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To cite this article: Nestor Fernandez, Pieter Theron, Christine Rollard & Sergio Leiva (2015) The family Carabodidae (Acari: Oribatida) IX. Redescription of *Carabodella calcarata* Mahunka, 1986 and *Hardybodes penicillatus* Mahunka, 1995, *International Journal of Acarology*, 41:7, 551-562, DOI: [10.1080/01647954.2015.1081406](https://doi.org/10.1080/01647954.2015.1081406)

To link to this article: <http://dx.doi.org/10.1080/01647954.2015.1081406>



Published online: 24 Aug 2015.



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## The family Carabodidae (Acari: Oribatida) IX. Redescription of *Carabodella calcarata* Mahunka, 1986 and *Hardybodes penicillatus* Mahunka, 1995

Nestor Fernandez<sup>a,b</sup>, Pieter Theron<sup>b</sup>, Christine Rollard<sup>c</sup> and Sergio Leiva<sup>d</sup>

<sup>a</sup>National Council of Scientific and Technological Research (CONICET), Evolutive Genetic Laboratory FCEQyN, Misiones National University, Posadas Misiones, Argentina (email: [nestorfernand51@yahoo.fr](mailto:nestorfernand51@yahoo.fr)); <sup>b</sup>Research Unit for Environmental Sciences and Management, North-West University, South Africa (email: [pieter.theron@nwu.ac.za](mailto:pieter.theron@nwu.ac.za)); <sup>c</sup>Muséum National d'Histoire Naturelle, Département Systématique et Evolution, Unité OSEB, Paris cedex 05, France (email: [chroll@mnhn.fr](mailto:chroll@mnhn.fr)); <sup>d</sup>National Institute Agricultural Technology (INTA), Experimental Rural Agency, Aimogasta, Argentina (email: [sergiodanteleiva@yahoo.ar](mailto:sergiodanteleiva@yahoo.ar))

(Received 27 March 2015; accepted 3 August 2015; published online 24 August 2015)

Redescriptions of the Carabodidae species *Carabodella calcarata* and *Hardybodes penicillatus* were completed together with redefinition and comparison of the genera under investigation. Complementary study of *H. penicillatus* and *H. flabellatus* resulted in recognition of the same structures observed in *H. mirabilis* (type species of *Hardybodes*), while observations of *Carabodella calcarata* (type species of *Carabodella*) highlighted the substantial differences compared to *Hardybodes* and other genera of the Carabodidae family. We concluded that *Carabodella* and *Hardybodes* are separate genera with easily distinguishable features. The particular characteristics of leg III in *C. calcarata* suggests a unique leg folding process compared to other genera in the family.

**Keywords:** Acari; Oribatida; *Carabodella calcarata*; *Hardybodes penicillatus*; redescription

### Introduction

Subías (2004 updated 2015) considers *Carabodella* a sub-genus of *Hardybodes*, but the situation is complicated by: (1) a remark made by Mahunka (1986) with regard to *Carabodella* and its relation to *Austrocarabodes*: “the new genus is well characterized by the epimeral setal formula (one pair of setae on the first epimeres) and the strong spur on femur IV. It comes nearest to *Austrocarabodes* Hammer, 1966, however, the epimeral setal formula of the latter: 3-1-3-3, without a strong spur” Mahunka (1986, p. 58) (see the section “Discussion”); (2) in the description of *Hardybodes penicillatus* Mahunka, 1995 and *H. flabellatus* Mahunka, 1995, the author remarked: “These two new species were easy to place in the genus *Hardybodes* Balogh, 1970, although some corrections and additions to the generic diagnosis are necessary. Consequently, the peculiar form of the rostrum and the rostral setae is characteristic only for the type species (*H. mirabilis* Balogh, 1970). The notogaster is not always flat, in the new species its median part distinctly projects” (Mahunka 1995, p. 938) (see the section “Discussion”).

These factors made it necessary to study: (a) all species within the genus *Hardybodes*; (b) *Austrocarabodes ensifer* (Sellnick 1931); (c) the type species of the genus *Carabodella*.

A previous paper reviewing the family Carabodidae (Fernandez et al. 2013a) included a redefinition of the genus *Hardybodes* based on the type species and redescription of *H. mirabilis*. We also previously studied the genus *Austrocarabodes* (Fernandez et al. 2013b),

including a redefinition of the genus *Austrocarabodes* and redescription of *A. ensifer* (Sellnick 1931). Finally, for the current paper, we studied the unique species *Carabodella* (*C. calcarata*) and two other species of *Hardybodes* (*H. penicillatus* and *H. flabellatus*) with the intention of better understanding the situation.

*Hardybodes* contains four species (sensu Subías *op. cit.*) – *Hardybodes* (*H.*) *mirabilis* Balogh, 1970, *H.* (*H.*) *penicillatus* Mahunka, 1995, *H.* (*H.*) *flabellatus* Mahunka, 1995, and *H.* (*Carabodella*) *calcarata* (Mahunka) 1986.

Only the type material deposited in the Museum d'Histoire Naturelles Genève was available for study; unfortunately other type materials were impossible to obtain. A decision was therefore made to redescribe only one species from Brunei, *H. penicillatus*, and determine the characteristics of *H. flabellatus*. In doing so, some errors and omissions of important characters were noted.

### Material and methods

All specimens were studied using light microscopy; specimens 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 France S. A.S., Rungis, France) equipped with a drawing tube. To aid observations, some specimens were stained with chlorazol black E (Coineau 1974).

**Morphological terminology**

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

Over the years, many different terms were used with reference to similar structures when describing genera and species in the family Carabodidae. We thought it fit to propose generalized terminologies (Fernandez et al. 2013a) in order to compare genera and species within the family.

**Institutions**

MNHN Muséum National d'Histoire Naturelle, Paris, France.

MHNG Muséum d'Histoire Naturelles, Genève.

**Redescriptions of taxa****Genus *Carabodella* Mahunka 1986****Redefinition**

Prodorsum slightly convex; lamellar cuspis rounded; elevated interlamellar process absent; bothridia cup-shaped, bothridial ring present; superior cornea of naso present. Notogaster slightly ovoid, without anterior and posterior depressions; humeral apophysis clearly visible. Fourteen pairs of setae ( $c_1$ ,  $c_2$ ,  $da$ ,  $dm$ ,  $dp$ ,  $la$ ,  $lm$ ,  $lp$ ,  $h_1$ ,  $h_2$ ,  $h_3$ ,  $p_1$ ,  $p_2$ ,  $p_3$ ). Pedotectum I, II and discidium present. Epimeral setal formula 1-1-3-3 or 2-1-3-3. Four pairs of genital setae; one pair of aggenital setae; three pairs of adanal setae; two pairs of anal setae. Lyrifissure *iad* far removed from anal aperture. Legs: femur III lacking femoral groove, bearing two spurs, ventral setae situated between them; femur IV robust, long spur ventrally.

***Carabodella calcarata* Mahunka 1986  
(Figures 1–13; Table 1)****Diagnosis**

**Integument.** tuberculate.

**Setae:** simple: interlamellar, notogastral, epimeral, genital, aggenital, anal, adanal; curved: rostral; lanceolate barbate: lamellar. Dorsolateral lamellae; prominent internal cuticular thickening originating in posterior bothridial zone, terminating internally to rounded lamellar apex; shallow lamellar furrow running parallel to cuticular thickening. Rostral margin rounded. Sensillus thin, barbate, upward curving tip; dorsosejugal furrow convex; circumgastric furrow present; lyrifissures *im*, *ih*, *ips*. Tutorium strongly curving cuticular thickening; deep supratutorial depression; pedotectum I, prominent extended area; pedotectum II, small rounded lamina; discidium with small triangular protuberance; polyhedral or partially rounded cavities

observed behind acetabulum IV. Slightly elevated epimeres, delimiting shallow furrow (*bo.l.*, *bo. 2*, *bo.sj*); anterior genital furrow present; genital plate ovoid; small compared to anal plate; four pairs of genital setae; aggenital setae posterior to genital opening, near medial zone; three pairs of adanal setae; anal plate terminating in small sharp tip; two pairs of anal setae; lyrifissure *iad* posterolaterally to  $ad_3$  setae. Preanal organ present; circumgastric depression present.

