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Research article

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A mountain of millipedes X: Species of Pyrgodesmidae and Cryptodesmidae in the Udzungwa Mountains, Tanzania (Diplopoda, Polydesmida)

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Abstract. Three new species of the family Pyrgodesmidae Silvestri, 1896 from the Udzungwa Mountains are described: *Cryptocorypha geminiramus* sp. nov., *Cryptocorypha cactifer* sp. nov., and *Cryptocorypha exovo* sp. nov. Several additional, unidentifiable pyrgodesmids from the Udzungwa Mountains are recorded. *Elythesmus enghoffi* Hoffman, 1978 (Cryptodesmidae Karsch, 1880), is recorded from the East Usambara (type locality), West Usambara, Uluguru, Nguru (Kanga) and Udzungwa Mountains, and its variation in size and body ring numbers is analyzed. The surface sculpture of pro- and metazonites is discussed.

Keywords. Taxonomy, new species, intraspecific variation, Eastern Arc Mountains, Usambara, Uluguru, Nguru.

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Introduction

This is the tenth in a series of articles on the millipede fauna of the Udzungwa Mountains. Previous articles in the series have dealt with the families Odontopygidae Attems, 1909 (Enghoff 2014, 2016a, 2016b, 2016c, 2018a, 2020; Enghoff & Frederiksen 2015), Paradoxosomatidae Daday, 1889 (Enghoff 2018b) and Gomphodesmidae Cook, 1896 (Olsen *et al.* 2020). The present contribution is about Udzungwa species of two families of the order Polydesmida Leach, 1815, suborder Polydesmidea Leach, 1815. For general information on the Udzungwa Mountains, see Enghoff (2014) and Scharff *et al.* (2015).

Hoffman (1980: 146) in his classical “*Classification of the Diplopoda*” wrote about the suborder Polydesmidea: “Whatever satisfaction might be felt about the classification of the foregoing two suborders [Chelodesmidea Cook, 1895 and Paradoxosomatidea] is replaced here by dissatisfaction and pessimism. The groupings set forth in the following pages are to a large extent an exercise in futility”. It is difficult to disagree with this statement. In the compilatory monograph of Attems (1940), Pyrgodesminae Silvestri, 1896 was a subfamily in Cryptodesmidae Karsch, 1880, characterized by the ventrad direction

of the preanal ring, as opposed to a more caudad direction in the subfamily Cryptodesminae Karsch, 1880. Not surprisingly, such a weak distinction between two subfamilies has proven unsustainable. Hoffman (1980) placed Cryptodesmidae in the superfamily Polydesmoidea together with Polydesmidae, Doratodesmidae Cook, 1896, Haplodesmidae Cook, 1896 and Opisetretidae Hoffman, 1980, while Pyrgodesmidae Silvestri, 1896 was placed in the superfamily Stylodesmoidea Cook, 1896 together with Cyrtodesmidae Cook, 1896. The hitherto only comprehensive phylogenetic analysis of polydesmidean (and dalodesmidean) relationships by Simonsen (1990) largely supported Hoffman's arrangement: Cryptodesmidae in the superfamily Polydesmoidea, together with Polydesmidae, Haplodesmidae, and Dalodesmidae Cook, 1896; Pyrgodesmidae in the superfamily Pyrgodesmoidea, together with Ammodesmidae Cook, 1896 and Cyrtodesmidae. This pattern was adopted in the recent classification of Diplopoda de Blainville in Gervais, 1844 (Golovatch & Enghoff in Enghoff *et al.* 2015) with the exception that Dalodesmidae was 'returned' to the suborder Dalodesmidea. However, Simonsen's analysis was based on limited evidence, and a comprehensive phylogenetic analysis involving molecular evidence is much needed. Such an analysis is far beyond the scope of the present article, and the two genera treated here are for the time being maintained in the families in which they have been classified by previous authors.

Material and methods

All studied specimens come from the zoological collections of the Natural History Museum of Denmark, University of Copenhagen (NHMD, formerly ZMUC). A very large part of the specimens were collected in pitfall traps by Jagoba Malumbres-Olarte, see Kunene *et al.* (2022).

Specimens were stored and examined in 70% ethanol under a stereo microscope. Specimens for scanning electron microscopy (SEM) were cleaned with ultrasound, transferred to 96% ethanol, then to acetone, air-dried, mounted on aluminium stubs or on triangles of flexible aluminium tape, in turn mounted on stubs, coated with platinum-palladium and studied in a JEOL JSM-6335F scanning electron microscope. In the case of *Elythemus enghoffi* Hoffman, 1978, some specimens were treated with trypsin or commercial detergent in order to remove the dark layer with which this species is coated, but results were disappointing.

Images were processed with Photoshop, in some cases involving stacking of multiple images, and plates were composed with Microsoft Publisher. Abbreviations for body parts are explained in the main text and the figure captions.

Results

Taxonomy

Class Diplopoda de Blainville in Gervais, 1844

Order Polydesmida Leach, 1815

Family Pyrgodesmidae Silvestri, 1896

Genus *Cryptocorypha* Attems, 1907

Type species

Cryptocorypha stylopus Attems, 1907, Java, by monotypy.

Other included species

Twenty-eight, including three new species described below. See Golovatch (2019) and Likhitrakarn *et al.* (2019).

Remarks

This genus was recently reviewed by Golovatch (2019) building on several other recent treatments (Golovatch *et al.* 2017; Likhitrakarn *et al.* 2019).

