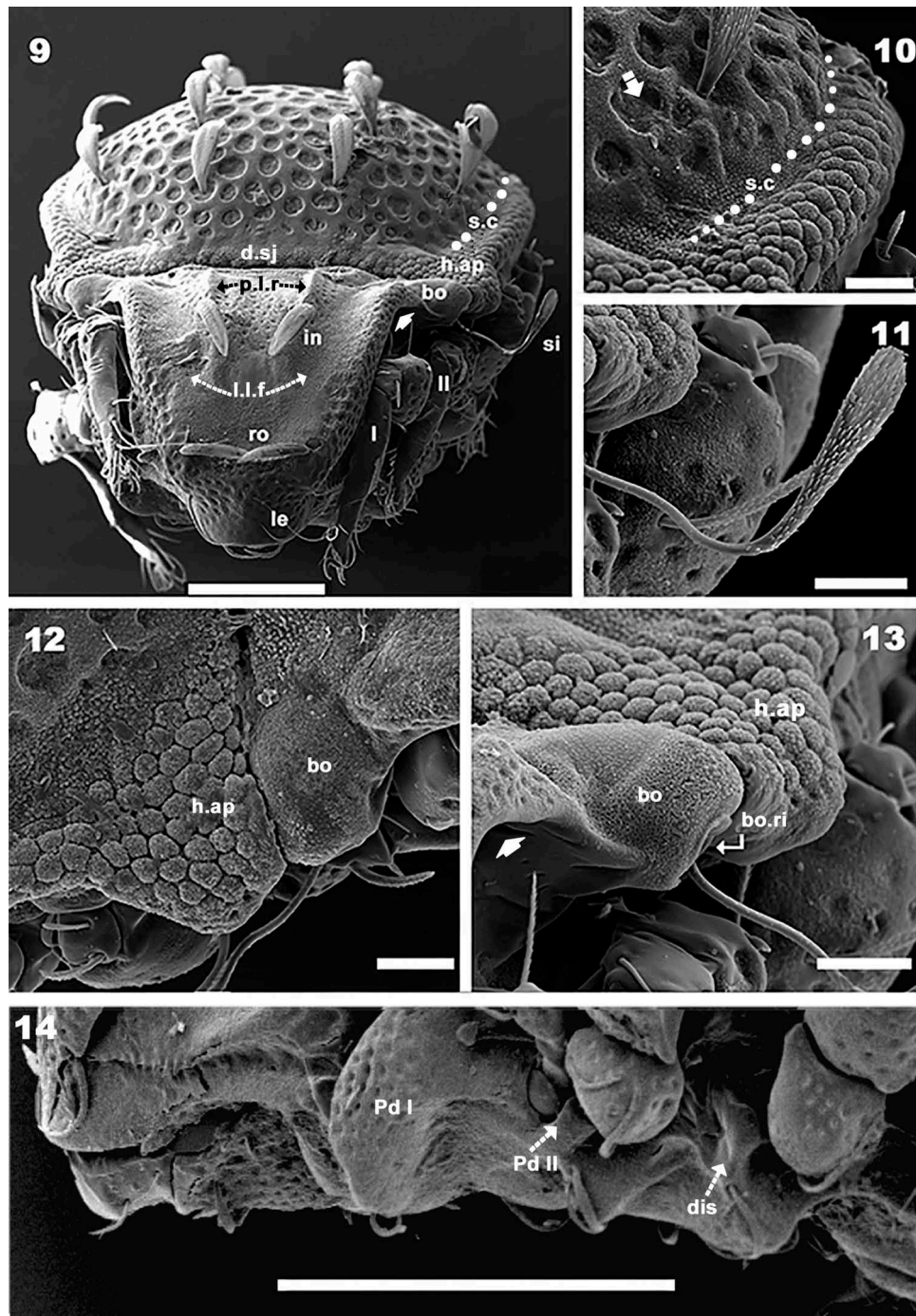
**Figure 6–8.** *Phyllocarabodes costaricensis* sp. nov. Adult female, Optical observations. **6.** dorsal view; **6'.** detail prodorsal area; **7.** ventral view; **8.** Lateral view. Abbreviations: see section on “Material and methods”. Scale bars: 6, 6' = 100 µm; 7 = 130 µm; 8 = 120 µm.

(Figures 15 and 17), lamellar zone, tutorial zone, pedotecta I, femur I–IV (Figure 27); punctate: between elevated notogastral zone and marginal notogastral zone (Figures 1 and 6 indicated by —); granulate: epimeral zone (Figures 32, 33 and 39).

**Setation.** Large variation: *in* setae: *salix* leaf-shaped with small barbules and raised central region, length 36–44 µm, width 10 µm ( $n = 6$ ) (Figures 2 and 9). Notogastral setae, length 34–40 µm, width 14 µm (Figures 1, 3 and 9); adanal  $ad_1$ ,  $ad_2$ ,  $ad_3$ , length 28–34 µm, width 7 µm (Figures 28 and 32): ovoid leaf-shaped, central zone elevated with barbules and slightly rugous margin. Setae *ro*: elongate leaf-shaped, central zone slightly elevated with small barbules and rugous margin, length 55–61 µm, width 8 µm (Figures 1, 5 and 9). Setae *le*: long phylliform with small dentitions, length 54.5–60.5 µm, width 2.5 µm (Figure 4). Anterior three pairs of *ge* setae: large, broad, curving setiform. Three posterior pairs of *ge* setae: setiform with longitudinal ribs, length 18–24 µm, width 2 µm (Figures 37, 44 and 45) (see ventral region). Subcapitular *h*

setae: leaf-shaped with small barbules, length 23–29 µm, width 4–5 µm (Figures 24 and 25). Subcapitular *m* setae: slightly inflated setiform (Figures 40). Epimeral setae: elongate leaf-shaped, with barbs (Figures 33). Anal setae spiniform (Figure 34). Subcapitular *a* setae slightly flabellate (Figure 42). Setae *ag* setiform with longitudinal ribs and marginal dentition (Figure 29).

**Prodorsum.** Prodorsum trapezoidal (dorsal view) (Figures 1 and 6); triangular, rounded apex in frontal view (Figure 9); polyhedral in lateral view (Figure 27). Elevated interlamellar process (*e.i.p*) flat, slightly convex (Figures 1, 9 and 27); posterior notogastral depression absent (Figures 1 and 6). Conspicuous prodorsal longitudinal ridge (*p.l.r*) (Figures 1 and 6, 6', 9, 15) originating near posterior transversal furrow (*t.p.p.f*) (Figure 1); *in* setae inserted on *p.l.r*. Prodorsal longitudinal ridge exceeding level of *in* setal insertions, but not extending to level of *ro* setal insertion (Figures 1 and 9); forward and slightly medially directed curved *in* setae



**Figure 9–14.** *Phyllocarabodes costaricensis* sp. nov. Adult female, SEM observations. **9.** frontal view; **10.** lateral view, posterolateral notogastral zone; **11.** sensillus, lateral view; **12.** humeral apophysis; **13.** bothridium anterior lateral view, bothridial ring zone; **14.** lateral zone, Pd I, Pd II, dis. Abbreviations: see section on “Material and methods”. Scale bars: 14 = 200  $\mu$ m; 9 = 100  $\mu$ m; 10, 11, 12, 13 = 20  $\mu$ m.

(Figures 1, 6 and 9); ro setae directed anteriorly and slightly medially, apical tips overlapping (Figures 1, 9 and 21).

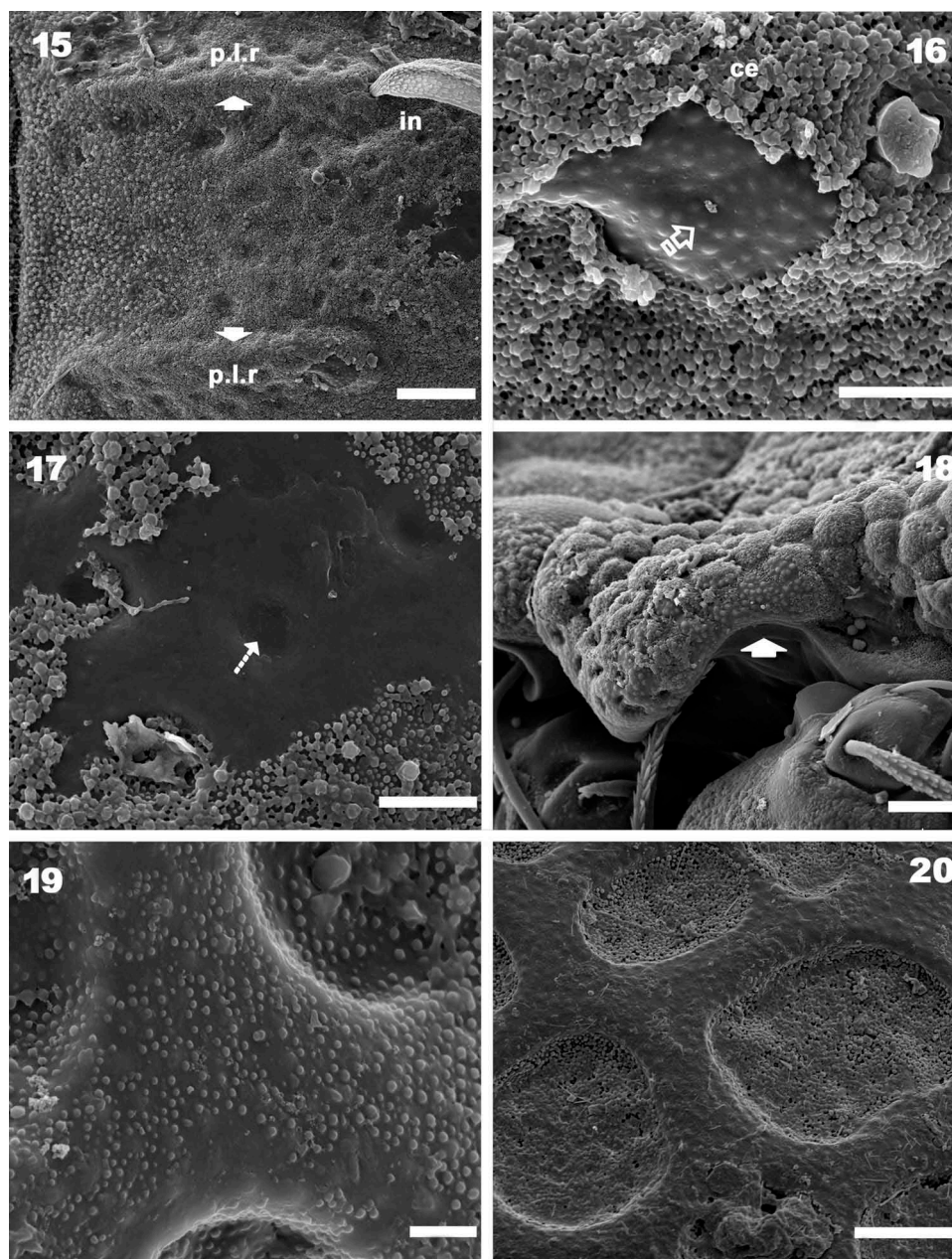
Sensillus (si) spatulate (Figure 11). Bothridial opening directed ventrally (Figures 13, 27, 31, 35 and 38), well defined, smooth bothridial ring (bo.ri), situated internally to bothridial opening with prominent bothridial tooth (bo.to) (Figures 8 and 35); bo.to easily distinguishable. Rostral margin rounded, protruding, resembling a duck bill, slightly rectilinear (Figure 9).