**Material examined**

“*Carabodella calcarata*, Paratype – Tanzania n° 54. – Tanzania, W Usambara Mts., Matundsi-Mashindei ridge, at 1300 m alt. 04.02. 1985. Submontane rain forest of the rocky Matundsi-Mashindei ridge, SW of Ambangulu Tea Estate. Berlese-funnel sample consisting a mass of fallen epiphytes, Leg 1. Peregovits.” Deposited in MHNG.

**Description**

**Measurements.** Length 660  $\mu\text{m}$ ; width 312  $\mu\text{m}$  (Figures 1, 2, 4).

**Colour.** Specimens without cerotegument: light brown; slightly shiny, when observed in reflected light (note that this material has been studied before and may be decoloured).

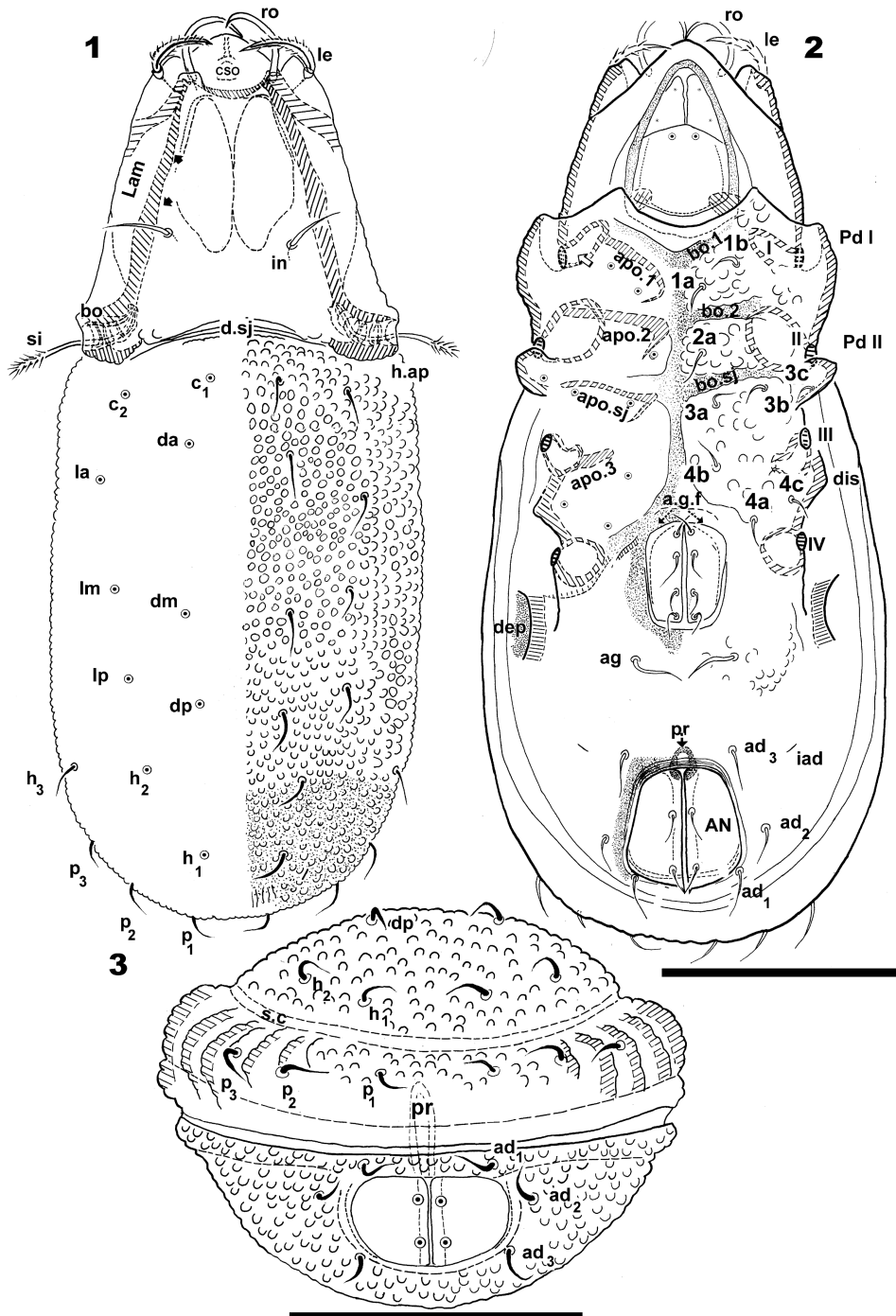
**Cerotegument.** Not present (see note above).

**Integument.** Tuberculate, more accentuate on notogaster (Figures 1–5)

**Setation.** Setae: simple: *in*, notogastral, epimeral, genital, aggenital, anal, adanal; curved: *ro*; lanceolate and barbate: *le*.

**Prodorsum.** Convex (Figures 1, 4), without any processes; *ro* setae situated on promontories curved, directing anteriorly; *le* directing laterally (Figures 3, 5); *le* setae directing anteriorly and medially (Figure 5). Dorsolateral lamellae (*Lam*); prominent internal cuticular thickening clearly visible (Figure 1, indicated by  $\uparrow$ ), originating on bothridial posterior zone and terminating in internal zone of rounded apex of lamellae (*la.ti*); shallow lamellar furrow (*l.l.f*), hardly discernible in dorsal view, clearly discernible in frontal view, running internally and parallel to cuticular thickening, terminating internally to rounded *la.ti* (Figure 5, indicated by  $\downarrow$ ). Rostral margin rounded (Figures 1, 2, 5). Bothridia cup-shaped, with bothridial ring (*bo.ri*) (Figure 4). Sensillus thin, barbate, dilated upward curving tip (Figure 1). Anterior to *ro* setae, superior cornea of naso (CSO) clearly visible (Figures 1, 5).

**Notogaster.** Oval, elongate in shape; without anterior notogastral depression (*n.a.d*) or posterior notogastral depression (*n.p.d*); dorsosejugal furrow (*d.sj*) convex, clearly visible (Figure 1). Circumgastric furrow (*s.c*) present,



Figures 1–3. *Carabodella calcarata* Mahunka 1986, adult. 1. dorsal view; 2. ventral view; 3. posterior view. Abbreviations: see “Materials and methods”. Scale bars: 1–2 = 165  $\mu$ m; 3 = 160  $\mu$ m.