An extensive diagnosis of the genus *Cryptocorypha* was provided by Golovatch (2019). This diagnosis (actually more like a general description) is reproduced here, with necessary updates to accommodate the new species, plus some linguistic and terminological adjustments, but without reference to specific species and illustrations:

A genus of small Pyrgodesmidae (3–15 mm long) with a strongly flat body and high paraterga. Adult body with 17 or 18 podous rings in both sexes, but more usually with 17 podous rings in ♂ and 18 podous rings in ♀. Head usually unmodified, only in several Afrotropical species with a paramedian pair of vertigial humps (only in ♂ or both in ♂ and ♀). Antennae C-shaped, mostly exposed, antennomere 6 the largest; interantennal isthmus $> 1.6 \times$ diameter of antennal socket. Collum flabellate, fully or almost fully covering head from above, fore margin regularly convex, not or nearly not lobulated, but with 6+6 (sub)equal sectors divided by 11 radii; central part usually with two transverse rows of 3+3 and 2+2 flat, roundish or transversely oval bosses or low tubercles; sometimes both rows and knobs vague. Postcollum metaterga each with three transverse rows of regular, non-differentiated, flat bosses or low rounded tubercles partly extending onto paraterga. Lateral margin of postcollum paraterga always indistinctly lobulated, without porosteles: paraterga 2 and 3 invariably trilobate, following ones 3-, 4- or 5-lobate, but poreless paraterga mostly showing fewer lobulations (typically three) than pore-bearing ones (typically four). Anterolateral lobulations absent, but 1–3 caudolateral ones mostly present. Tergal setae missing in most species. Pore formula normal (5, 7, 9, 11, 13, 15–18(19)), ozopores inconspicuous, open flush on tergal surface near base of penultimate lateral lobulation. Telson fully exposed in dorsal view, epiproct conical. Last tibia or both last and penultimate tibiae (♂ and/or ♀) often, but not always with an apicodorsal trichostele (= a long tactile seta on stalk or knob). Gonopods from relatively simple to complex, typically clearly transverse; coxae globose, each usually with one or a few strong setae, laterally papillate and microsetose, usually divided by a central sternal tubercle; cannulae unmodified curved tubes; telopodites remaining well-exposed beyond a small to modest gonocoel, each typically tri- or quadripartite, consisting of a distinct mesal solenomere branch mostly flanked by a more or less prominent, membranous, sometimes ornate, sac- or lobe-shaped, anterolateral velum, and a normally long and lateral exomere process. Sometimes velum and exomere fully fused into a single sac-shaped structure, or velum more or less strongly appressed to exomere or endomere, leaving gonopodal telopodite bi- or slightly tripartite. When telopodite clearly quadri- or tripartite, a more or less evident endomere branch normally also distinct. (Modified from Golovatch 2019.)

Transforming this extensive characterization into a differential diagnosis of *Cryptocorypha* is not possible, not the least considering the high degree of variability in gonopod structure among the included species. The genus obviously belongs to the “Pyrgodesmidae cryptodesmiformes”, an informal grouping named by Mauriès & Maurin (1981) for several genera of Pyrgodesmidae with a superficial resemblance to species of Cryptodesmidae. Neither Mauriès & Maurin (1981) nor any subsequent author has provided a more strict diagnosis of this grouping or an account of its content. As examples of cryptodesmiform pyrgodesmids Mauriès & Maurin (1981) mentioned the genera *Dusboscquiellina* Brolemann, 1926 and *Cachania* Schubart, 1955. Based on available literature (Brolemann 1926, Schubart 1955, Golovatch & VandenSpiegel 2014), *Cryptocorypha* differs from *Dusboscquiellina* by the unmodified third male femur (tuberculate in *Dusboscquiellina*) and from *Cachania* by the lobulated/striate collum (neither lobulated nor striate in *Cachania*).

While *Cryptocorypha* thus remains poorly diagnosed, it serves as a useful temporary ‘home’ for several Afrotropical and Oriental cryptodesmiform pyrgodesmids. Future revisionary and phylogenetic

studies will probably reshuffle the taxonomy of the species currently ascribed to the genus, as well as pyrgodesmid (and cryptodesmid, see Discussion) taxonomy in general.

Golovatch (2019) gave a provisional key to the 25 *Cryptocorypha* species recognized at that time, and Likhitrakarn *et al.* (2019) gave details about the species known to them.

Cryptocorypha geminiramus sp. nov.

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Figs 1–7

Diagnosis

Differs from all other species of *Cryptocorypha* Attems, 1807, except *C. chenovi* Golovatch *et al.*, 2013 from Vanuatu, by its small size (max. diameter of males 0.72 mm), vs 0.78–0.92 mm in the congeners from Udzungwa and min. 1.00 mm in other non-Udzungwan species (the diameter of *C. kumamotoensis* (Murakami, 1966) is unknown but the published male body length, 5 mm, suggests a diameter of >0.8 mm). Differs from all other species of *Cryptocorypha*, except *C. cactifer* sp. nov., *C. bocal* Golovatch, Nzoko Fiemapong & VandenSpiegel, 2017 from D.R. Congo, and *C. leia* Chamberlin, 1945 from Java, by the virtually identical, very slender solenomere and exomere. Differs from *C. cactifer* sp. nov. by the absence of setae in podous body rings and from *C. bocal* and *C. leia* by the very poorly developed velum on the gonopod telopodite.

Etymology

The species epithet (noun in apposition) refers to the virtually identical pair of slender branches (solenomere and exomere) of the gonopod telopodite.

Material examined (160 ♂♂, 19 ♀♀, 3 subad. ♀♀)

Holotype

TANZANIA • ♂; Morogoro Region, Udzungwa Mountains National Park, Kidatu; 07°40'45.5" S, 36°55'06.9" E; 1448 m a.s.l.; 21 Oct. 2014; J. Malumbres-Olarte leg.; Plot 5; NHMD 621823.

Paratypes

TANZANIA • 69 ♂♂, 8 ♀♀; same collection data for as holotype; summed catch from 10 pitfall traps; NHMD 621824 • 13 ♂♂, 2 ♀♀, 1 subad. ♀; same collection data as for holotype; 07°40'42.1" S, 36°55'06.8" E; 1482 m a.s.l.; 21 Oct. 2014; Plot 6, summed catch from six pitfall traps; NHMD 621825 • 18 ♂♂, 6 ♀♀, 2 subad. ♀♀; same collection data as for holotype; 07°41'12.9" S, 36°55'39.2" E; 978 m a.s.l.; 14 Sep. 2014; Plot 8, summed catch from eight pitfall traps; NHMD 621826 • 38 ♂♂, 3 ♀♀; same collection data as for holotype; 07°41'06.2" S, 36°54'52.4" E; 1527 m a.s.l.; 23 Oct. 2014; Plot 9; summed catch from nine pitfall traps; NHMD 621827 • 2 ♂♂; Morogoro Region, Udzungwa Mountains Natl Park, Mito Mitatu; 07°50'29.6" S, 36°52'01.2" E; 674 m a.s.l.; 26 Sep. 2014; J. Malumbres-Olarte leg.; Plot 13, pitfall trap, summed catch from two pitfall traps; NHMD 621828 • 15 ♂♂; same collection data as for preceding; 07°50'26.1" S, 36°51'33.0" E; 1006 m a.s.l.; 26 Sep. 2014; Plot 14, summed catch from five pitfall traps; NHMD 621829 • 2 ♂♂; same collection data as for preceding; 07°50'14.3" S, 36°50'46.8" E; 1207 m a.s.l.; 16 Dec. 2013; T. Pape and N. Scharff leg.; Plot MM1, summed catch from two pitfall traps; NHMD 621830 • 1 ♂; same collection data as for preceding; 14 Mar. 2014; NHMD 621831 • 1 ♂; Udzungwa Mountains, Mwanihana Forest above Sanje; 1650 m a.s.l.; 18 Aug. 1982; M. Stoltze and N. Scharff leg.; pitfall trap; NHMD 621832.