**Notogaster.** In dorsal view anterior notogaster rectangular, with lateral protruding humeral tubercle (h.ap); posterior oval (Figure 1); in lateral view convex (Figures 8 and 27). Anterior and posterior depressions absent (Figure 1); d.sj large, more or less rectilinear, clearly delimited. Circumgastric furrow (s.c)

trajectory not extending to posterior; central elevated notogastral zone visible in Figures 1, 9, 10 and 27 (indicated with white dots, also indicating different diameters. Dots small in zone where s.c not visible or very shallow). Central notogastral zone “light bulb-shaped”, convex with foveate microsculpture (see “Discussion” section), starting slightly posterior to d.sj and ending close to marginal setae; flattened zone between end point of foveate microsculpture and marginal zone (indicated in Figures 1 and 6 by  $\blacktriangle$ ).

Ten pairs of ovoid leaf-shaped setae, described above (Figures 1, 3, 6, 9 and 27). Polyhedral shaped humeral apophysis (h.ap), easily observed; anterior zone overlapping posterior bothridial zone (Figures 1, 9, 12 and 13) (See discussion); completely different ornamentations in bo and h.p zones (Figures 12 and 13); posterior h.ap. zone concave (Figure 18 indicated by  $\blacktriangle$ ),





**Figure 15–20.** *Phyllocarabodes costaricensis* sp. nov. Adult female, SEM observations. **15.** prodorsum: interlamellar zone with *p.l.r.*; **16.** prodorsum: cerotegumental layer and cuticular microsculpture; **17.** prodorsum: detail of cuticular microsculpture; **18.** humeral apophysis, posterior view; **19.** notogastral microsculpture; **20.** notogastral microsculpture. Abbreviations: see section on “Material and methods”. Scale bar: 15 = 20  $\mu$ m; 18, 20 = 10  $\mu$ m; 16, 17 = 5  $\mu$ m; 19 = 2  $\mu$ m.

adapted to accommodate leg III during leg folding and coaptation (Fernandez et al. 2013a).

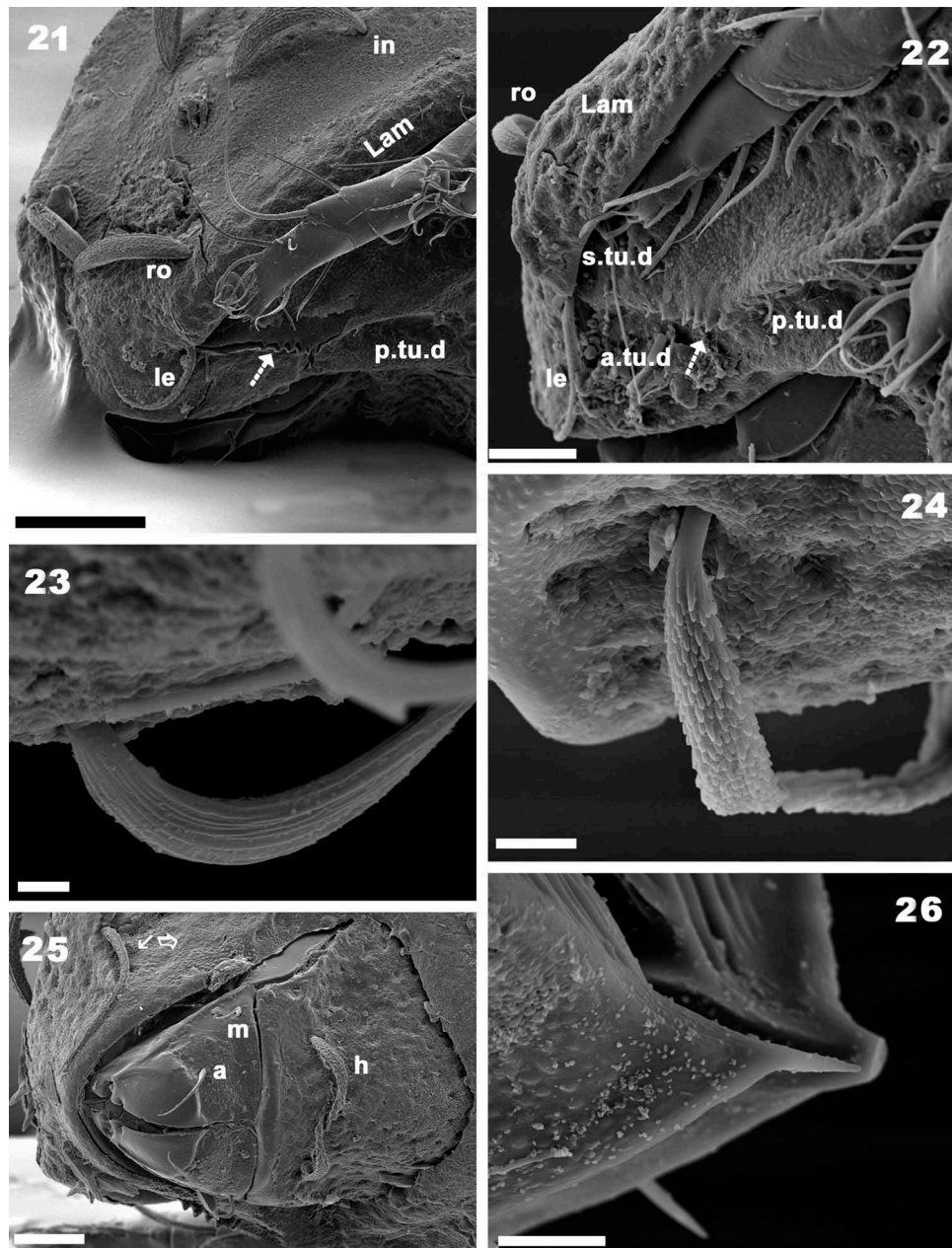
**Lateral region.** Clearly discernible curved lamellae (*lam*); *le* setae curving (Figure 4), inserted on apical lamellar zone (Figures 21 and 22); *h.ap* concave in posterior view (Figure 18). Tutorium (*tu*): large curving lamina, margin undulate, cuticle foveate; with aligned dentition (Figures 21 and 22, indicated by  $\square$ , 27). Supratutorial depression (*s.tu.d*) well developed; two large pocket depressions between *Tu* and *Pd I*; large depression (*a.tu.d*) ventral to tutorial dentition; deep *p.tu.d* (Figures 21 and 22). *Pd I*: large extended lamina; *Pd II*: small rectangular lamina (Figures 8, 14 and 27); discidium (*dis*) hardly discernible, small triangular to rounded apex (Figures 8 and 14).

Bothridia rounded, curling to resemble a mouse ear; bothridial opening directing downwards (Figures 13, 31, 35 and 38); bothridial ring (*bo.ri*) smooth externally and internally (Figures 8, 31, 35 and 38), incomplete; with bothridial tooth (Figures 8, 31, 35 and 38). *Si* cylindrical, arching dorsally (Figures 9 and 11), with short barbs (Figure 11).

**Frontal view.** Figures 9, 10, 13 and 18 facilitate understanding of the shape and disposition of prodorsal and notogastral topography, as well as: *in* setae, *ro* setae, *lam*, *le* setae, *Tu*, *Pd I*, *h.ap* shapes and prodorsal and notogastral setal disposition.

Slightly elevated *e.i.p* with flattened surface, with specific microsculpture (Figure 9); *l.l.f* small depressed area; foveate zones and more or less smooth cuticular surfaces easily observed (Figures 9 and 10); *bo*, *h.ap*, and concave marginal zone (Figure 18 indicated by  $\blacktriangle$ ) situated anterior to bothridial area; the *bo.ri* clearly discernible (Figures 13, 31, 35 and 38). The *s.c* originates in posterior zone of *h.ap*, running externally to elevated notogastral zone (Figures 1, 9, 10 and 27). Trajectory of *s.c* incomplete, disappearing or becoming flattened on posterior elevated notogastral zone (Figures 1, 9, 10 and 27 indicated by line of large white dots). Colliculate and granulate microsculpture of *h.p*, *s.c* and *bo* clearly differentiated (Figures 9, 10, 12 and 13); foveate microsculpture of elevated central notogastral zone clearly visible (Figure 10 indicated by  $\uparrow$ ).

**Ventral region.** Subcapitular setae *h*, *m*, *a* differing in shape (See setation); *h* setae directing paraxially (Figures 24 and 43); *m* setae



**Figure 21–26.** *Phyllocarabodes costaricensis* sp. nov. Adult female, SEM observations. **21.** prodorsum anterolateral view; **22.** prodorsal anterior zone, lateral view; **23.** genital seta; **24.** subcapitulum lateral view; **25.** posterior anal apical zone. Abbreviations: see section on “Material and methods”. Scale bar: 21 = 50 µm; 25 = 25 µm; 22 = 20 µm; 24, 26 = 5 µm; 23 = 2 µm.

directing laterally (Figure 40); *a* setae directing anteriorly (Figure 42). Epimera slightly elevated, delimited by shallow furrow (*bo.1*, *bo.2*, *bo.sj*, *bo.3*). Epimera 3 and 4 fused (Figures 7 and 39); medial epimeral zone with longitudinal depression (Figure 39); *apo.1*, *apo.2*, *apo.sj* and *apo.3* clearly discernible (Figure 7). Epimeral setae (Figures 30 and 33); setal formulae: 1-1-3-3; all setae same shape and length (Figures 27 and 36); *3b*, *3c* closely adjacent, more or less parallel (Figure 33). Genital plate small in relation to anal plate (Figure 39). Six pairs of genital setae, differing in shape (See setation) (Figure 44); three anterior pairs are large, wide and curving (Figure 45); three posterior pairs longer, more or less flabellate (Figure 37). Discidium small, hardly discernible. Clearly observed depression surrounding genital opening; *a.g.f* clearly observed, extending from anterior to genital plate to posterior epimeral margin (Figure 39, trajectory indicated by large white dots). *Ag* setae (Figure 29), *ad* setae (Figure 28), situated some distance apart (Figure 39); aggenital setae situated posterior to genital opening, in shallow depressed area, directed posteriorly and paraxially; posterior aggenital insertion on series of promontories laterally and