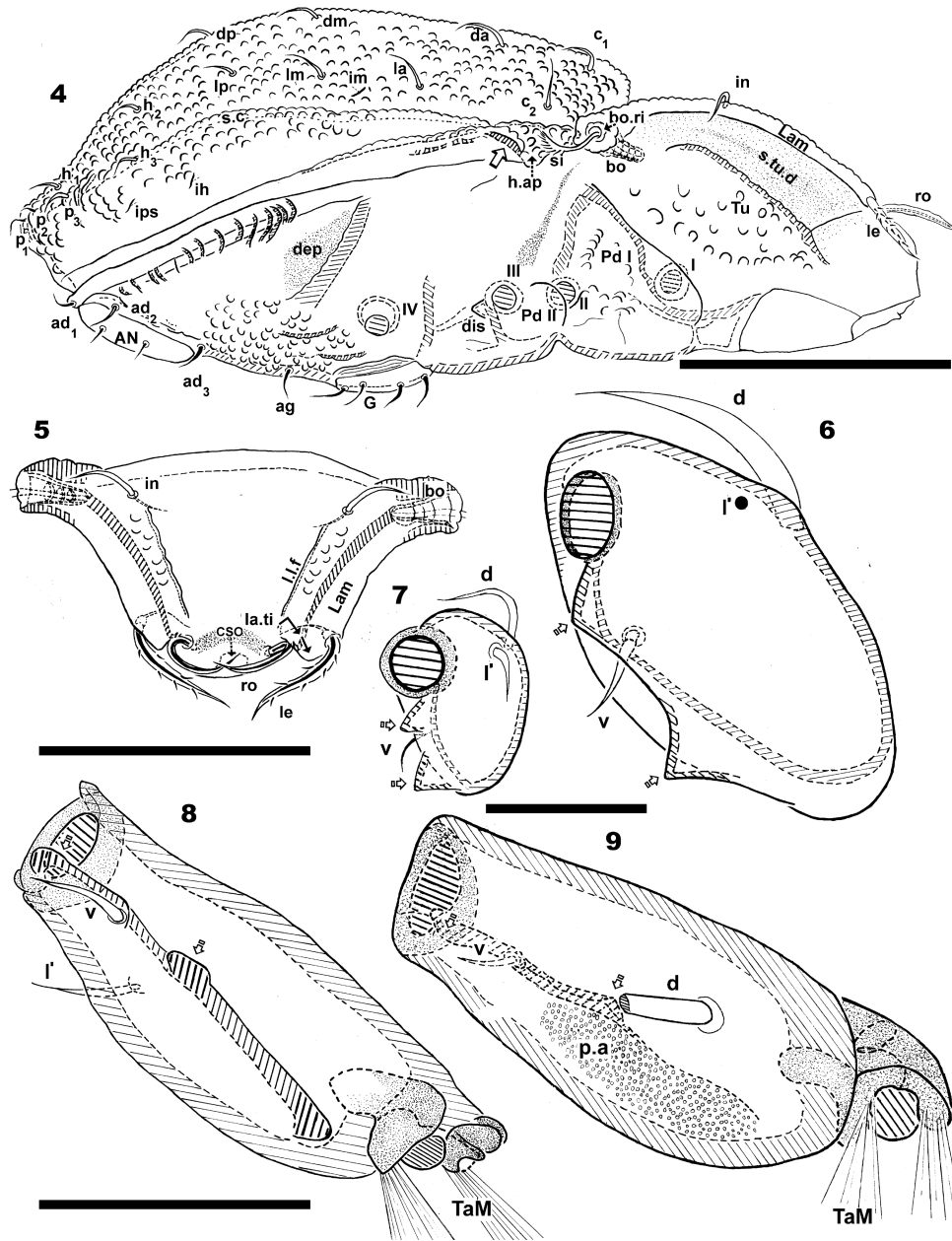
hardly discernible in dorsal view; easily observed in posterior view (Figure 3). Humeral apophysis (*h.ap*), clearly visible in lateral view; hardly discernible in dorsal view (Figures 1, 4), with large rod-like ridge clearly discernible in lateral view (Figure 4, indicated by  $\Rightarrow$ ).

Fourteen pairs of simple notogastral setae (*c*<sub>1</sub>, *c*<sub>2</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>); lyrifissures *im*, *ih*, *ips* clearly visible (Figure 4).

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

Pedotectum I (*Pd I*): prominent extended area, rounded end, covering first acetabulum (Figure 4). Pedotectum II (*Pd II*): small rounded lamina (Figure 4). Sejugal





Figures 4–9. *Carabodella calcarata* Mahunka 1986, adult. 4. lateral view; 5. frontal view; 6. femur III, antiaxial inclined view; 7. Femur III, frontal inclined view; 8. Femur III ventral view; 9. femur III dorsal inclined view. Abbreviations: “Materials and methods”. Scale bars: 4 = 200  $\mu$ m; 5, 6, 8, 9 = 45  $\mu$ m; 7 = 30  $\mu$ m.

depression (*sj*) deep, clearly visible. Three pairs of lyrifissures, *im*, *ih*, *ips*. Humeral apophysis (*h.ap*) triangular in shape, tip overlapping posterior bothridial zone (Figure 4); upper margin linear; inferior margin oblique–rectilinear. Rod-shaped thickening crossing *h.ap* (Figure 4, indicated by  $\Rightarrow$ ).

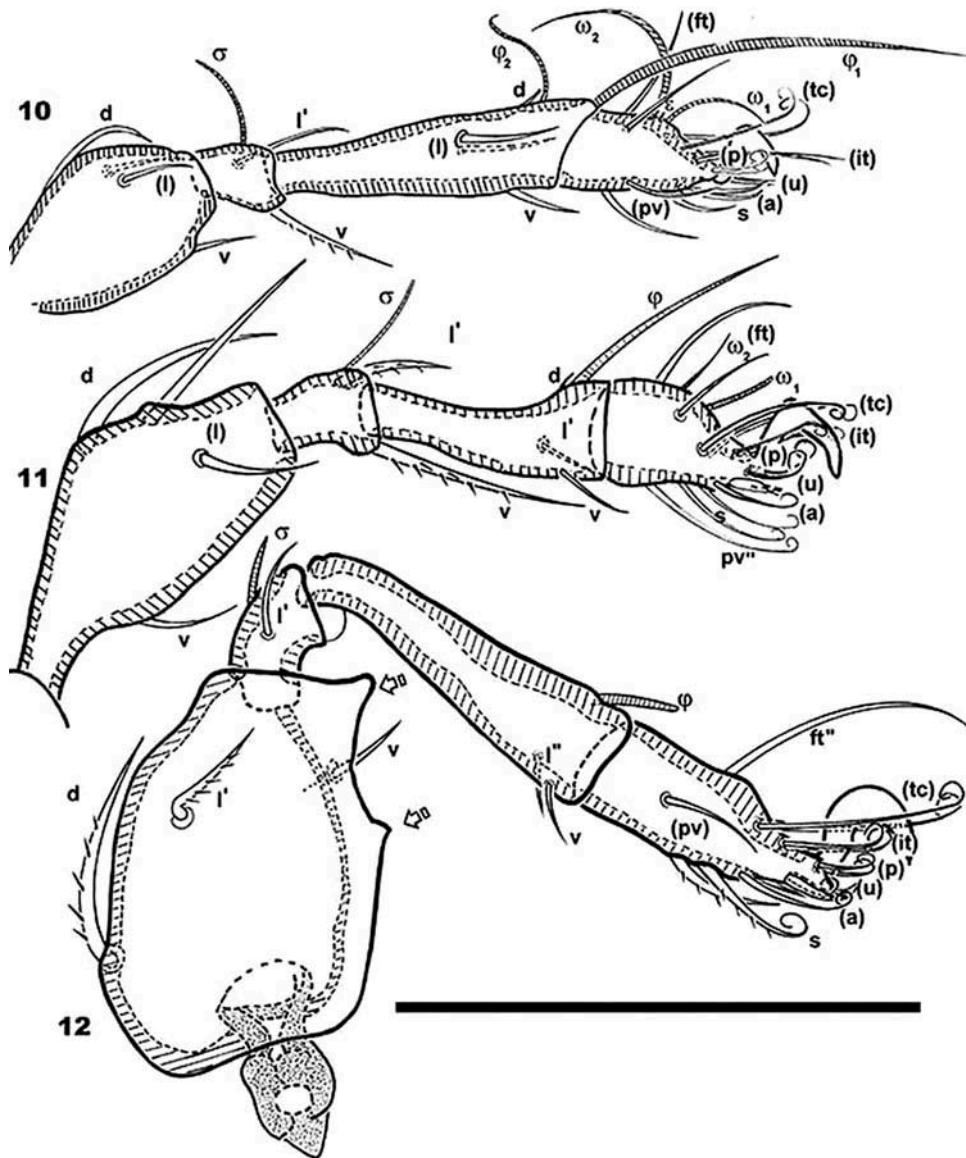
Discidium: small triangular protuberance near acetabulum III. Many polyhedral or partially round cavities (*dep*) situated behind acetabulum IV (Figure 4).