Description

SIZE. Males: Length 3.2–3.8 mm; maximal body width (across metazona) 0.59–0.72 mm in males from Kidatu; males from Mito Mitatu up to 4.6 mm long. 17 podous + 1 apodous ring + telson. Females: Length 4.6–6.1 mm. One specimen (from Kidatu, Plot 9) 6.6 mm long (0.92 mm wide). Width 0.83–1.10 mm. One specimen (from Kidatu, Plot 5) 1.36 mm wide. 18 podous + 1 apodous ring + telson.

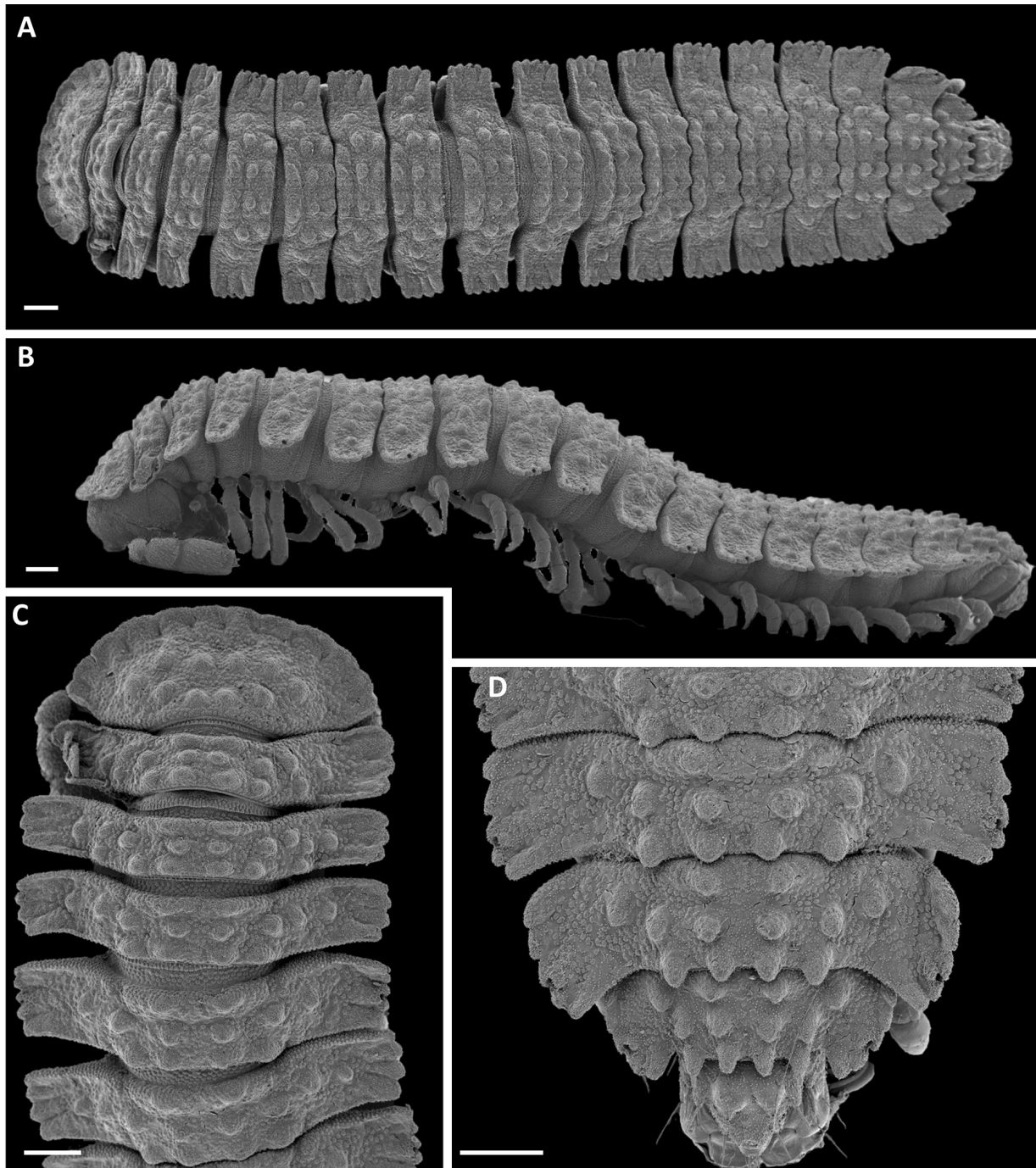


Fig. 1. *Cryptocorypha geminiramus* sp. nov., paratype (NHMD 621824), ♂, from Kidatu. **A.** Dorsal view. **B.** Lateral view. **C.** Collum and rings 2–6, dorsal view. **D.** Rings 15 (part)–18 and telson, dorsal view. Scale bars = 0.1 mm.

COLOUR. Entirely pallid or with faint brown pigment, especially on paranotal margins and on level 1 tubercles.