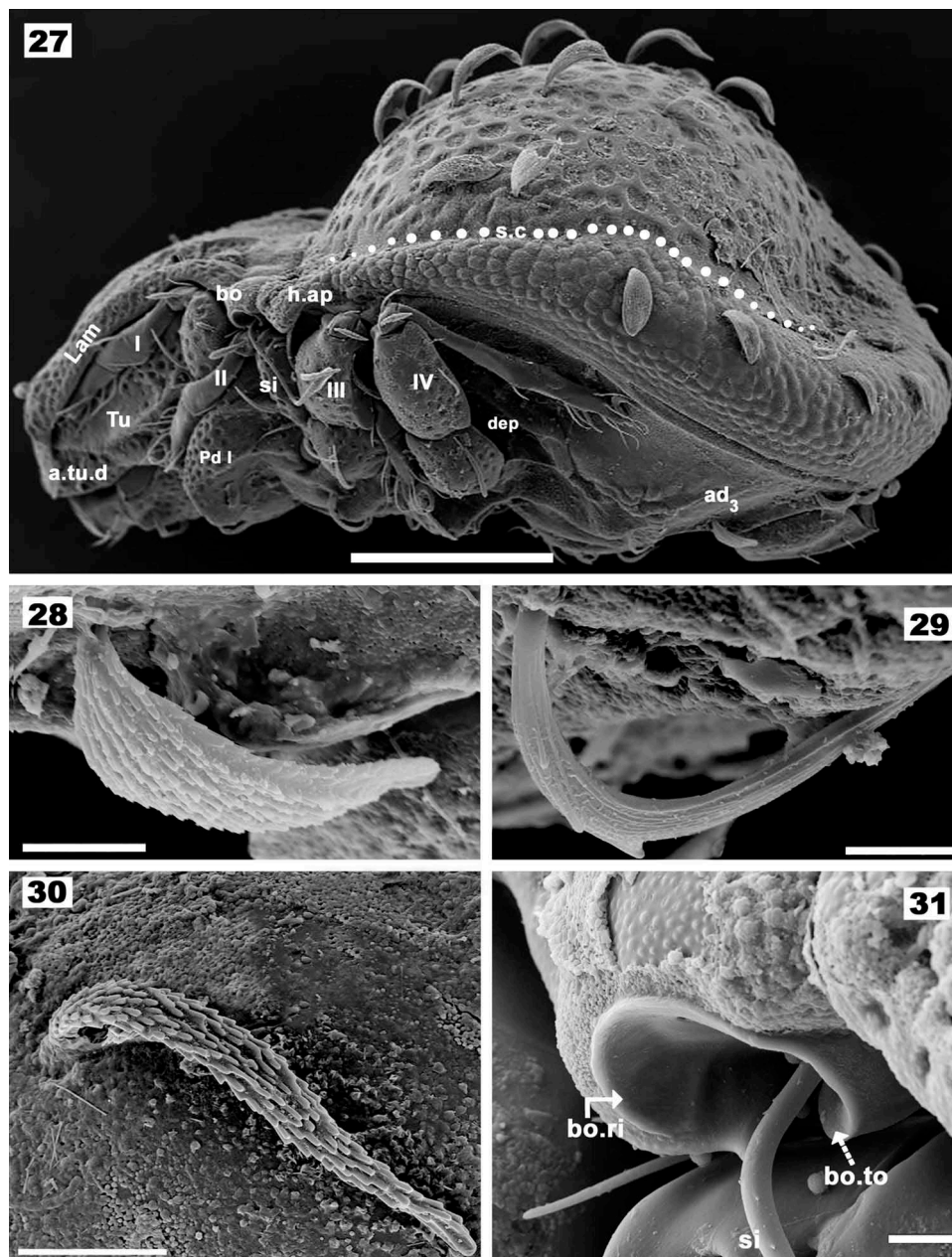
paraxially to these setae (Figure 39 indicated by ↗). Between genital and anal plate, shallow, polyhedral depression (Figure 39 indicated by ♦). Three pairs of paraxially directing adanal setae: *ad<sub>3</sub>-ad<sub>1</sub>* (Figures 28 and 32). Anal plate polyhedral, sharply tipped (Figures 26 and 39). Two pairs of anal setae (Figure 39). Lyrifissure *iad* situated laterally at level *ad<sub>3</sub>* setae (Figure 7). Several depressions (*dep*) clearly visible (Figures 27 and 39).

**Legs (Figures 35–38).** All legs monodactyle. Setal formulae I (1-3-2-4-16-1) (1-2-2); II (1-2-3-3-17-1) (1-1-2); III (2-3-1-2-14-1) (1-1-0); IV (1-2-2-2-13-1) (0-1-0).

#### Remarks

The following characteristics permit easy differentiation of *Ph. Costaricensis* from other congeners: variation in cuticular microsculpture; shape and disposition of prodorsal and notogastral setation; disposition and shape of *bo* and *h.ap*; presence of





**Figure 27–31.** *Phyllocarabodes costaricensis* sp. nov. Adult female, SEM observations. **27.** lateral view; **28.** adanal setae; **29.** aggenital setae, detail; **30.** epimeral seta 2a; **31.** bothridium and bothridial ring. Abbreviations: see section on “Material and methods”. Scale bar: 27 = 100  $\mu$ m; 28, 30 = 10  $\mu$ m; 29, 31 = 5  $\mu$ m.

bothridial ring and bothridial tooth; epimeral setal formula 1-1-3-3; setae 3b and 3c situated closely adjacent.

Interesting anomalies are observed on the prodorsal longitudinal ridge (*p.l.r.*), where *in* setae are usually found. In this instance, two pairs of *in* setae are situated on the ridge; one in normal position and behind them, another smaller pair (Figure 6’).

**New taxon description**  
***Zimbabwae kenyaensis* sp. nov.**  
 (Figures 46–71, Table 1)

**Etymology**

The specific epithet is derived from Kenya, country of origin of type material.

**Material examined**

**Holotype:** Female “KEN 77-63. Nakuru distr. Mau escarpment, près de Enangipen. Tamisage dans la forêt alt. 2700 m. 6.XI. 1977. LEG V. Mahnert & J.L. Perret”; material deposited in the Collection of tNHMG, Switzerland; preserved in 70% ethanol.

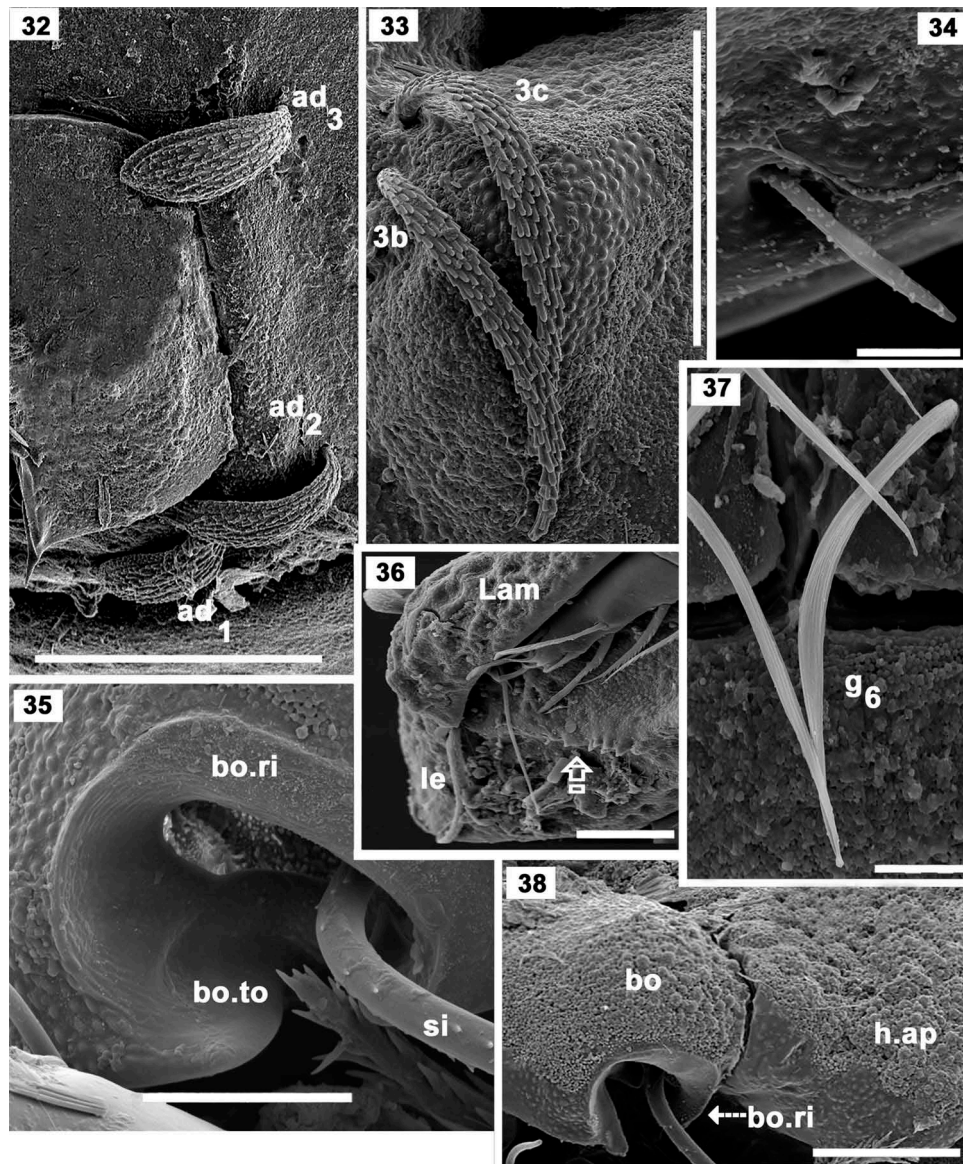
**Paratype** Two adult females, same locality and date as Holotype; deposited in Collection of NHMG; preserved in 70% ethanol. Material studied with SEM: three specimens, not deposited.

**Diagnosis (adult female)**

**Microsculpture.** *Colliculate:* posterior notogastral zone, between *s.c* and *p*<sub>1</sub>, *p*<sub>2</sub>, *p*<sub>3</sub>, *h*<sub>3</sub>. *Pustulated:* *bo*, ventral and lateral depressions, subcapitulum, near setae *a*, *m*, *h*; *Tu*, *s.tu.d*, *p.tu.d*, *a.tu.d*. *Rugose:* *e.i.p*, surrounding *in* setal insertion; notogaster near *c*<sub>3</sub> setae; lamellae near *le* setae; epimera, genital plate. *Foveate:* *e.i.p* zone promontories; posterior notogastral zone; *prm dp* setae and zone between *prm dp*, *prm dm* setae and *prm h*<sub>1</sub>, *prm h*<sub>2</sub>, *prm lp* setae; apical zone of lamellae, subcapitulum, anterior to insertion *h* setae. *Punctate:* prodorsum near *in* setae; notogastral zone between foveae; externally to *s.c*. *Smooth:* *bo.ri*, *bo.to*.