*Ventral region* (Figure 2). Epimera slightly elevated, delimited by shallow furrow (*bo.1*, *bo.2*, *bo.sj*); epimeres

3–4 fused; *apo.1*, *apo.2*, *apo.sj* and *apo.3* clearly discernible.

Epimeral chaetotaxy 2-1-3-3; laterally occurring structure, possibly insertion or shaved setae (Figure 2 indicated by  $\Rightarrow$  see Remarks). *Pd I*, *Pd II* and *dis* easily discernible. Anterior genital furrow (*a.g.f*) present, but hardly discernible; various angles of observation are necessary in order to establish the shape.

Genital plate ovoid; small in comparison with anal plate; four pairs of setae; all setae more or less equal in size. Aggenital setae situated posterior to genital opening, near medial zone. Three pairs of adanal setae. Anal plate terminating in small sharp tip, two pairs of anal setae.



Figures 10–12. *Carabodella calcarata* Mahunka 1986, adult. 10. leg I, anti-axial view; 11. leg II, anti-axial view; 12. leg III anti-axial view. Abbreviations: see “Materials and methods”. Scale bars: 10–12 = 50  $\mu$ m.

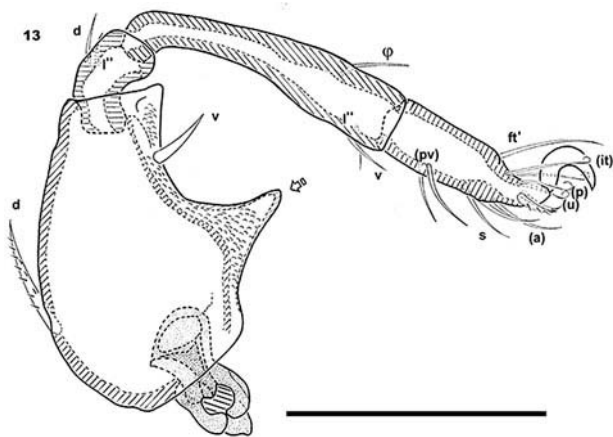


Figure 13. *Carabodella calcarata* Mahunka 1986, adult. Leg IV anti-axial view. Abbreviations: see “Materials and methods”. Scale bars: 13 = 40  $\mu$ m.

Lyrifissure *iad* easily discernible, situated posterior and laterally to  $ad_3$  setae. Preanal organ (*pr*) clearly visible as a rounded structure.

*Posterior aspect* (Figure 3). Notogaster circular. Circumgastric depression (*s.c*) visible as a conspicuous furrow. Cuticular ridges occurring in  $p_1, p_2, p_3$  setal zone; preanal organ (*pr*) clearly discernible.

#### Legs (Figures 6–13)

*Leg I* (Figure 10). Femur with four setae. Genu with fine, setiform  $\sigma$ , of medium length;  $v$  setae longest, barbed; (*l*) setae smooth. Tibia: long, tactile  $\phi_1$  on dorsal apophysis;  $\phi_2$  medium sized, small setae *d* situated posteriorly, close to  $\phi_2$ . Tarsus with medium length, setiform  $\omega_1$  and  $\omega_2$ ;  $\epsilon$

Table 1. *Carabodella calcarata* Mahunka, 1986.

	Femur	Genu	Tibia	Tarsus	Claw
<b>Leg I</b>					1
Setae	<i>d,(l),v</i>	<i>l',v</i>	<i>d,(l),v</i>	<i>(pv),s,(a),(u),(p),(it),(tc),(ft),ε</i>	
Solenidia		$\sigma$	$\varphi_1, \varphi_2$	$\omega_1, \omega_2$	
<b>Leg II</b>					1
Setae	<i>d,(l),v</i>	<i>v,l'</i>	<i>d,l',v</i>	<i>(p),(it),(tc),(ft),(u),(a),s,pv''</i>	
Solenidia		$\sigma$	$\varphi$	$\omega_1, \omega_2$	
<b>Leg III</b>					1
Setae	<i>d,l',v</i>	<i>l'</i>	<i>l'',v</i>	<i>(it),(tc),ft'',(p),(u), (a),s,(pv)</i>	
Solenidia		$\sigma$	$\varphi$	0	
<b>Leg IV</b>					1
Setae	<i>d,v</i>	<i>d,l''</i>	<i>l'',v</i>	<i>(p),(it),ft',(u),(a),s,(pv)</i>	
Solenidia		0	$\varphi$	0	

small, hardly discernible; setae *(u),(a)* and *s*, more or less equal in size; *(p)* small.

**Leg II** (Figure 11). Femur with long setae. Genu  $\sigma$ , medium sized; *v* setae large, barbed. Tibia short;  $\varphi$  medium length, setiform, associated with small setae *d*. Articulation between tibia and tarsus by means of small synarthrodial membrane permitting limited movement (Fernandez et al. 2013a). Tarsus medium sized;  $\omega_1, \omega_2$  small.

**Leg III** (Figures 6, 7, 8, 9, 12). Femur with particular characters not found in other genera of the family Carabodidae studied to date. Polyhedral in shape, lacking femoral groove (*f.g.*), two spurs present (indicated by  $\hat{\cup}$  in Figures 6, 7, 8, 9, 12). Setae *v* situated between spurs. Frontal view (Figure 7) permitting observation of positioning of spurs ( $\hat{\cup}$ ) and *v* setae. Antiaxial (Figure 12) and antiaxial lateral inclined views (Figure 6) as well as ventral view (Figure 8) allowing observation that setae *v* are situated ventrally, but paraxially to spurs ( $\hat{\cup}$ ). Dorsal view (Figure 9) allowing observation of relative position of dorsal setae *d* and porose area (*pa*) (situated paraxially to spurs) ( $\hat{\cup}$ ); *d* and *l''* setae barbed. Genu with *l''* and  $\sigma$  medium length. Tibia with *l''* and *v*;  $\varphi$  baculiform. Tarsus, *(it), (tc), ft''*.

**Leg IV** (Figure 13). Leg with particular characteristic: femur with prominent spur (indicated by  $\hat{\cup}$ ), similar shape as femur III but larger, *d* setae barbed. Genu with medium-sized *d* setae. Tibia  $\varphi$  medium size. Tarsus (*tc*) and *ft''* setae absent.

**Setal formulae** (trochanter to tarsus). I (1-4-2-4-16-1) (1-2-2); II (1-4-2-3-14-1) (1-1-2), III (2-3-1-2-14-1) (1-1-0); IV (1-2-2-2-12-1) (0-1-0) (see Table 1).

#### Remarks

Very fine observation of the cuticle was necessary, as it was opaque. Two setae were found on the side of the first epimere; but on the other side, in lateral position, a

structure is present which is possibly a razed seta or an insertion. The difficulty of observation and small number of specimens makes it impossible to be certain of the number of epimeral setae. For these reasons, in the redescription, we add the epimeral setal formula (1-1-3-3) given by Mahunka (1986) (See the section "Discussion").