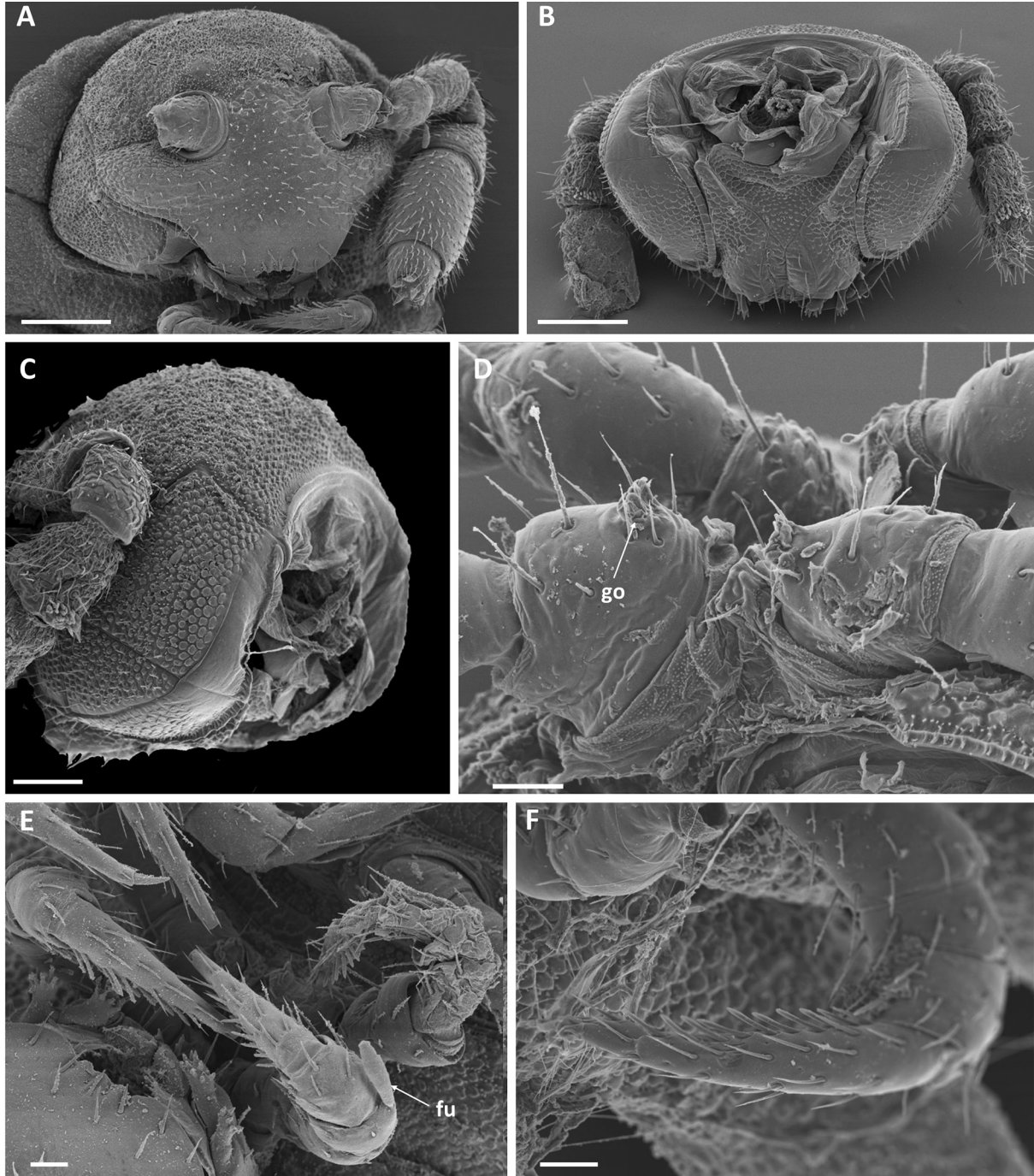


Fig. 2. *Cryptocorypha geminiramus* sp. nov. A–E. Paratype (NHMD 621824), ♂, from Kidatu. F. Paratype (NHMD 621829), ♂, from Mitu Mitato. A. Head, frontal view. B. Head, (sub)posterior view. C. Head, sublateral view (left side). D. Bases of first and second pairs of legs. E. First and second pair of legs. F. Leg of second pair, tarsus. Abbreviations: *fu* = epibiotic fungus, possibly *Basiodiobolus* sp.; *go* = gonopore. Scale bars: A–B = 0.1 mm; C = 0.05 mm; D–F = 0.02 mm.

SURFACE SCULPTURE (Figs 1, 3). Entire exposed dorsal surface covered in a three-level ornamentation: Level 1: Rounded, hemispherical to subspherical tubercles of ca 35 μm diameter arranged in two or three transverse rows on all body rings. These tubercles are covered with level 3 spherules. Level 2: Very small, smooth, circular, flattened ‘buttons’ of ca 8 μm diameter, covering entire dorsal surface except level 1 tubercles and lateral parts of paraterga. Level 3: A dense cover of minute stalked spherules of ca 1.5 μm diameter over entire dorsal surface, including level 1 tubercles, mostly arranged in neat lines