**Setation.** Epimeral, aggenital, genital setae *simple*; *in* setae *leaf-shaped*, *rugous*, with small barbs and central longitudinal furrow; *ro*, notogastral setae *simple*, small asperities; *h*, *m*, *a* setae *simple*,





**Figure 32–38.** *Phyllocarabodes costaricensis* sp. nov. Adult female, SEM observations. **32.** anal zone with adanal setae; **33.** epimeral setae *3b*, *3c*; **34.** anal setae. **35.** bothridium, lateral view; **36.** prodorsum, apical zone; **37.** genital setae, *g<sub>6</sub>*; **38.** bothridium dorsolateral view. Abbreviations: see section on “Material and methods”. Scale bar: 32 = 50  $\mu$ m; 38, 36 = 20  $\mu$ m; 33, 35 = 10  $\mu$ m; 34, 37 = 5  $\mu$ m.

lateral vein; *le* setae wide, leaf-shaped, dentate margin, with small central teeth; *an* setae small spur.

**Prodorsum.** Rectangular between *d.sj* and level of promontories, posterior to elevated interlamellar process; anterior more or less trapezoidal, with semicircular margins. Elevated interlamellar process with irregular promontories and depressions, divided into two lateral zones by flat medial depression. Three protuberances observed: one sigmoid lateral protuberance, situated internally to *in* setae insertion level; second, rounded to irregular protuberance, situated lateral to *in* setal insertion; third protuberance, rounded in dorsal view, situated marginally, lateral to the second promontory. Relatively deep shallow lamellar furrow; ovoid CSO between *ro* setae. Posterior prodorsal depression divided into two (anterior and posterior) by translamellae. Lamellae running dorsolaterally, with large, slightly curving translamella. Lamellar tips connected to cuticular extension bar. Cylindrical, barbed sensillus, curving dorsally. Bothridial ring and bothridial tooth smooth.

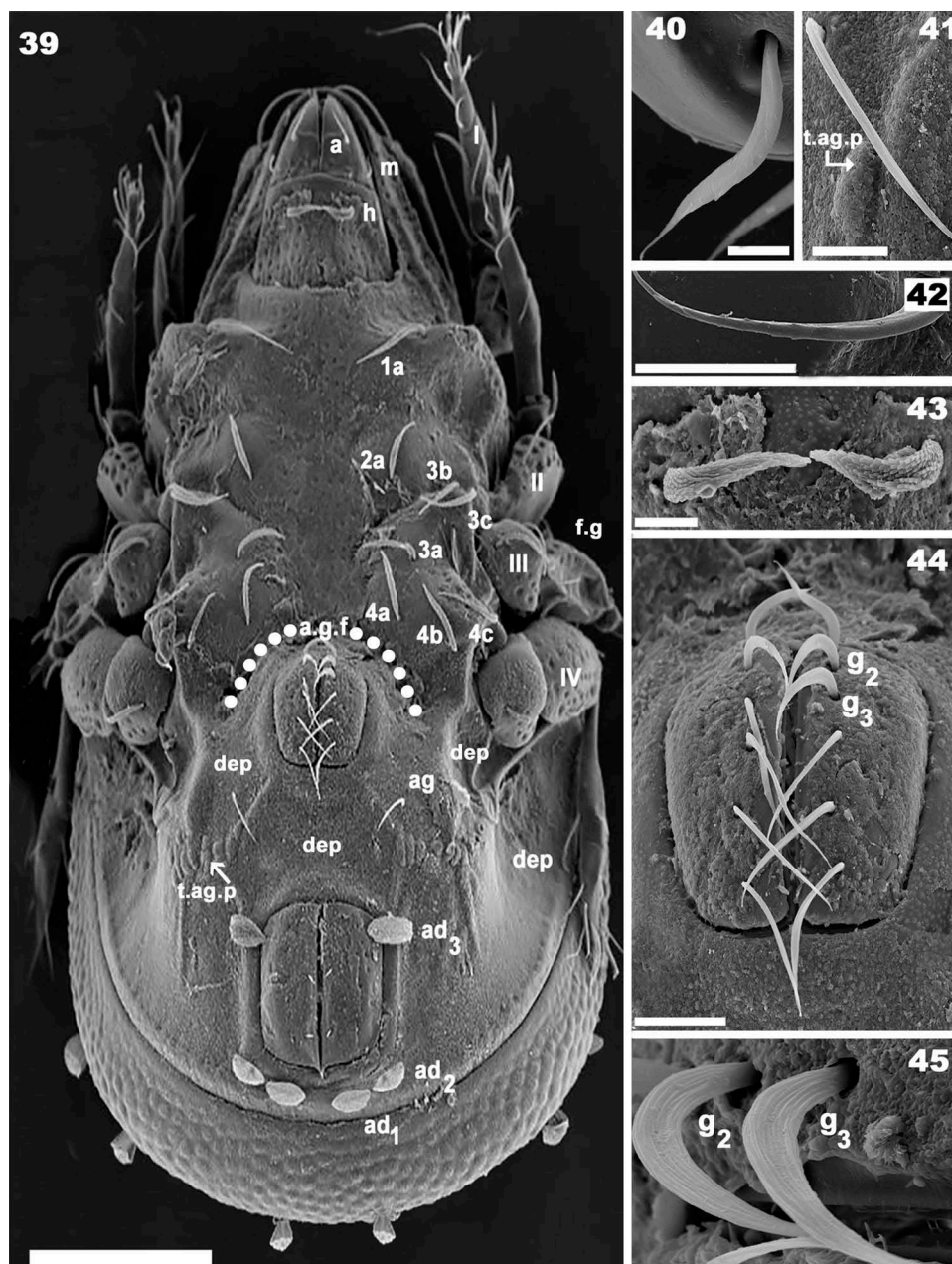
**Notogaster.** Anterior zone trapezoidal; medial to posterior zone ovoid; rectilinear, narrow *d.sj*; *n.a.d* large, extending posteriorly, exceeding level of *da*, *la* setal insertions; elevated Y-shaped cuticular ridge dividing *n.a.d* into two longitudinal zones. Y-shaped structure extending anteriorly almost to *d.sj*; two superior Y-branches

posteriorly exceeding *da* setal insertion; depression between branches of Y in central superior zone. Fifteen pairs of setae: *c<sub>1</sub>*, *c<sub>2</sub>*, *c<sub>3</sub>*, *da*, *dm*, *dp*, *la*, *lm*, *lp*, *h<sub>1</sub>*, *h<sub>2</sub>*, *h<sub>3</sub>*. All setae except *p<sub>1</sub>*, *p<sub>2</sub>*, *p<sub>3</sub>* inserted on promontories. Promontories *prm da* and *prm la*, *prm lm* setae connected by oblique promontory. Circumgastric depression between *la*, *lm*, *lp*, *h<sub>2</sub>*, *h<sub>1</sub>* and *h<sub>3</sub>*, *p<sub>3</sub>*, *p<sub>2</sub>*, *p<sub>1</sub>* setae; trajectory of circumgastric depression changing to sigmoid slightly anterior to *h<sub>3</sub>* setae. Projecting humeral apophysis with oblique depression; short transverse furrow anterior and posterior to *c<sub>3</sub>* setae.

**Ventral region:** slightly elevated epimera; setae on rounded promontories; longitudinal furrow on paraxial zone of epimera 1–3; epimeral chaetotaxy 3-1-3-3. Epimeral setae *1a*, *2a*, *3a*, *4a* small. Discidium well discernible; *a.g.f* present, connected to lateral genital depression by tube-shaped structure; four pairs of long genital setae; *ag* setae posterior to external genital opening; situated laterally and close to *ad<sub>3</sub>*; setae *ag* and *ad<sub>3</sub>*, *ad<sub>2</sub>*, *ad<sub>1</sub>* differ in shape; polyhedral, sharply tipped anal plate; two pairs of anal setae. Polyhedral depressions situated laterally to genital and anal zones and between openings.

#### Description

**Measurements.** SEM 620  $\mu$ m (605–642)  $\times$  315  $\mu$ m (310–330) (*n* = 6). Light microscopy: 630  $\mu$ m (615–645)  $\times$  322  $\mu$ m (317–341) (*n* = 3).



**Figure 39–45.** *Phyllocarabodes costaricensis* sp. nov. Adult female, SEM observations. **39.** ventral view; **40.** subcapitular setae *m*; **41.** aggenital setae, general view with transverse cuticular promontories; **42.** subcapitular setae *a*; **43.** subcapitular setae *h*; **44.** genital plate; **45.** detail genital *g1–g3* setae. Abbreviations: see section on "Material and methods". Scale bar: 39 = 100  $\mu$ m; 44 = 20  $\mu$ m; 42–43 = 10  $\mu$ m; 40, 41, 45 = 5  $\mu$ m.

**Shape.** Prodorsum polyhedral and notogaster ovoid (Figure 46).

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

**Cerotegument.** Grainy, only present on posterior prodorsal depression (*p.p.d*<sub>1</sub>, *p.p.d*<sub>2</sub>) and notogaster, zone of *s.c* (Figures 51 and 56).

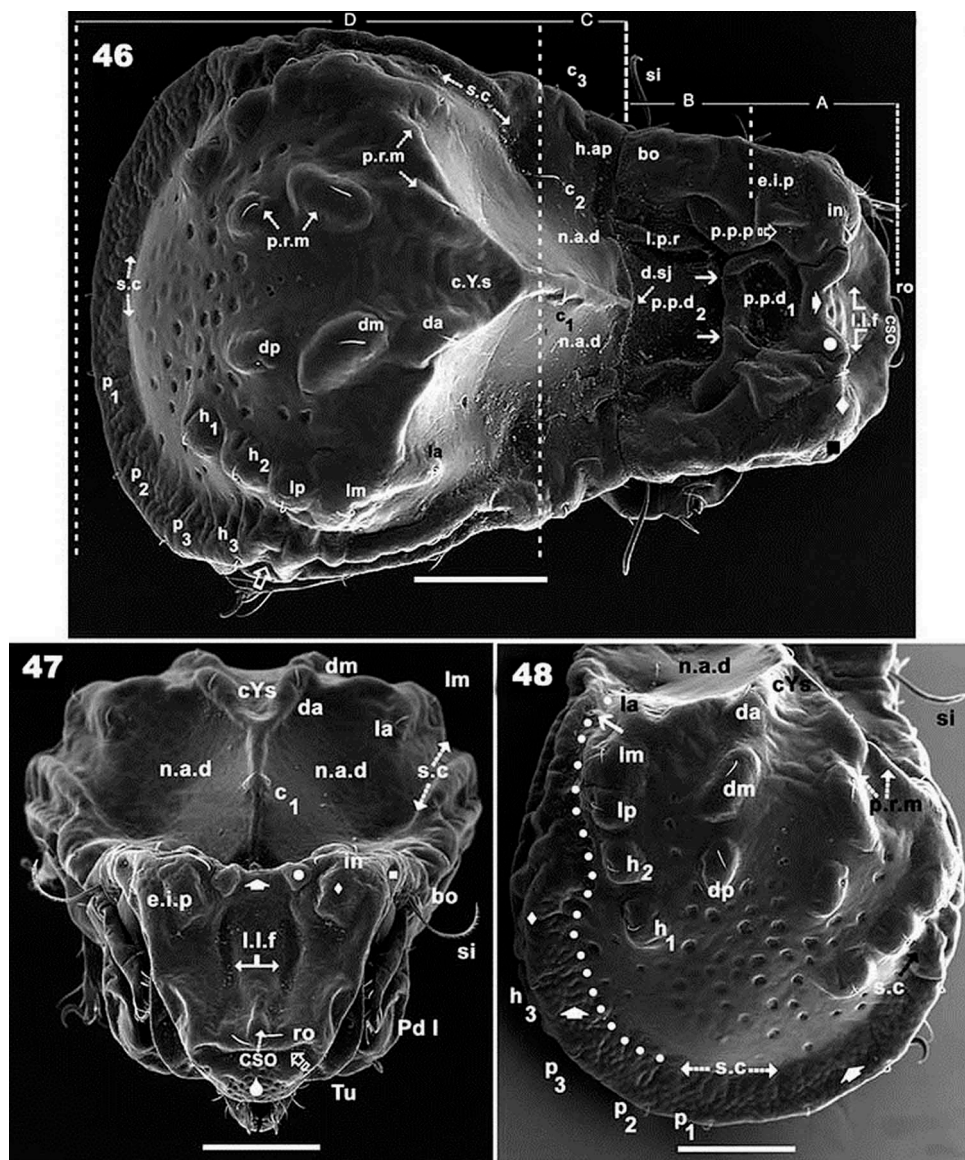
**Integument.** Microsculpture: *colliculate*: posterior notogastral zone between *s.c* and setae *p*<sub>1</sub>, *p*<sub>2</sub>, *p*<sub>3</sub>, *h*<sub>3</sub> (Figure 48 indicated by ▲), *Pustulate*: *bo*, *h.ap* (anterior zone) (Figure 61, indicated by ♀), zone of *ppd*<sub>2</sub> (Figure 51, indicated by ◆◆), *s.tu.d* zone (Figure 60), posterior zone *Pd I* (Figure 60). *Rugose*: *e.i.p* surrounding in setae insertions (Figure 46), notogaster near *c*<sub>3</sub> (Figure 58), zone *ag*, *ad* setae (Figure 71), surrounding in setae (Figure 64). *Foveate*: (Figures 48 and 66) fovea rounded to polyhedral in shape: posterior zone, promontories *dp*, *h*<sub>1</sub> setal promontories extending to *s.c* (Figure 48), subcapitulum (Figure 70), anterior zone to *ro* setae (Figure 47 indicated by ◆◆). *Smooth*:

prodorsum (Figure 47), anterior notogastral zone (Figures 46 and 47), ventral zone (Figure 68).

**Setation.** Notogastral setae (Figures 52, 60 and 67), *ro* (Figure 53), epimeral (Figure 69), *ag*, *ad* (Figure 71): *simple with very fine barbs*; genital setae *simple* (Figure 68); *in* setae *leaf-shaped, rugous, with small asperities and central longitudinal furrow* (Figure 64); *le* setae *wide, leaf-shaped, margin dentate, with small central teeth* (Figure 54); anal setae *spiniform* (Figure 68).

**Prodorsum.** Dorsal view: generally polyhedral in shape, zone B (indicated by dotted transverse line in Figure 46), rectangular between *d.sj* and level of promontories posterior to *e.i.p* (*p.p.p*); zone A (indicated in Figure 46 by dotted transverse line), more or less trapezoidal with semicircular margins. Frontal view (Figure 47), triangular with irregular semicircular margins; *d.sj* concave (Figure 46); elevated *e.i.p* with irregular promontories and depressions, divided into two lateral zones by concave medial depression (Figures 46, 47 and 51 indicated by ▲).





**Figure 46–48.** *Zimbabwea kenyaensis* sp. nov. Adult female, SEM observations. **46.** dorsal view; **47.** frontal view; **48.** posterior dorsal view. Abbreviations: see section on “Material and methods”. Scale bar: 46–48 = 100  $\mu$ m.

**Table 1.** *Zimbabwea kenyaensis* sp. nov.: leg setae and solenidia.

Leg I	Femur	Genu	Tibia	Tarsus	Claw
setae	<i>d,v</i>	<i>l,v</i>	<i>d,v</i>	( <i>ft</i> ), $\epsilon$ ,( <i>tc</i> ),( <i>it</i> ),( <i>p</i> ),( <i>u</i> ),( <i>a</i> ), <i>s,pv'</i>	1
solenidia		$\sigma$	$\varphi_1,\varphi_2$	$\omega_1,\omega_2$	
Leg II					
setae	<i>dp,da,ls</i>	( <i>l</i> ), <i>v</i>	<i>d,(v)</i>	( <i>pv</i> ), <i>s,(a)</i> ,( <i>u</i> ),( <i>p</i> ),( <i>it</i> ),( <i>tc</i> ),( <i>ft</i> )	1
solenidia		$\sigma$	$\varphi$	$\omega_1,\omega_2$	
Leg III					
setae	<i>d,l',v</i>	<i>l'</i>	<i>l',v</i>	( <i>pv</i> ), <i>s,(a)</i> ,( <i>u</i> ),( <i>p</i> ),( <i>it</i> ),( <i>tc</i> ), <i>ft'</i>	1
solenidia		$\sigma$	$\varphi$	–	
Leg IV					
setae	<i>d,v</i>	<i>d,l'</i>	<i>l',v</i>	( <i>pv</i> ), <i>s,(a)</i> ,( <i>u</i> ),( <i>p</i> ),( <i>tc</i> ), <i>ft'</i>	1
solenidia		–	$\varphi$	–	

Each zone comprising three protuberances. One sigmoid to irregular lateral protuberance (Figures 46 and 47) situated internally to *in* setae insertion level (Figures 46 and 51). In frontal view (Figure 47 indicated by large white ●), these promontories appearing rectangular to polyhedral, separated from *in* setal insertion by simple furrow. Second protuberance situated lateral to *in* setal insertion, rounded to irregular in dorsal view (Figures 47 and 51 indicated by ♦); appearing rectangular to polyhedral in frontal view (Figure 47 indicated by ♦), separated from first protuberance by large furrow and *in* setal insertion. Third promontory, rounded in dorsal view,

situated marginally, lateral to the second promontory (Figure 46, indicated by ■), forming rounded “ear-shaped” depressed zone in frontal view (Figure 47, indicated by ■). On *e.i.p*, posterior to protuberances, more or less rectangular depressed area *p.p.p* present, with anterior zone of complicated shape (Figures 46 and 51 indicated by ♀, this last figure shows different angles of right and left sides). On anterior zone of *e.i.p*, well defined, deep, curving *l.l.f* (Figures 47 and 60); ovoid, well defined *CSO* between *ro* setae (Figure 47).

Large prodorsal posterior depression behind *e.i.p*, divided into two by translamella (Figure 46, indicated by 1), forming one anterior (*p.p.d*<sub>1</sub>) and one posterior (*p.p.d*<sub>2</sub>) depression; *p.p.d*<sub>1</sub> small, polyhedral to rounded, with well delimited internal ovoid structure (Figure 46); *p.p.d*<sub>2</sub> large, rectangular, with lateral posterior ridge (*l.p.r*) (Figure 46).

*Lam* running dorsolaterally (Figure 60); translamella large, slightly curving (Figure 46). Curving *in* setae (Figures 47, 60 and 64) (length 14–18  $\mu$ m); inserted anteriorly on *e.i.p*, directed obliquely (Figures 47, 60 and 64); *ro* setae (Figures 46, 47 and 53) (length 18–24  $\mu$ m), directed anteriorly and paraxially (Figures 46 and 47); lateral *le* setae situated anterior to lamellae (Figures 54 and 60) (length 23–29  $\mu$ m) (broader zone 8–12  $\mu$ m). Lamellae terminating in prominent *la.ti*, tips connected to cuticular extension bar (Figure 54 indicated by ▲) (See Lateral region).

Barbed, cylindrical sensillus (*si*) (77–83  $\mu\text{m}$ ), curving dorsally (Figures 55 and 61). Bothridial opening directing ventrally (Figures 60 and 61); smooth, clearly defined bothridial ring (*bo.ri*), with *bo.to* (Figures 61 and 62). Furrow running externally to *bo.ri* (Figure 61 indicated by indicated  $\blacktriangle$ ). Rostral margin slightly rounded (Figure 47).

**Notogaster.** Anterior *n.a.d* longitudinally divided into two (Figures 46, 47 and 50) by anterior extension ridge of *c.Ys*, extending close to *d.sj*. Fifteen pairs of setae: *c*<sub>1</sub>, *c*<sub>2</sub>, *c*<sub>3</sub>, *da*, *dm*, *dp*, *la*, *lm*, *lp*, *h*<sub>1</sub>, *h*<sub>2</sub>, *h*<sub>3</sub>, *p*<sub>1</sub>, *p*<sub>2</sub>, *p*<sub>3</sub>; setae *c*<sub>1</sub> length: 13–15  $\mu\text{m}$  (Figure 60); *c*<sub>2</sub>, *c*<sub>3</sub> length: 10–14  $\mu\text{m}$  (Figure 58); setae *da*, *dm*, *dp* length: 22–28  $\mu\text{m}$  (Figure 67); setae *la*, *lm*, *lp* length: 20–26  $\mu\text{m}$ ; setae *h*<sub>1</sub>, *h*<sub>2</sub> length: 10–13  $\mu\text{m}$ ; setae *h*<sub>3</sub>, *p*<sub>1</sub>, *p*<sub>2</sub>, *p*<sub>3</sub> length: 18–19  $\mu\text{m}$  (Figure 52).

Setae *c*<sub>1</sub> situated on anterior extension ridges (*c.Ys*) (Figures 46, 47 and 50); *c*<sub>2</sub> setae situated on minute promontories (*prm*) on *n.a.d* (Figures 46 and 60); *c*<sub>3</sub> setae inserted on rounded lateral promontories (Figures 58 and 60); *da* setae situated on elongated promontories, on lateral branch of *c.Ys* (Figures 46, 47, 48 and

67); *dm* setae situated on large elongated promontories (Figures 46, 48 and 67); *dp* setae on small rounded promontories (Figures 46, 48 and 67); *la* setae situated on elongated promontories with rounded edges, anterior to oblique *prm* connecting *c.Ys* and *lm* promontories (Figures 46, 48, 50 and 60); *lm*, *lp* setae situated on contiguous rounded polyhedral promontories; the first large, the second small; promontories separated by transverse furrow (Figures 46, 48 and 60); *h*<sub>1</sub>, *h*<sub>2</sub> on individual rounded promontories separated by furrow (Figures 46 and 48); *h*<sub>3</sub> situated on slightly elevated rounded promontories (Figures 46, 48, 52 and 60). Circumgastric depression originating laterally anterior to *la* setal insertion level (Figures 46 and 56); *s.c* deflected by promontories (Figures 46, 47, 48 and 65) to *h*<sub>3</sub> setal insertion level; setae *p*<sub>1</sub>, *p*<sub>2</sub>, *p*<sub>3</sub> aligned, situated behind *h*<sub>3</sub> (Figures 46, 48 and 52). Clearly defined *s.c* (Figures 47 and 50) visible from posterior zone *h.ap*, and surrounding notogaster (Figures 46, 47 and 48), between *la*, *lm*, *lp*, *h*<sub>2</sub>, *h*<sub>1</sub> and *h*<sub>3</sub>, *p*<sub>3</sub>, *p*<sub>2</sub>, *p*<sub>1</sub> setae (Figures 46 and 48).