#### Taxon redescription

##### Genus *Hardybodes* Balogh 1970

The genus was redefined on the basis of the type species *Hardybodes mirabilis* Balogh 1970 by Fernandez et al. (2013a), pages 45–46 as: "Body shape ovoid. Prodorsum lacking interlamellar processes; a pair of prodorsal cavities and median eye pillar present; lamellae laterodorsal, laterally clearly discernible with *le* apically; internal lamellar paraxial border clearly visible and on prodorsal surface is delimited by shallow dorsal lamellar furrow ending in internal part of a smaller tip. Interlamellar setae on lamellar surface. Dorsosejugal furrow narrow, well delimited. Bothridial ring incomplete, with bothridial tooth. Notogaster convex without anterior depression. Fifteen pairs of notogastral setae. Tutorium, pedotectum I, pedotectum II and discidium present. Epimeric setae 3-1-3-3; anterior genital furrow present; genital setae: 4; Ag:1; Ad:3; An:2."

Redefinition of *Hardybodes* based on all presently known species in genus:

Body shape ovoid. Prodorsum lacking interlamellar processes; pair of ovoid medial eye structures present, connected to prodorsal surface by cavities, or situated internally without external cavities; laterodorsal lamellae clearly discernible with *le* apically; internal lamellar paraxial border clearly visible, on prodorsal surface delimited by shallow dorsal lamellar furrow, terminating in internal part of sharper lamellar tip. Interlamellar setae on lamellar surface. Dorsosejugal furrow narrow, well delimited. Bothridial ring incomplete, with bothridial tooth. Notogaster convex without anterior depression. Fifteen pairs of notogastral setae. Tutorium, pedotectum I,



pedotectum II and discidium present. Epimeral setae 3-1-3-3; anterior genital furrow present; G: 4; Ag:1; Ad:3; An:2.

***Hardybodes penicillatus* Mahunka, 1995**  
(Figures 14–31, Table 2)

*Redescription of adult*

*Diagnosis (adult female)*

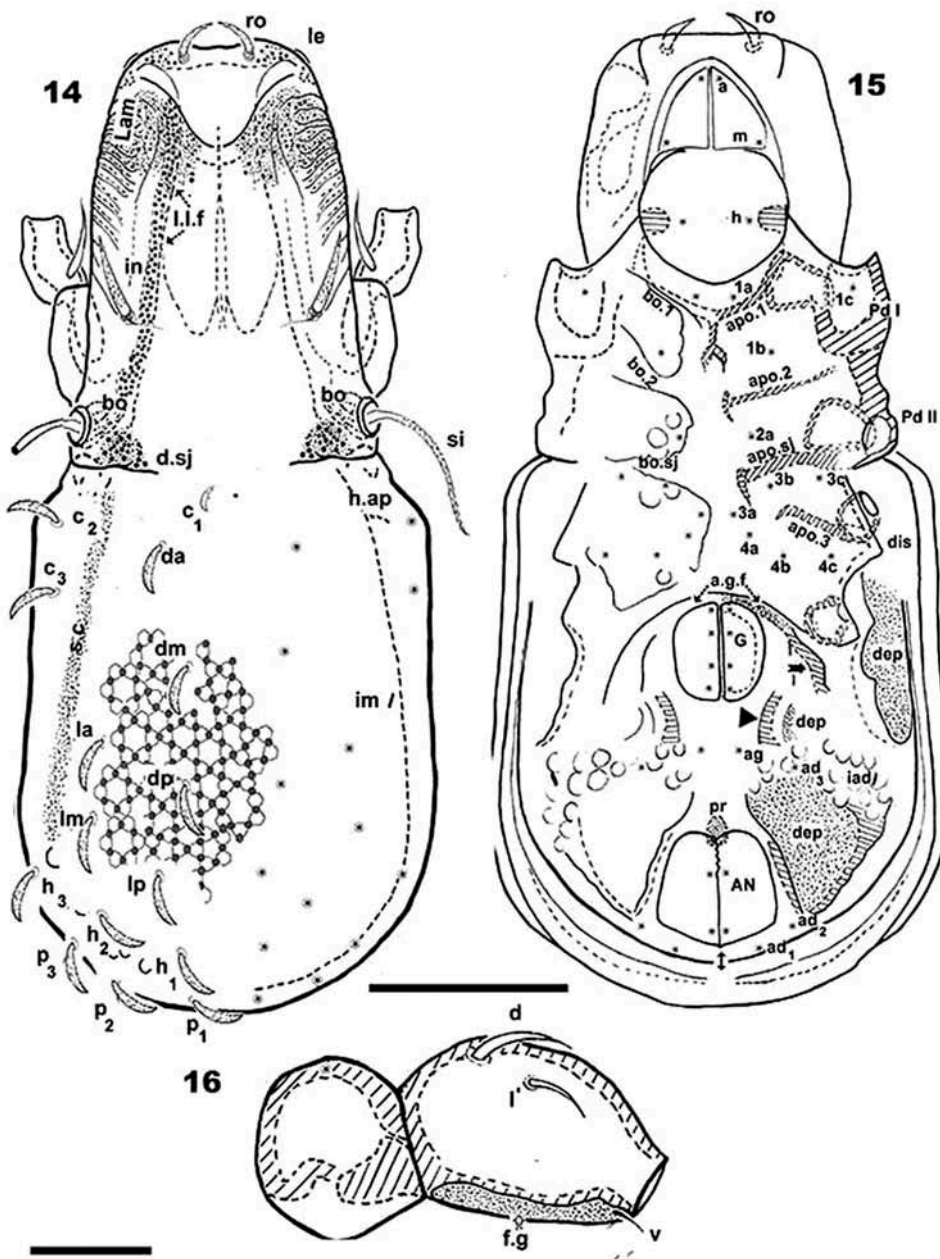
*Integument: tuberculate:* small on prodorsum, lamellar and bothridial zone; large: ventral region. *Cuticular ridges:* obliquely aligned, on lateral lamellar margin. *Polygonate*

*network:* principally hexagonal structures, related to each other by rounded structures.

*Setation:* simple: epimeral, aggenital, anal, adanal (not included in Figures, only insertions indicated); simple, slightly barbed: *ro*, *in*; lanceolate barbate: *le*; plumose: genital (not included in Figures, only insertions indicated); lanceolate, small asperities: notogastral.

*Prodorsum:* slightly convex. Rostral margin slightly concave. Bothridia cup-shaped, slightly curved. Sensillus thin, barbate. Paired internally bilobed structure, clearly discernible in frontal and lateral view; dorsal opening and median pillar eye, not present.