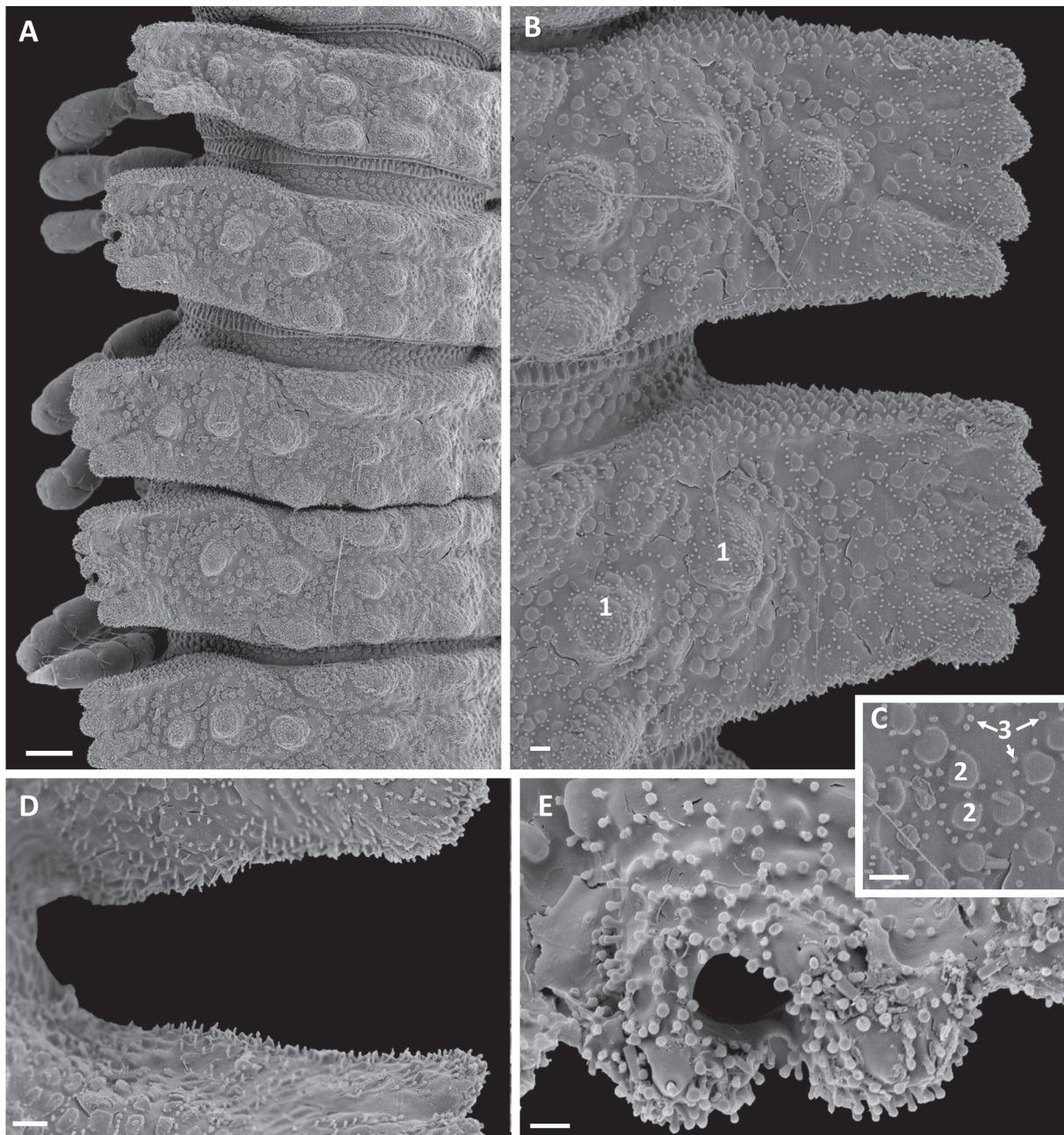


Fig. 3. *Cryptocorypha geminiramus* sp. nov., paratype (NHMD 621824), ♂, from Kidatu. **A.** Rings 4–8, (latero)dorsal view. **B.** Paraterga 8–9, dorsal view. **C.** Enlarged detail of B, showing level 2 buttons and level 3 spherules. **D.** Anterior and posterior edge, respectively, of successive paraterga, ventral view. **E.** Left ozopore on ring 5, oblique lateral view. Abbreviations: 1 = level 1 tubercles; 2 = level 2 buttons; 3 = level 3 spherules. Scale bars: A = 0.05 mm; B–D = 0.01 mm; E = 0.005 mm.

(which possibly correspond to the limits between individual cuticular microscutes), but denser and more irregularly arranged on lateral margins of paraterga. These are the “microvilli” of Likhitrakarn *et al.* (2019).

HEAD (Figs 2A–C, 7A–B). Smooth between antennae and below, in this area with numerous short setae; posterior part of head microtuberculate including a dense cover of level 3 spherules. Interantennal