Promontories bearing *da* and *lm* setae connected by oblique promontories (Figure 60 indicated by  $\blacktriangle$ ). Humeral apophysis

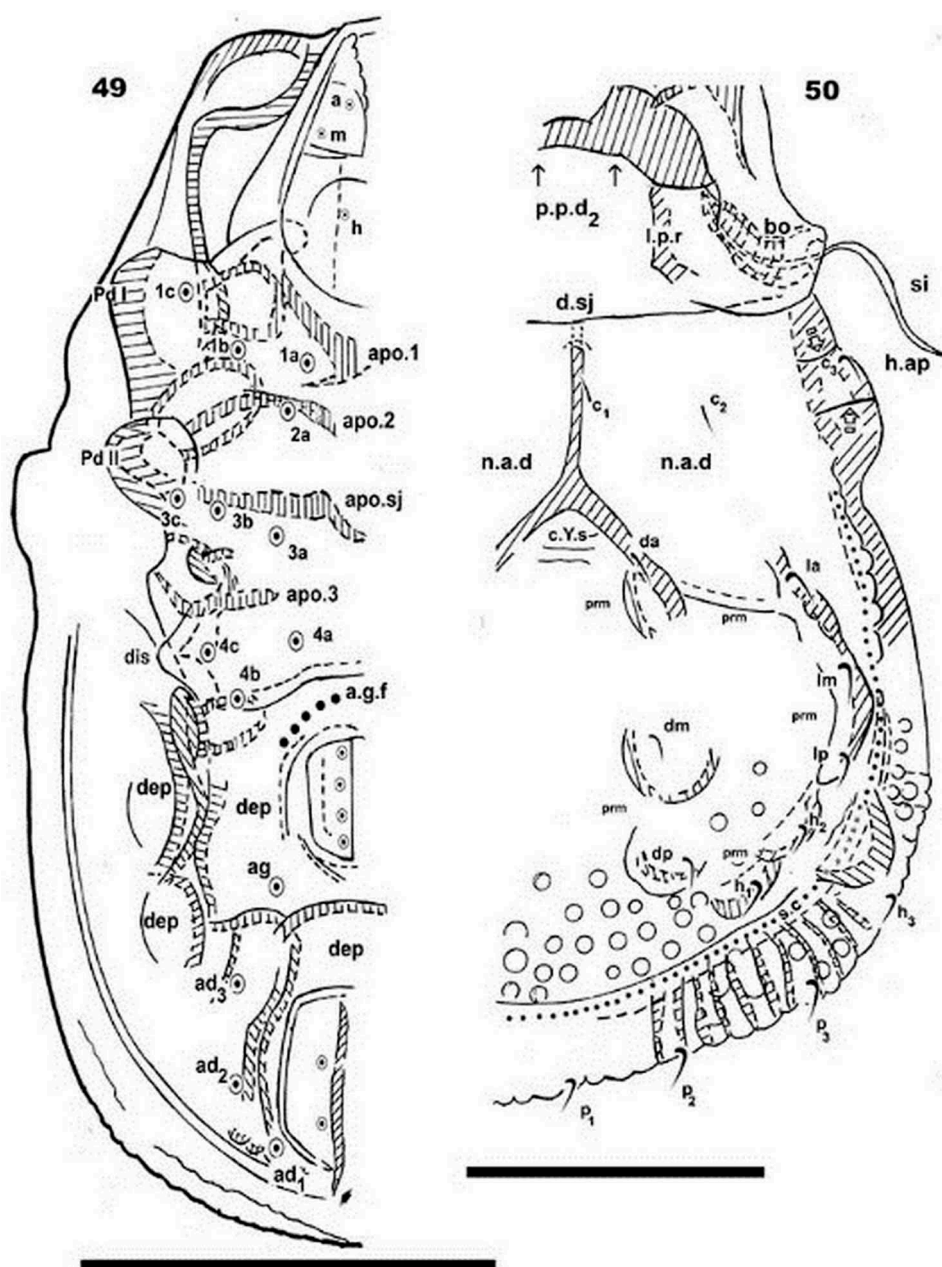
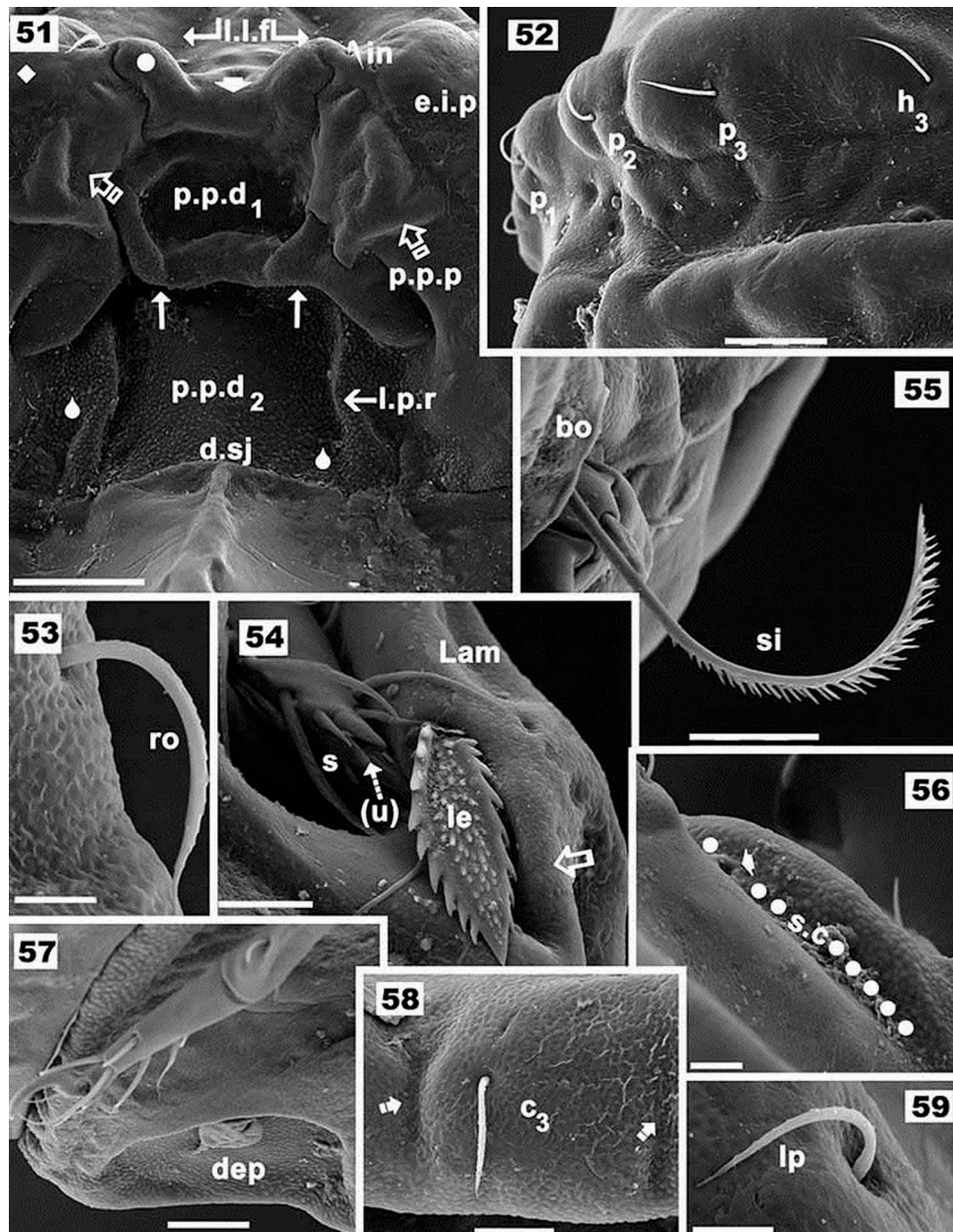


Figure 49–50. *Zimbabwea kenyaensis* sp. nov. Adult female, optical observations. 49. ventral view; 50. dorsal view. Abbreviations: see section on “Material and methods”. Scale bars: 49 = 270  $\mu\text{m}$ ; 50 = 230  $\mu\text{m}$ .





**Figure 51–59.** *Zimbabwea kenyaensis* sp. nov. Adult female, SEM observations. 51. prodorsum, anterior region; 52. notogaster, lateral posterior region; 53. rostral setae; 54. lamellar setae; 55. sensillus; 56. notogaster, lateral region; 57. ventral posterior zone depressions; 58. humeral apophysis, region setae  $c_3$ ; 59. notogaster, insertion zone  $lp$  setae. Abbreviations: see section on “Material and methods”. Scale bars: 51 = 50  $\mu\text{m}$ ; 52, 55, 57 = 20  $\mu\text{m}$ ; 54, 56, 58 = 10  $\mu\text{m}$ ; 53, 59 = 5  $\mu\text{m}$ .

( $h.ap$ ) long, large projection (Figures 46, 47, 48 and 60);  $gla$  situated on  $c.s$  slightly posterior to level of  $la$  setal insertions (Figure 56 indicated by  $\blacktriangle$ , 62).