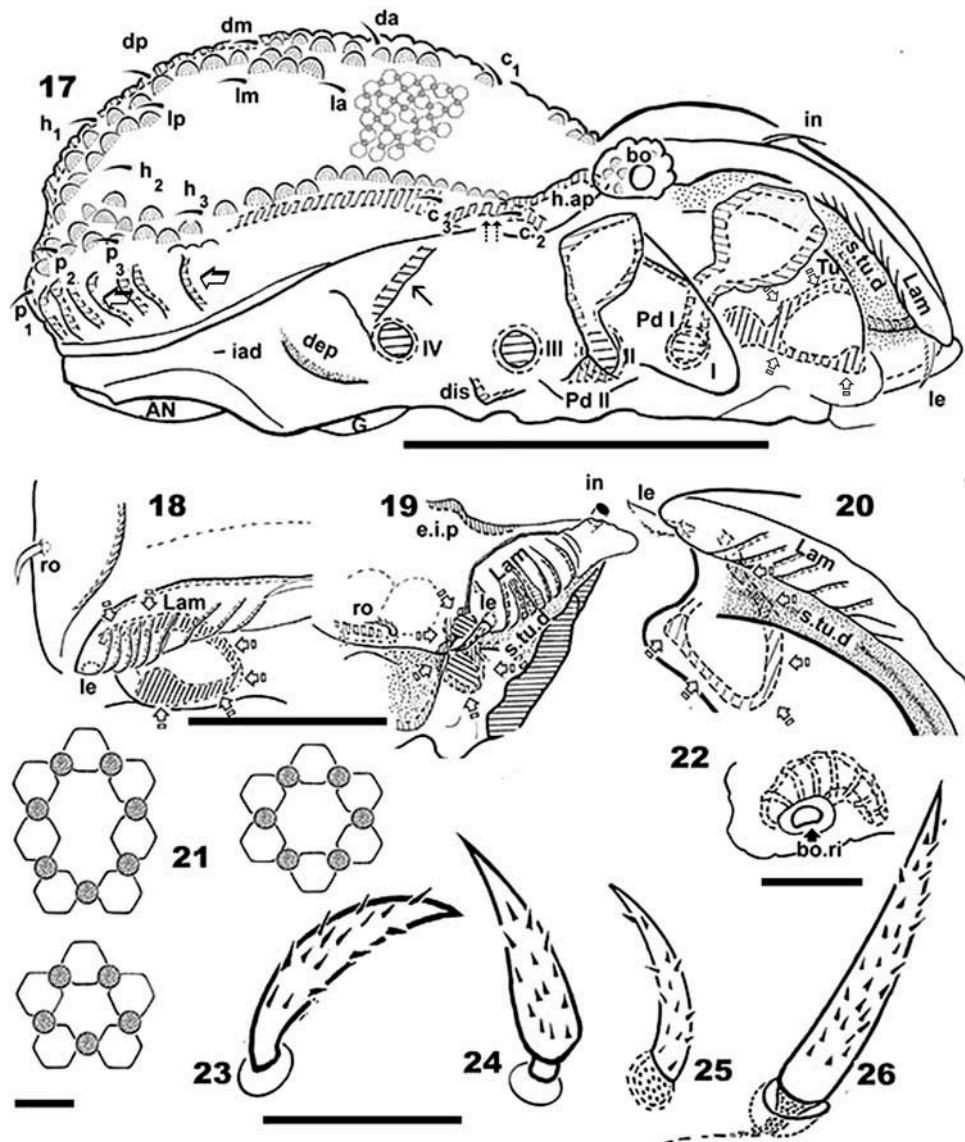
*Notogaster:* oval elongate; lacking notogastral anterior depression and notogastral posterior depression;



Figures 14–16. *Hardybodes penicillatus* Mahunka 1995, adult. 14. dorsal view; 15. ventral view; 16. femur III. Abbreviations: see “Materials and methods.” Scale bars: 14–15 = 70 μm; 16 = 20 μm.

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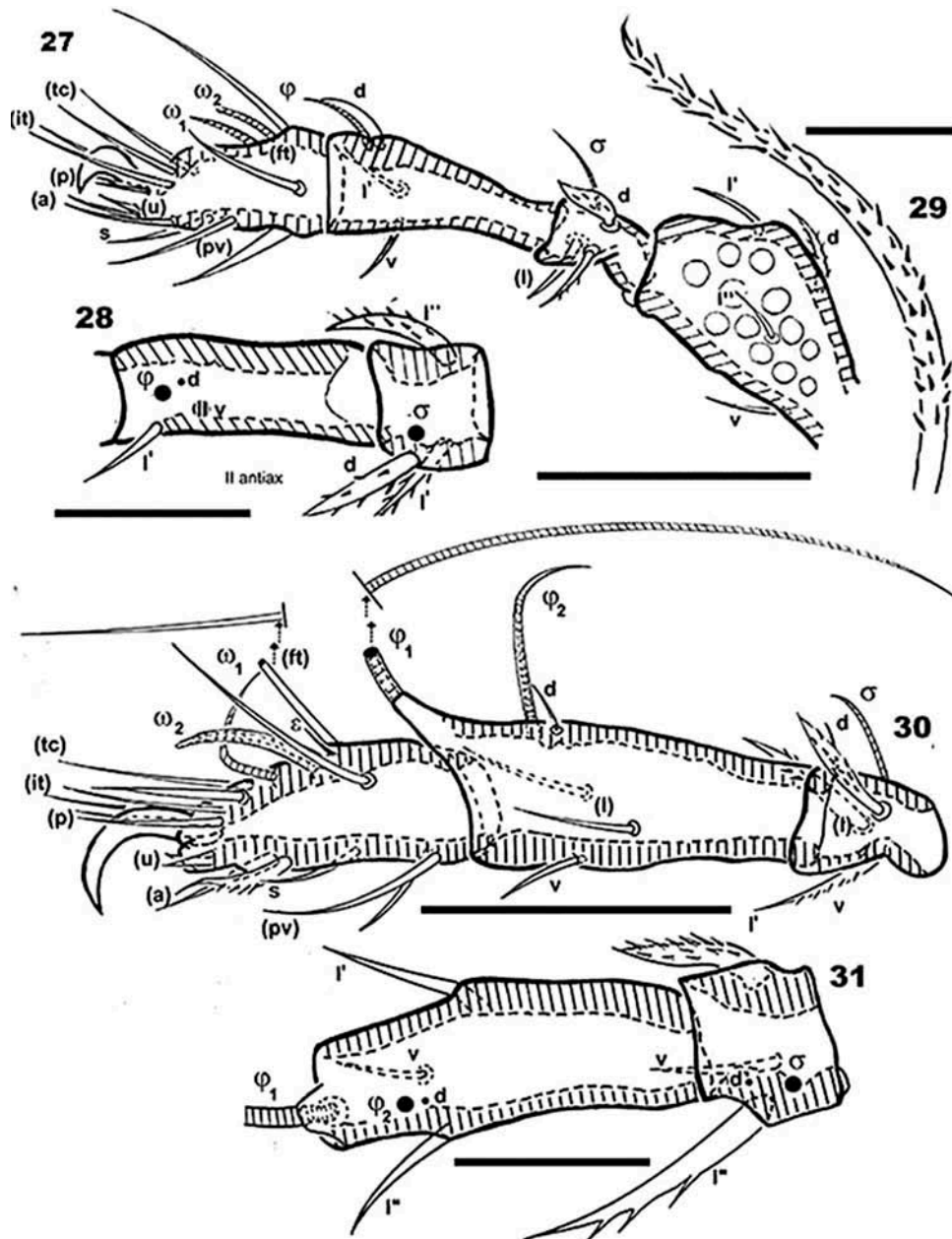
Figures 17–26. *Hardybodes penicillatus* Mahunka 1995, adult. 17. lateral view; 18 anterior zone of prodorsum, laterally inclined view; 19. anterior zone of prodorsum, frontally inclined view; 20. anterior zone of prodorsum, lateral view; 21. polygonal network; 23–24. notogastral setae; 25. rostral setae; 26. interlamellar setae. Abbreviations: see “Materials and methods.” Scale bars: 17 = 130  $\mu\text{m}$ ; 18–20, 22–26 = 30  $\mu\text{m}$ ; 21 = 10  $\mu\text{m}$ .

dorsosejugal furrow present, not discernible in medial zone; circumgastric furrow, clearly visible; humeral apophysis elongate with rod-shaped thickening. Fifteen pairs of notogastral setae ( $c_1$ ,  $c_2$ ,  $c_3$ ,  $da$ ,  $dm$ ,  $dp$ ,  $la$ ,  $lm$ ,  $lp$ ,  $h_1$ ,  $h_2$ ,  $h_3$ ,  $p_1$ ,  $p_2$ ,  $p_3$ ); lyrifissures not discernible.