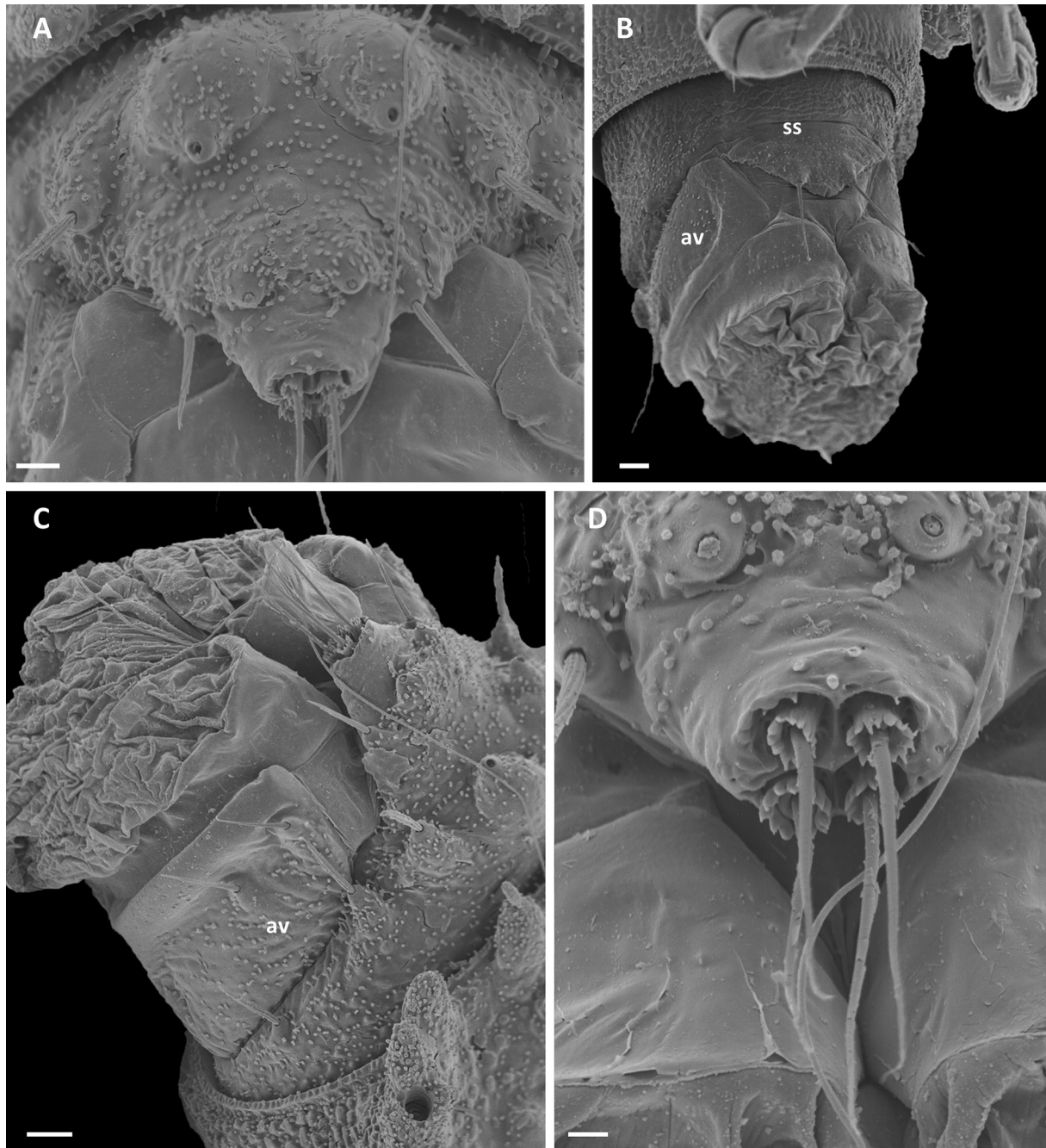


Fig. 4. *Cryptocorypha geminiramus* sp. nov., paratype (NHMD 621824), ♂, from Kidatu, telson. **A.** (Posterior)-dorsal view **B.** Ventral view. **C.** Oblique lateral view. **D.** Spinnerets. Abbreviations: *av* = anal valve; *ss* = subanal scale. Scale bars: A = 0.01 mm; B–C = 0.02 mm; D = 0.005 mm.

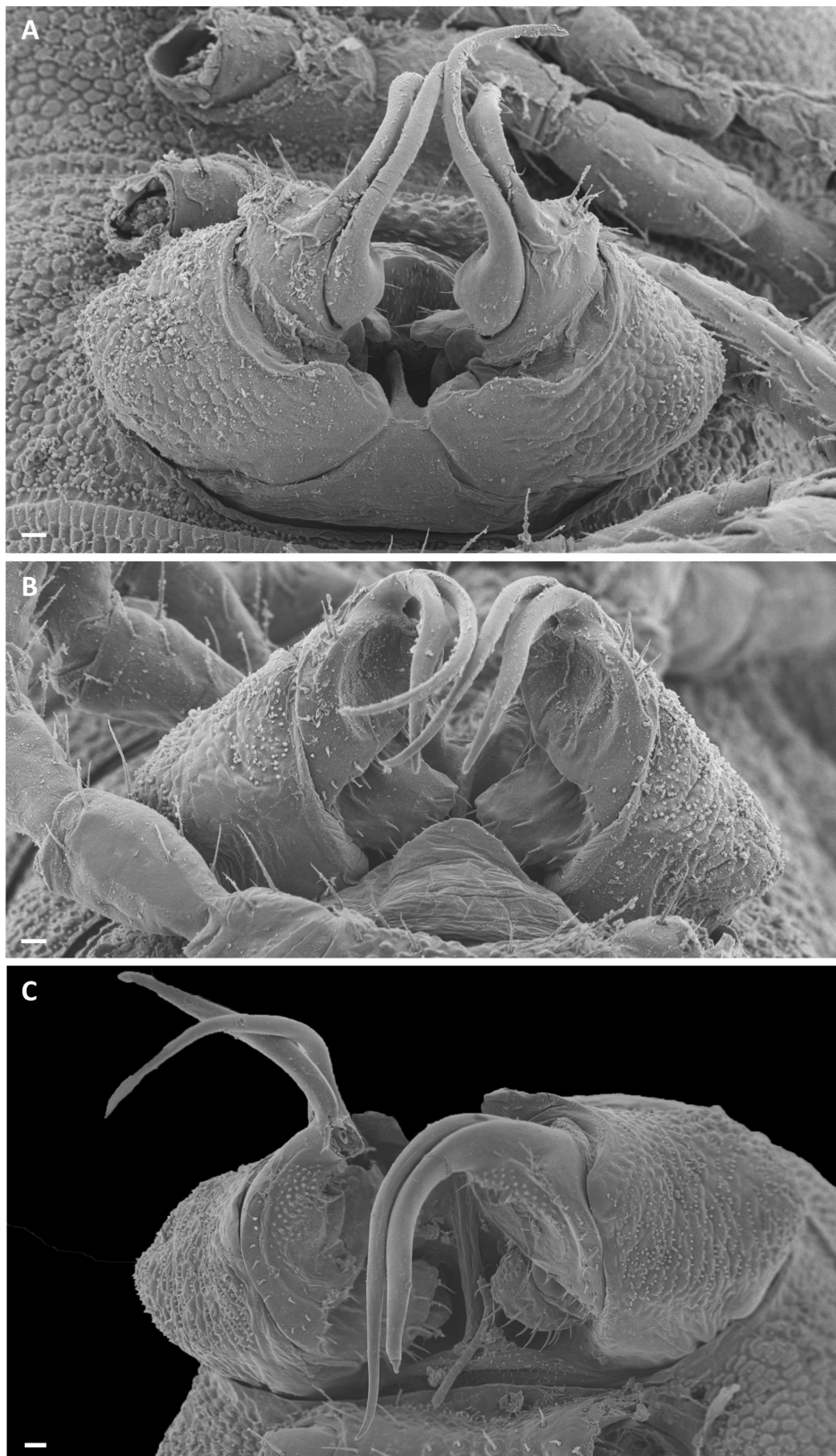


Fig. 5. *Cryptocorypha geminiramus* sp. nov., gonopods in situ. **A–B.** Paratype (NHMD 621824), ♂, from Kidatu. **A.** Ventro-anterior view. **B.** Subposterior view. **C.** Paratype (NHMD 621829), ♂, from Mitu Mitatu, latero-posterior view. Scale bars = 0.01 mm.