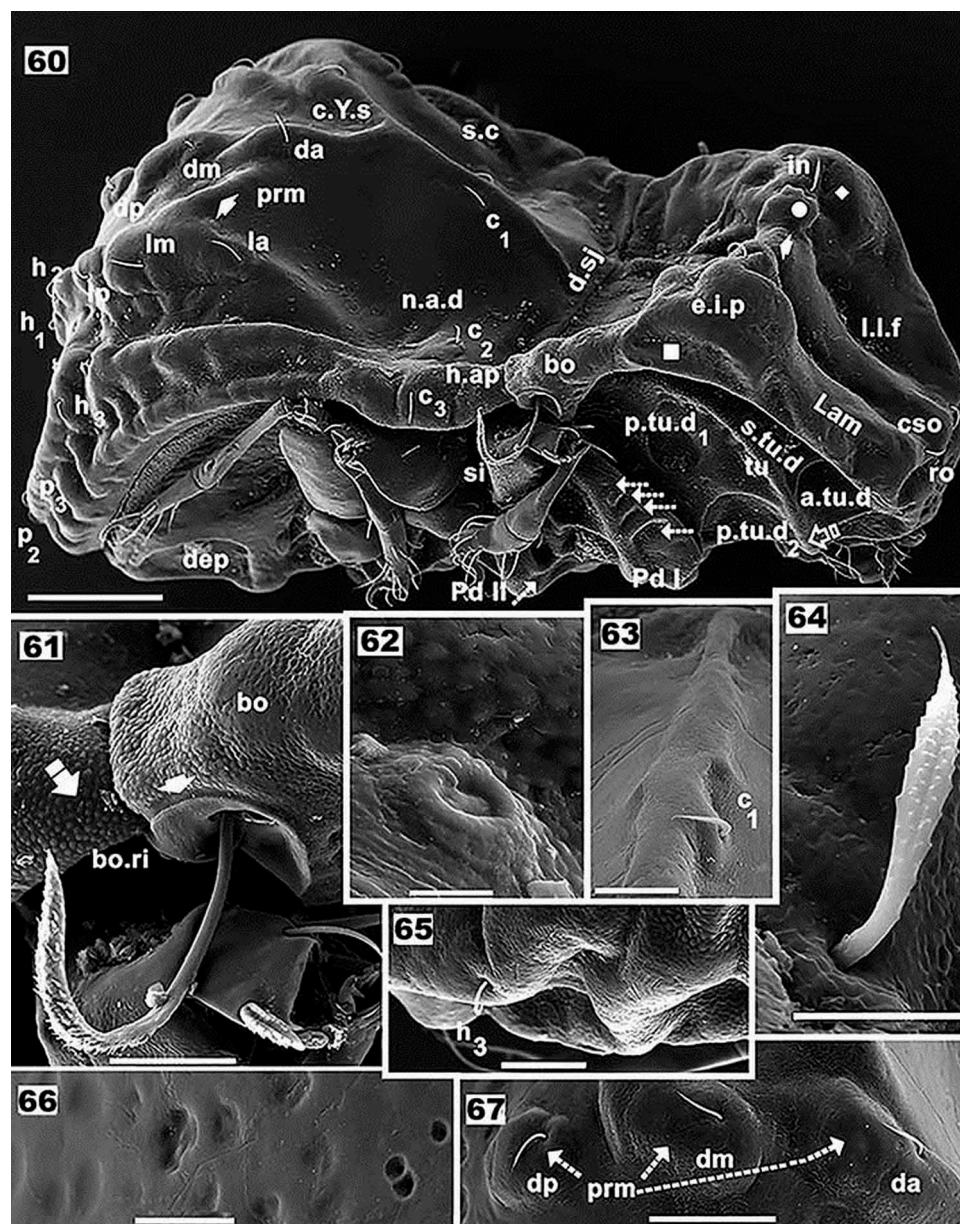
**Lateral region.** Lamella ( $lam$ ) easily discernible, with cuticular microsculpture of rounded elongate depressions, large elevations and foveae (Figure 60); bothridial zone pustulate and rugous (Figures 60 and 61);  $le$  setal insertion hardly discernible (Figure 60); lamellar tip ( $la.ti$ ) merged with cuticular surface by cuticular extension bar (Figure 54, indicated by  $\blacktriangle$ , 68); Tutorium ( $Tu$ ) conspicuous, large lamina with curving margin and smooth cuticle, but with some fovea (Figure 60). Two lateral posterior tutorial depressions,  $p.tu.d_1$  and  $p.tu.d_2$  (Figure 60); supratutorial depression ( $s.tu.d$ ) (Figure 60) completely concealing leg I during leg folding; one pocket depression ( $a.tu.d$ ) observed inside  $s.tu.d$  (Figure 60);  $Pd\ I$ : large polyhedral lamina (Figure 60) extending externally; triangular in dorsal view, with wide anterior zone and series of four longitudinal depressions (Figure 60, indicated by  $\leftarrow$ ).  $Pd\ II$ : rounded lamina (Figure 60).

**Posterior view.** Promontories well defined. Trajectory of  $s.c$  between  $prm\ la$ ,  $prm\ lm$ ,  $prm\ lp$ ,  $prm\ h_1$ ,  $prm\ h_2$  and lateral setal inferior promontories  $prm\ h_3$ ,  $prm\ p_3$ ,  $prm\ p_2$ ,  $prm\ p_1$ , clearly observable (Figure 48 with dotted line). Colliculate cuticular microsculpture between  $s.c$  and  $p_1$ ,  $p_2$ ,  $p_3$  and  $h_3$  seta clearly discernible, with a prominent extension in posterior zone (Figure 48 indicated by  $\blacktriangle$ ,  $\blacklozenge$ ). Foveate microsculpture and rounded cavities (Figures 48 and 66) reaching  $s.c$  at  $dm$ ,  $lp$  setal promontory level.

**Ventral region.** Complex epimeral system with raised and depressed areas (Figure 68 indicated by  $\blacklozenge$ ); epimeral setae observed on rounded promontories; epimera 3 and 4 clearly discernible, unfused. Epimeral chaetotaxy 3-1-3-3. Epimeral setae  $2a$ , small (Figure 68);  $dis$  small, easily observed (Figure 68);  $a.g.f$  clearly visible, situated anterior to genital plate (Figure 60 indicated by large white dot);  $a.g.f$  connected to genital lateral depression by tube-shaped structure (Figure 60 indicated by  $\blacklozenge$ ).

Genital plate ovoid; four pairs of genital setae arranged in simple line;  $ag$  setae situated at level of genital plate tip, lateral





**Figure 60–67.** *Zimbabweae kenyaensis* sp. nov. Adult female, SEM observations. **60.** lateral view; **61.** bothidium and sensillus; **62.** notogastral *glia*; **63.** notogaster, zone of  $c_1$  setal insertions, lateral view; **64.** interlamellar setae; **65.** notogaster, lateral region; **66.** cuticular microsculpture; **67.** zone of setal promontories, setae *da*, *dm*, *dp*. Abbreviations: see section on “Material and methods”. Scale bar: 60 = 100  $\mu$ m; 67 = 50  $\mu$ m; 61, 63, 65, 66 = 20  $\mu$ m; 64 = 10  $\mu$ m; 62 = 5  $\mu$ m.

to genital opening, near  $ad_3$ ; setae  $ag$ ,  $ad_3$ ,  $ad_2$ ,  $ad_1$ , more or less same shape and length; anal plate polyhedral, sharply tipped with two pairs of anal setae. Polyhedral depressions (*dep*) situated laterally to genital and anal zones, between openings. Subcapitulum diarthric; large depression at lateral level of subcapitulum (Figure 68 indicated by  $\blacktriangle$ ).

**Legs.** Setal formulae I (1-2-2-2-15-1) (1-2-2); II (1-3-3-3-15-1) (1-1-2); III (2-3-1-2-14-1) (1-1-0); IV (1-2-2-2-12-1) (0-1-0).

**Remarks.** *Zimbabweae kenyaensis* sp. nov. is closely related to *Zimbabweae pluosiae*, but a series of differences exist between them. These species are very complex and SEM is indispensable in facilitating their study. Principal differences are found in the prodorsal zone:  $p.p.p$  differ in shape;  $p.p.d_2$  large; lateral external  $l.p.r$  with several different structures; promontories in the zone of *in* setae are triangular (indicated by large white dot), separated by a furrow from those that are rounded polyhedral (indicated by  $\blacklozenge$ ). Foveate zone anterior to CSO. Notogaster, *c.Y.s* anterior extension differ in shape, transversal promontories on zone anterior to  $c_1$

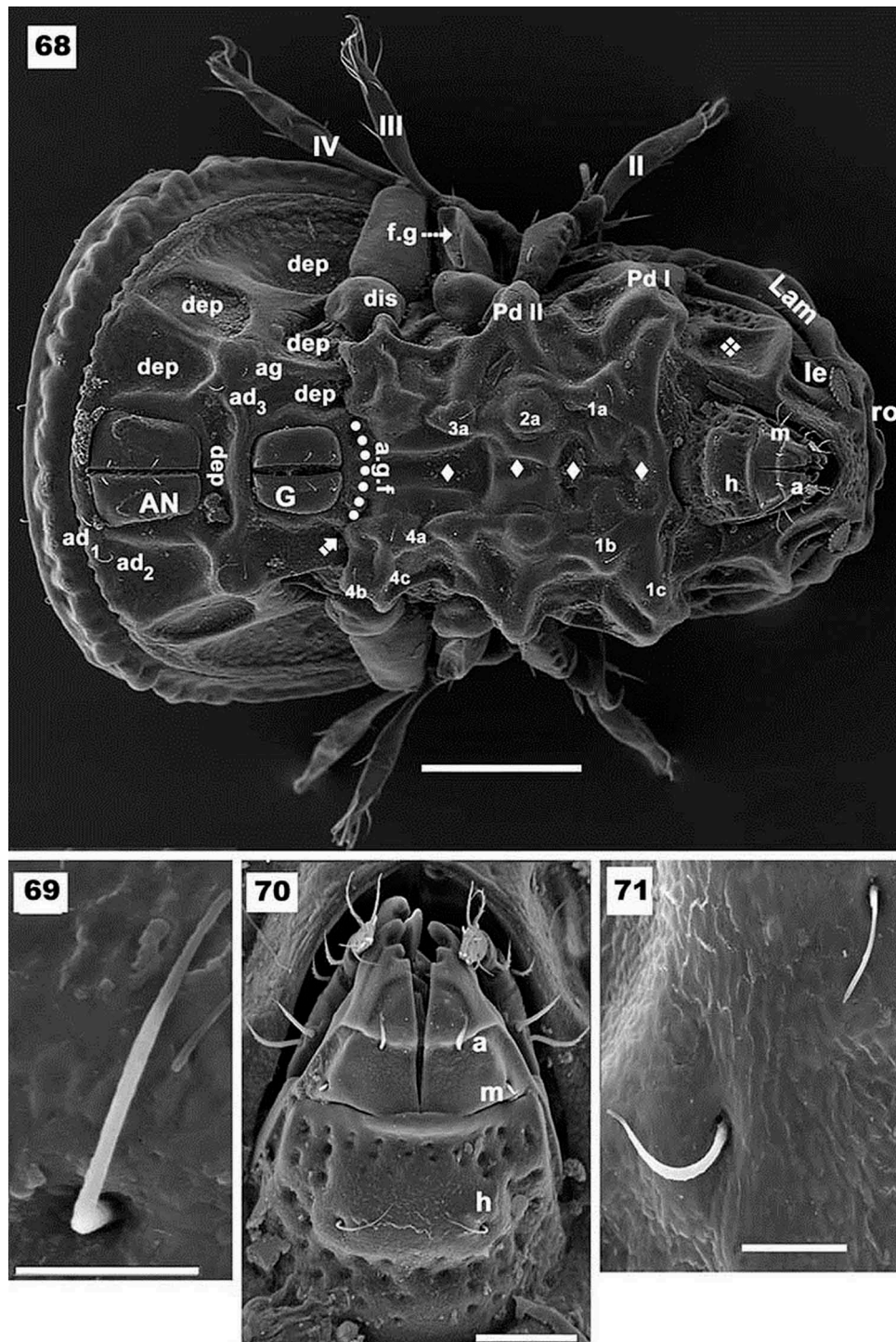
insertion extend to  $prm$  *lm*; *bo.ri* with external furrow. Ventral region: epimeral zone with large promontories; setae *ad*, *ag*, differ in shape to *Z. pluosiae*.