**Lateral region:** turtorium: deep supratutorial depression (*s.tu.d*) with internal pocket depression. Pedotectum I (*Pd I*) prominent, with oblique cuticular ridge; Pedotectum II triangular, structure; discidium, small triangular protuberance. Rounded cavities behind acetabulum IV.

**Ventral region:** epimera slightly elevated, shallow furrow; epimere 4 fused; epimeral chaetotaxy 3-1-3-3; anterior genital furrow anterior to genital opening; genital plate ovoid; small compared to anal plate; four pairs of setae.

Aggenital setae, posterior to genital opening and near medial zone; three pairs of adanal setae; anal plate terminating in small sharp tip; two pairs of anal setae. Preanal organ a clearly visible rounded structure. Leg I: genu, solenidium  $\sigma$  setiform, fine, medium length; dorsal setae small, situated anterior to  $\sigma$ ; tibia, solenidium  $\phi_1$  on apophysis, lengthy, tactile;  $\phi_2$  medium length; dorsal setae small, in close proximity and posterior to  $\phi_2$ ; tarsus, solenidium  $\omega_1$ ,  $\omega_2$  medium length; famulus small; unguinal setae, small. Leg II: genu, solenidium  $\sigma$ , medium sized; dorsal setae, insertion level laterally to solenidium; tibia, solenidium  $\phi$  medium length; dorsal setae same length; tarsus medium sized; solenidia  $\omega_1$ ,  $\omega_2$  same length. Leg III: femur, ventral femoral groove, inner setae. Leg IV, femur normal.



Figures 27–31. *Hardybodes penicillatus* Mahunka 1995, adult. 27. leg II, antiaxial view; 28. tibia II, dorsal view; 29. sensillus, lateral view; 30. leg I, antiaxial view; 31. genu, tibia I, dorsal view. Abbreviations: see “Materials and methods.” Scale bars: 27 = 30  $\mu\text{m}$ ; 28 = 20  $\mu\text{m}$ ; 29, 31 = 15  $\mu\text{m}$ ; 30 = 25  $\mu\text{m}$ .

#### Material examined

*Hardybodes penicillatus* Mahunka 1991. Bru-88-35. Brunei (Belai District): “Badas Forest Reserve” à env. 10 Km sur la route secondaire qui bifurque, à 32 Km de Kuala Belai, vers le sud, forêt “Kerangas” (=“Tropical heath forest”) formée presque exclusivement par *Agathis dammara* (Lambert) L.G.Rich (Araucariaceae) prélèvement de sol au pied de *Agathis dammara*, 10 m; 23.XI. 1988. Leg. B. Hauser – Holotype and 2 Paratypes. Material Deposited in MHNG.

#### Description

**Measurements.** Length 326 (302–372)  $\mu\text{m}$ ; wide 156 (142–170)  $\mu\text{m}$  (Figures 14, 15).

**Colour.** Specimens without cerotegument: light brown; slightly shiny when observed in reflected light (this material has been previously studied and therefore decoloured).

**Cerotegument.** Not present (see note made above, with regard to colour).

Table 2. *Hardybodes penicillatus* Mahunka 1995.

	Femur	Genu	Tibia	Tarsus	Claw
<b>Leg I</b>					1
Setae	<i>d,(l),v</i>	<i>d,(l),v</i>	<i>d,(l),v</i>	<i>(pv),s,(a),(u),(p),(it),(tc),(ft),ε</i>	
Solenidia		σ	Φ <sub>1</sub> ,Φ <sub>2</sub>	ω <sub>1</sub> ,ω <sub>2</sub>	
<b>Leg II</b>					1
Setae	<i>d,(l),v</i>	<i>d,(l)</i>	<i>d,l',v</i>	<i>(p),(it),(tc),(ft),(u),(a),s,(pv)</i>	
Solenidia		σ	φ	ω <sub>1</sub> ,ω <sub>2</sub>	
<b>Leg III</b>					1
Setae	<i>d,l',v</i>	<i>l'</i>	<i>l',v</i>	<i>(it),(tc),ft',(p),(u),(a),s,(pv)</i>	
Solenidia		σ	φ	0	
<b>Leg IV</b>					1
Setae	<i>d,v</i>	<i>d,l''</i>	<i>l',v</i>	<i>(p),(it),ft',(u),(a),s,(pv)</i>	
Solenidia		0	φ	0	

*Integument.* Complex: (a) *tuberculate, small*: prodorsum lamellar and bothridial zone (Figure 14); (b) *tuberculate, large*: ventral region (Figure 15). (c) *obliquely aligned cuticular ridges*: lateral lamellar margin (Figure 14); (d) *polygonate network*: on dorsal notogastral surface, complex organization of principally hexagonal forms, related by rounded structures. The polygonal network is formed by the association of five, six or seven hexagonal forms (Figure 21). Rounded structures, linking polygonal structures, are darker and present fine punctuation.

*Setation.* Simple: epimeral, aggenital, anal, adanal (not included in Figures, only insertions indicated); simple, slightly barbate: *ro, in*, (Figures 25, 26); lanceolate barbate: *le* (Figure 17); plumose: genital (not included in Figures, only insertions indicated); lanceolate small asperities: notogastral (Figure 23, 24).

*Prodorsum.* Slightly convex (Figure 17); *ro* setae curving, directed anteriorly; *in* setae inserted on the lamellae, dorsally in medial posterior prodorsal zone, directing laterally and anteriorly (Figure 14). Dorsolateral lamellae (*Lam*); clearly visible shallow lamellar furrow (*ll,f*), terminating internally at rounded *la.ti* (Figures 14, 19). Rostral margin slightly concave (Figures 14, 19). Bothridia cup-shaped, curving slightly, with bothridial ring (*bo.ri*) (Figure 22). Sensillus thin, barbate (Figure 29). Paired internal bilobed structures present, hardly discernible in dorsal view, but conspicuous in frontal and lateral views (Figures 17, 18, 19, 20 indicated by ⚡). These structures resemble the internal part of medial eye (*oc*) observed in *H. mirabilis* and *Bovicarabodes* spp., but lacking dorsal opening or median eye pillar (Fernandez et al. 2013a) and are located further internally than in *H. mirabilis*.

*Notogaster.* Oval elongate, shape; without notogastral anterior depression (*n.a.d*) nor notogastral posterior depression (*n.p.d*); dorso-sejugal furrow (*d.sj*) not visible in medial zone (Figure 14). Circumgastric furrow (*s.c*), well visible in dorsal view (Figure 14). Humeral apophysis (*h.ap*) prominent (Figure 14).

Fifteen pairs of thickened notogastral 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>*); lyrifissures not discernible.

*Lateral region.* Bilobate structure of medial eye clearly visible on prodorsum (Figure 17 indicated by ⚡).

Tutorium (*Tu*) clearly visible as strongly curving cuticular thickening (Figure 17). Deep supra-tutorial depression (*s.tu.d*) with internal pocket depression. Pedotectum I (*Pd I*), prominent extended area, rounded tip, covering first acetabulum (Figure 17), with oblique cuticular ridge on posterior zone; Pedotectum II (*Pd II*) triangular structure (Figure 17). Humeral apophysis (*h.ap*) elongate, tip overlapping posterior bothridial zone (Figure 17). Upper margin irregularly rounded; inferior margin rounded; rod-shaped thickening crossing *h.ap* well discernible (Figure 17, indicated by ↑↑↑).