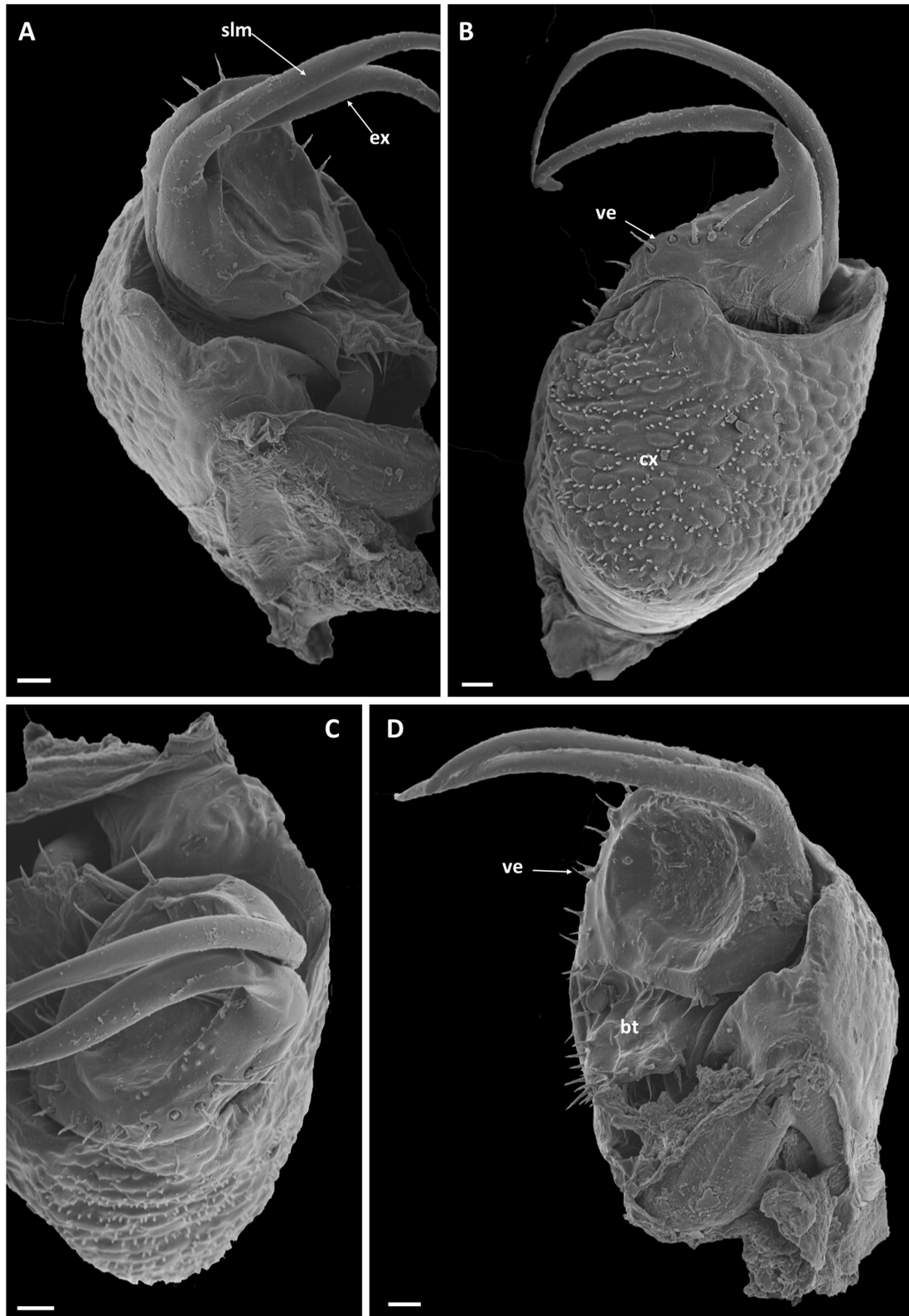


Fig. 6. *Cryptocorypha geminiramus* sp. nov., paratype (NHMD 621824), ♂, from Kidatu. **A–C.** Left gonopod. **A.** (Sub)mesal view. **B.** Lateral view. **C.** (Sub)ventral view. **D.** Right gonopod, Postero-mesal view. Abbreviations: *bt* = basal part of telopodite; *cx* = coxa; *ex* = exomere; *slm* = solenomere; *ve* = velum(?). Scale bars = 0.01 mm.

isthmus 1.4 times diameter of antennal socket. Antennae short, stout, bent in C-shape, antennomere 6 by far the largest.

COLLUM (Figs 1A–C, 7A–B). Completely covering head from above, with broadly rounded anterior margin, faintly divided into 12 lobules, lateralmost lobules smaller than the others; two transverse rows of 2+2 and 3+3 level 1 tubercles; level 2 buttons and level 3 spheres as on ensuing metatergites.

POSTCOLLAR PODOUS BODY RINGS. Without setae. With three transverse rows of level 1 tubercles. No. of tubercles in the three rows: ring 2: 2/6/8; ring 3: 2/8/8, ring 4: 2/8/4, rings 5, 7, 9–10, 12–13, 15–17 (poriferous podous rings): 2/6/4; rings 6, 8, 1, 4: 2/8/4. Paraterga almost horizontal, rectangular, with three (rings 2–4), four (rings 6, 8, 11, 14), or five (rings 5, 7, 9–10, 12–13, 15–17/18) lateral lobes; no lobes on anterior and posterior margins; anterior margin densely microtuberculate. Pore formula