## Discussion

### Deposition of type species

According to the first of the series of papers by Balogh and Mahunka (1969a; Acari: Oribatids collected during the second expedition, I), as indicated in page 2, type material was deposited in the Hungarian Natural History Museum, Budapest: “The Holotypes and the greater part of the Paratypes are deposited in the Zoological Collection of the Hungarian Natural History Museum, Budapest; one Paratype each, whenever it has been possible to do so, forwarded to the collections of Dr. J. Aoki, Tokyo; Dr. E. Piffel, Vienna; Dr. A. Rajske, Poznan; and Dr. T.A. Woolley, Louisiana”. In the second paper (Balogh and Mahunka 1969b, Acari: Oribatids collected by the second expedition, II), page 31 reads as “The type-material of the described taxa is deposited as itemized in the preceding publication.”, and on





**Figure 68–71.** *Zimbabwea kenyaensis* sp. nov. Adult female, SEM observations. **68.** ventral view; **69.** epimeral setae 3a; **70.** subcapitulum, ventral; **71.** Ag–ad<sub>3</sub> setal zone. Abbreviations: see section on “Material and methods”. Scale bar: 68 = 100 µm; 69 = 20 µm; 70 = 10 µm; 71 = 5 µm.

page 48, regarding the type material of *Phyllocarabodes octogonalis* n. sp.: “Material examined: 1 ex. (Holotype: 0-606-68): No. 459-1. 1. ex. Paratype: 0-607-68): from the same locality”.

Though not clearly stated, we thus deduced that the material was deposited in the Hungarian Natural History Museum, Budapest. However, our subsequent enquiries to this museum regarding a loan of this material resulted in a negative reply.

We spent many years searching for specimens resembling the type and recently, in samples from Costa Rica, we obtained interesting material similar to the type species of *Phyllocarabodes*. In the following, we analyse information about Carabodidae relating to the genus *Carabodes*. Subsequently, we supply a redefinition of the genus *Phyllocarabodes*, compare it to *Carabodes*, and provide our opinion on its taxonomy.

#### Family Carabodidae, genus *Carabodes*

The genital setal formula provided for *Carabodes* by Grandjean 1949, was (1-2-4-4). Subsequent studies by Andre (1975), Bellido (1978) and Ermilov (2011) confirmed this formula.

While Mahunka (1986) did not record two pairs of aggenital setae in any carabodid genera, Reeves and Behan-Pelletier (1998) provided a detailed redefinition of *Carabodes*, and found two pairs of aggenital setae in some species. The following species share this character state: *C. brevis* Reeves, *C. erectus* Reeves, *C. falcatus* Jacot, *C. phylliformis* Reeves, *C. polyporetes* Reeves, *C. gibbiceps* Berlese, *C. cherokee* Reeves, *C. clavatus* Jacot, *C. niger* Banks, *C. coweetaensis* Reeves, *C. nantahalaensis* Reeves, *C. interruptus* Reeves and *C. floridus* Berlese (Reeves & Behan-Pelletier, 1998).

### Post-embryonic development

Information about immatures was obtained from Grandjean (1949, 1953) and André (1975) on *Carabodes labyrinthicus*; Bellido (1978) on *C. willmanni*; Reeves (1992) on *C. erectus*; Reeves and Behan-Pelletier (1998) and Ermilov (2011) on *C. subarcticus*.

We conclude that preceding authors (Grandjean 1949; 1953; André 1975; Bellido 1978; Reeves 1992, 1997; Reeves and Behan-Pelletier 1998) provided a good general overview of *Carabodes* and its principal characteristics and variations, but considered *Pentabodes* and *Phyllocarabodes* (amongst others) as separate taxa.

### Genus *Phyllocarabodes*

The taxonomy of *Phyllocarabodes* Balogh & Mahunka 1969 is complicated by an incomplete original description, and its unexplained inclusion in *Carabodes* as subgenus by Subías (2004, updated 2017) seemingly without study of the type material or additional specimens.


The taxonomy of *Pentabodes*, *Antillobodes* and *Phyllocarabodes* is confusing as indicated by the following: Mahunka, in his revision of the family Carabodidae in 1986, redescribed *Pentabodes* and *Phyllocarabodes* as different genera. Subías 2004 (until 2015) indicated "*Carabodes (Phyllocarabodes)*" Balogh J & Mahunka, 1969b (5 spp.) (= *Antillobodes* Mahunka, 1985) (= *Pentabodes* P. Balogh, 1984 "sin. nov."), without any further explanation.

Synonymy of *Phyllocarabodes*, *Pentabodes* and *Antillobodes* will be studied and discussed in a future paper. We have studied the type material of *Antillobodes*, but to date have been unable to obtain type material of *Pentabodes*, though we anticipate specimens among material collected in Colombia, housed in the Collection of the Museum National d'Histoire Naturelles (MNHN, Paris).

### Taxonomy of *Phyllocarabodes*

The description of *Phyllocarabodes octogonalis* Balogh & Mahunka 1969b included only two figures (their Figure 34 and 35), and the captions to the figures only state: "34–35: *Phyllocarabodes octogonalis* n. sp.". Figure 34 is a dorsal view, but Figure 35 is of a notogastral or prodorsal seta (Balogh and Mahunka 1969b). Based on this incomplete description, the following problems arise when analysing further data on *Ph. octogonalis*:

The ornamentation of *Ph. octogonalis* was discussed by Balogh P. (1986) in his description of *Ph. ornatus*, and a comparison is given of the ornamentation of these two species. Balogh (1986) mentioned a tuberculate ornamentation of *Ph. octogonalis* in his text and figures whereas Mahunka depicted and described *Ph. octogonalis* with a smooth surface. Hence the true nature of the surface is unclear.

Prodorsum and prodorsal setae. In Balogh and Mahunka (1969b), Figure 34 shows an interesting particularity: the dotted parallel lines behind *in* setae. We consider these lines to represent the elevated prodorsal longitudinal ridge (*p.r.l*) found between *in* setae and posterior zone of prodorsum (present paper: Figures 1 and 6, 6' indicated by *p.r.l* and ). Balogh P. (1986) did not refer to this structure in his text, but in Figure 5 of *Ph. octogonalis*, a sigmoid line was added behind the *in* setae. Mahunka (1986) indicated: "Prodorsum: lamellae with sharp cuspis, rostral setae thin, arising near to them, lamellar seta phylliform, originating in the interlamellar area". In their description, Balogh and Mahunka (1969b) stated: "Hairs *ro* and *la* narrowly, hairs *in* widely, phylliform". However, in illustrations, two pairs of setae are visible (*in* and *ro*), but not *le*. From Mahunka (1986) it is unclear if and where *in* setae were observed. Balogh P. (1986) also did not mention these setae in his comparison of *Ph. octogonalis* and *Ph. ornatus*.

Balogh and Mahunka (1969b) as well as Mahunka (1986) gave only vague information on interlamellar, lamellar and rostral setae which makes it difficult to homologize the setae as they show different positions in the different species

The situation of notogaster and notogastral setae is treated very superficially by Balogh and Mahunka (1969b), Mahunka (1986) and Balogh (1986), providing limited information on notogastral setae and not providing any discussion regarding the relative positions of the setae, nor of the characteristics of the notogaster (see section on "Conclusion").

Balogh and Mahunka (1969b) gave an epimeral formula of 1-1-3-3 while Mahunka (1986) provided a formula of 2-1-3-3. We doubt the existence of the second seta on epimeron I as indicated by Mahunka (1986) as the position of these setae is very particular and unusual.

In Mahunka (1986), the text and figures indicate two setae on the first epimere (setae indicated on Figure 62), and in Figure 63 a large seta situated on *Pd.I*, which was not observed by Balogh and Mahunka (1969b), nor by Balogh P. in 1986, but included by Mahunka (1986). Six pairs of genital setae are consistently observed in all three species of the genus *Phyllocarabodes* (*Ph. octogonalis*, *Ph. ornatus*, *Ph. costaricensis*).

Ten pairs of notogastral setae are observed in *Phyllocarabodes*, but with an unusual distribution. To provide notation for these setae, it is necessary to study ontogenetic development (Grandjean 1953; Travé 1964). Setal distribution is not related to the setal distribution of the genus *Carabodes*.

Genital formulae of *Phyllocarabodes* and *Carabodes* cannot be compared as ontogenetic studies of *Phyllocarabodes* are lacking.

In *Phyllocarabodes*, part of the notogaster is "light bulb-shaped", starting slightly behind the *d.sj* and extending to the posterior notogastral marginal setal zone. This zone is surrounded laterally by *s.c* that posteriorly is nearly erased or very flat, and is not clearly discernible (Figures 1 and 27) (present paper). This zone is tuberculate in *Ph. octogonalis* and *Ph. ornatus* (*sensu* Balogh P. 1986) and displays foveate microsculpture in *Ph. costaricensis*. The disposition of the notogaster posterior to the elevated zone is very different to that observed in known species of *Carabodes*. The shape of the notogaster and elevated zone can be compared to Figures 3, 5 and 8 of *C. chandleri* in Reeves 1992; *C. erectus* Figures 18 and 19 in Reeves 1992; *C. interruptus* Figures 26 and 28 in Reeves 1992; *C. pentasetosus* Figures 34 and 36 in Reeves 1992; *C. labyrinthicus* (Michael); *C. rugosior* Berlese; *C. granulatus* Banks Figures 39, 40 and 41, respectively, in Reeves and Behan-Pelletier (1998).

In *Phyllocarabodes*, the zone where *h.ap* and *bo* overlaps is distinct, as the anterior part of the *h.ap* is perfectly embedded in the posterior part of *bo*. This differs from that in *Carabodes* and can be compared to *Carabodes hoh* (Reeves & Behan-Pelletier 1998) (Figures 36 and 42) and *C. colorado* (Reeves & Behan-Pelletier 1998) (Figure 18) to observe the difference. In *Phyllocarabodes*, the bothridium (Figure 35, present paper) is distinct from that in *Carabodes*: the opening is directed downwards, mouse-ear shaped and incomplete, with smooth particular *bo.ri* and large *bo.to*.

These profound differences in body shape clearly support the idea that *Phyllocarabodes* is a distinct genus and not just a subgenus of *Carabodes*. We therefore redefine the genus as follows.

### Redefinition: *Phyllocarabodes*

Elongate animals. Prodorsum elongate, with parallel ridges situated at level of *in* setae; extending from close to *d.sj* and exceeding *in* setal insertion level; *ro* setae longer than *in*; *le* setal insertion anterior to *ro* setal insertion; ventral tutorial zone dentate; *Pd I* medium-sized, *Pd II* very small, *dis* tiny, hardly discernible. Ten pairs of notogastral setae with particular distribution (notation cannot be accurately provided without ontogenetic studies); central zone of notogaster rounded or "light bulb-shaped", partially surrounded by *s.c*; *s.c* partially erased or flat posterior to elevated central zone; elevated notogastral zone microsculpture differing from rest of notogaster; epimeral setal formula 1-1-3-3; longer epimeral setae; *3b*, *3c* adjacent; six pairs of genital setae.

We consider *Phyllocarabodes* differentiated from *Carabodes* based on important differences in: shape of prodorsum and notogaster, disposition of prodorsal and notogastral setae (very different to



*Carabodes*). All three known species of *Phyllocarabodes* have six pairs of genital setae.

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