Discidium: small triangular protuberance near acetabulum III. Rounded cavities (*dep*), situated behind acetabulum IV. Oblique linear cuticular thickening superior and posteriorly directing toward acetabulum IV (Figure 17 indicated by ↗). Zone with many cuticular thickenings between *bng* and *p* setal zone (Figure 17 indicated by ⇒).

*Ventral region* (Figure 15). Epimera slightly elevated, delimited by shallow furrow (*bo.1, bo.2, bo.sj*); epimere 4 fused; *apo.1, apo.2, apo.sj* and *apo.3* well discernible.

Epimeral chaetotaxy 3-1-3-3. *Pd I, Pd II* and *dis*, clearly discernible. Anterior genital furrow (*a.g.f*) distinct, situated in normal position; following *a.g.f* cuticular thickening (Figure 15 indicated by ⇒). Genital plate ovoid; small in comparison with anal plate; four pairs of setae, all more or less equally sized (not included in Figures, only insertions indicated). Aggenital setae situated posterior to genital opening and near medial zone. Anterior and laterally to *ag* setae, curved cuticular thickening (Figure 15 indicated by ▼). Three pairs of adanal setae; *ad<sub>3</sub>*, close to *ag* distant to *ad<sub>2</sub>* and *ad<sub>1</sub>*; *iad* lateral, slightly posterior to *ad<sub>3</sub>*. Anal plate terminating in small sharp tip (Figure 15 indicated by ⚡). Two pairs of anal setae. Preanal organ (*pr*), well visible as a rounded structure. Prominent polygonal depressions (*dep*) posterior to acetabulum IV, laterally to anal opening, and



laterally to curved cuticular thickening (indicated by ▼ in Figure 15).

*Leg I* (Figures 30, 31). Femur with four setae; *d* setae with very small barbs. Genu with  $\sigma$  setiform, fine, medium length; *d* setae small, situated anterior to  $\sigma$ ; (*l*) setae with large barbs;  $\nu$  medium length, barbed. Tibia  $\varphi_1$  long, tactile, on dorsal apophysis;  $\varphi_2$  medium length, small setae *d* situated in close proximity and posterior to  $\varphi_2$ . Tarsus  $\omega_1$  and  $\omega_2$  medium length;  $\varepsilon$  small, hardly discernible; (*u*) small.

*Leg II* (Figures 27, 28). Femur with medium-sized barbed *d* setae. Genu,  $\sigma$  medium sized; *d* setae situated more or less laterally, at  $\sigma$  insertion level (Figure 28). Tibia  $\varphi$  medium length, associated with setae *d*, similar length (Figure 28). Tarsus medium sized;  $\omega_1$ ,  $\omega_2$  same length.

*Leg III* (Figure 16). Femur with femoral groove, setae  $\nu$  inside *f.g.*. Other segments normal chaetotaxy (Table 2).

*Leg IV*. Normal shape and chaetotaxy (Table 2).

*Setal formulae* (trochanter to tarsus). I (1-4-4-4-16-1) (1-2-2); II (1-4-3-3-15-1) (1-1-2), III (2-3-1-2-14-1) (1-1-0); IV (1-2-2-2-12-1) (0-1-0). (Table 2).

#### Remarks

Our purpose was not to completely revise *H. flabellatus* (holotype and two paratypes studied), our observations were made in order to establish whether the characteristics correspond with those of *H. penicillatus*. We confirm the following characters principally related to those of *Hardybodes* to be: elevated interlamellar process; medial eye structures on prodorsum; number of notogastral setae; leg characteristics. Characters at specific level indicated by Mahunka (1995) permit easy identification of the species.

We have slightly modified the description of the genus given in 2013 and adapted to new studies.

#### Discussion

Analysing the problems surrounding *Carabodella* and *Hardybodes* is difficult, as current knowledge differs greatly to that available in 1986 or 1995, and comparison of animals with very different characteristics can be problematic.

The problem is principally related to partial observation or prior errors in observation. A complicating factor is that restricted specimen numbers are available for study, as well as observational difficulty of several characters due to conservation condition of materials (see Fernandez et al. 2013a, 2013b).

In the original revision of the family Carabodidae (Fernandez et al. 2013a), we described the protection mechanism as well as the importance of the femoral

groove observed on femur III. At first, we assumed this to be a common mechanism for all Carabodidae, and the femoral groove a common structure. However, we can say that we were mistaken, and in depth studies are necessary before generalizations are made.

*Carabodella calcarata* lacks the femoral groove on leg III, and instead two spurs are present. Ventral setae observed inside the femoral groove in other genera are in this instance located between these spurs. Evidently, only this character differentiates *Carabodella* from *Austrocarabodes* and *Hardybodes*, as they were related by Mahunka in 1986 and Subias (*op.cit.*).

The shape of femur IV in *Carabodella* further complicates the leg folding process as protection mechanism. Undoubtedly, the entire mechanism (if it exists) is expected to be very dissimilar. Unfortunately, the limited number of animals available for study generated more questions than answers. Before making generalizations across a family, in-depth study of genera is necessary, as processes may be unique or inherent to a specific genus.

With regard to the epimeral setal formula, indicated by Mahunka (*op.cit.*) as a character separating *Austrocarabodes* from *Carabodella*, we have many doubts. We found asymmetric variations in the number of setae on epimere 1 on the only specimen studied. That number differs from that observed by Mahunka (*op.cit.*). We believe that this character is unsuitable to be used at generic level, without having studied a significant number of specimens. This character is normally subject to intra-specific variations.

All three species within the genus *Hardybodes* have previously been studied. *Hardybodes mirabilis* was problematic in many respects (see Fernandez et al. 2013a, p. 48 “Historical review” and p. 49 “Discussion”).

First, we redescribed the type species *H. mirabilis* and compared prodorsal structures related to medial eye with that observed in *Bovicarabodes* (Fernandez et al. 2013a). At the same time, we studied two other species of the genus, *H. flabellatus* and *H. penicillatus*, and for this present article we again studied the type material of the latter two species. This allowed us to delve deeply into the differences identified by Mahunka (1995) between the three species of the genus: “the peculiar form of rostrum and the rostral setae is characteristic only for the type species.” This observation evidently refers to the structure of the “medial eye.”

We state that the structure observed in *H. mirabilis* is situated more superficially than in *H. penicillatus* and *H. flabellatus*. No cavities or medial eye pillar is present. The bilobed structure in *H. mirabilis* exists and is conspicuous, as in the type species, as well as in lateral views on *H. flabellatus* and *H. penicillatus*. It is not related to the prodorsal surface by means of cavities. The particular form found on the prodorsum of *H. mirabilis* is related to its position, but the structures of the medial eye are present in all three species. Mahunka (1995) (Figures 60 and 65) hinted at the structure above, but overlooked its importance.



We consider the shape and position of rostral setae to be characteristic at specific level. The small differences found at the level of the elevated interlamellar process and the notogaster are specific, not generic. Diagnostic features/characteristics at generic level are very intricate, and in most instances difficult to interpret. We do not agree with combinations specified by Subías (*op.cit*) that include *Carabodella* as a sub-genus of *Hardybodes*, as both genera present characteristics that permit differentiation.

### Acknowledgements

Peter J. Schwendinger, Curator of the Department of Arthropodology and Entomology at the Museum d'Histoire Naturelles, Geneva, is especially thanked for his support in facilitating our research, without whose assistance it would have been an impossible task. 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.

### Funding

This work is based on research supported in part by the National Research Foundation of South Africa (UID) 85288.

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