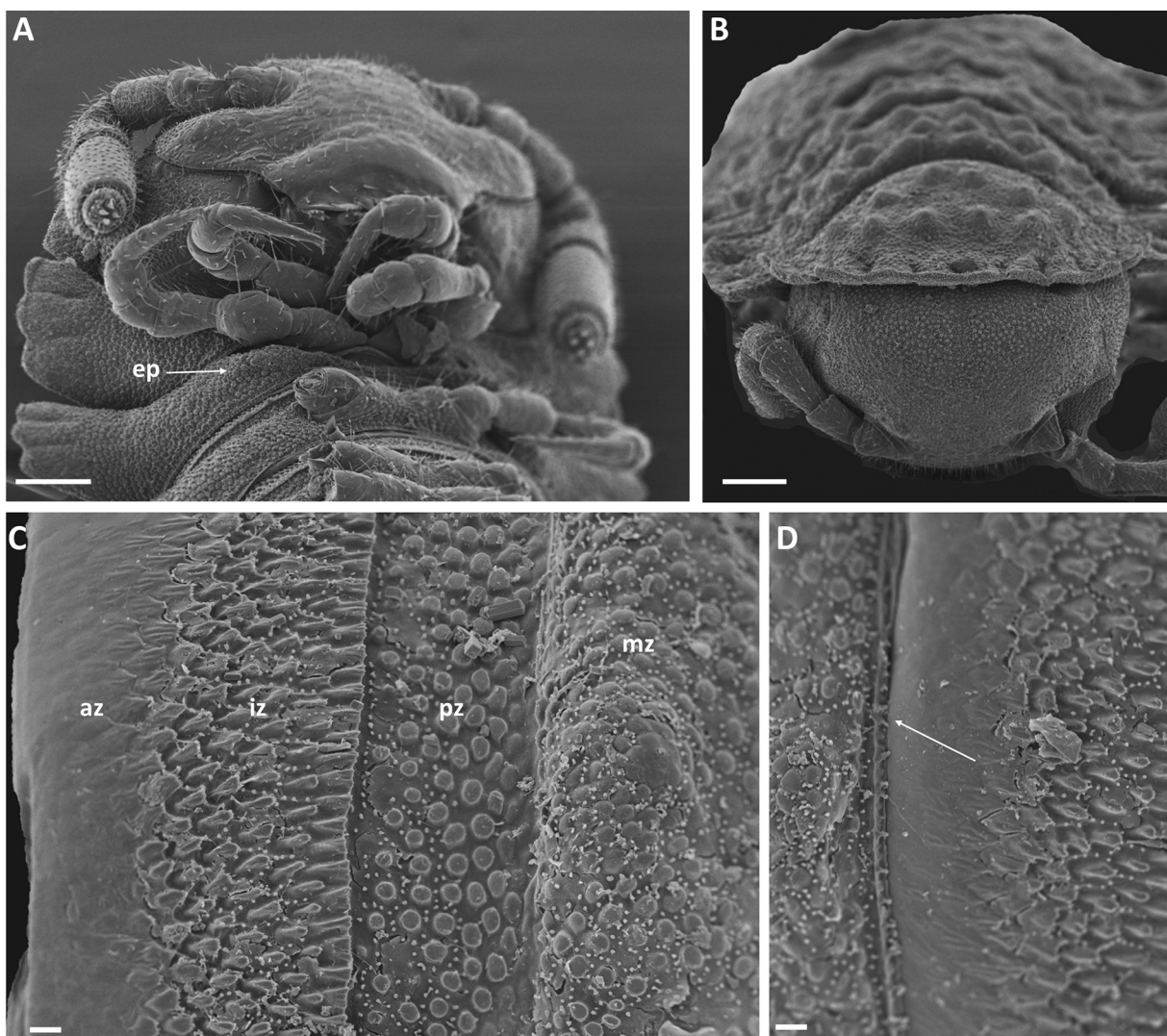


Fig. 7. *Cryptocorypha geminiramus* sp. nov., ♀♀, from Kidatu. **A.** Paratype (NHMD 621824). **B–D.** Paratype (NHMD 621825). **A.** Head and rings 1–3, ventral view. **B.** Head and anterior rings, anterior view. **C.** Prozonal sculpture. **D.** Limbus (arrow). Abbreviations: *az* = anterior zone; *ep* = epigynal ridge; *iz* = intermediate zone; *mz* = metazona; *pz* = posterior zone. Scale bars: A–B = 0.1 mm; C–D = 0.01 mm.

normal (5, 7, 9–10, 12–13, 15–18); ozopores (Fig. 3 D) on lateral margin, deeply embedded between third and fourth paratergal lobe and surrounded by a dense cover of level 3 spherules. Ventral side of metaterga, including mesalmost part of paraterga, with dense pavement of level 2 buttons, in part (especially on paraterga) interspersed with level 3 spheres. Towards anterior and posterior margins of paraterga, level 3 spheres drawn out into short rods, giving surface hairy look (Fig. 3C). Prozona (Fig. 7C) clearly divided into three zones. Anterior zone almost smooth, with indistinct cover of low swellings; in intermediate zone these swellings are replaced by triangular denticles, interspersed with level 3 spherules; posterior zone sharply demarcated from intermediate zone, with dense cover of level 2 buttons and level 3 spherules. Sterna smooth. Limbus (Fig. 7D) extremely narrow, with scattered rodlike denticles.

APODOUS RING (Fig. 1D–E). With three transverse rows of each 4 level 1 tubercles; tubercles in posterior row each with a minute clavate seta (Fig. 1E). Four lateral lobes.

TELSON (Fig. 4). Preanal ring (‘epiproct’) visible from above, triangular, with a dense cover of level 3 spherules, with two setiferous level 1 tubercles on the dorsal surface, setiferous denticle on each lateral margin, each followed by 2 successively smaller setiferous tubercles on lateral flank; also, transverse row of 4 setae near posterior tip; posterior tip with 4 long trichoid spinnerets each surrounded by crownlike collar. Anal valves (paraprocts) each with 2 non-marginal setae. Subanal scale (hypoproct) broadly triangular, with scattered level 3 spherules and two long setae on small marginal tubercles.

LEGS. Unmodified in both sexes, except for flattened setae on tarsi of leg-pairs 1–2 in males (Fig. 2E–F).

GONOPODS (Figs 5–6). Coxa (*cx*) moderately globose, its surface scaly and with scattered level 3 spherules, mesally forming shallow gonocoel. Telopodite projecting strongly from gonocoel, very evident in lateral and ventral views. Basal (‘prefemoral’) part of telopodite (*bt*) massive, with several distolateral setae, giving rise to two very long, subparallel, slender, simple, pointed, slightly arcuate processes – mesal solenomere (*slm*) and lateral exomere (*ex*). Broad, setose lobe (*ve*) at mesal base of telopodite probably corresponds to ‘velum’ described in several other species of *Cryptocorypha*.

Females

With a low epigynal ridge (*ep*) on ring three (Fig. 7A). Non-sexual characters as in males. A subadult female (from Kidatu, Plot 6) is 4.5 mm long, 0.72 mm wide, 17 podous + 1 apodous ring + telson. This is the only non-adult specimen of this species seen.

Remarks

A key to species of *Cryptocorypha* was provided by Golovatch (2019). In the first couplet of the key Afrotropical and Asian species are separated, but the mentioned criteria concerning ring numbers are non-exclusive. If the Afrotropical alternative is chosen, *C. geminiramus* sp. nov. runs to *C. diffusa* (Brolemann, 1920) from which it differs by several characters, especially by strongly different gonopods. If the Asian alternative in the first couplet is chosen, *C. geminiramus* sp. nov. runs to couplet 17(18) where it fits neither alternative.

Cryptocorypha cactifer sp. nov.

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Figs 8–9

Diagnosis

Identical with *C. geminiramus* sp. nov. in almost all characters, but differs from the smaller *C. geminiramus* and from all other species of *Cryptocorypha* by the presence of setae on podous body rings (Fig. 8).

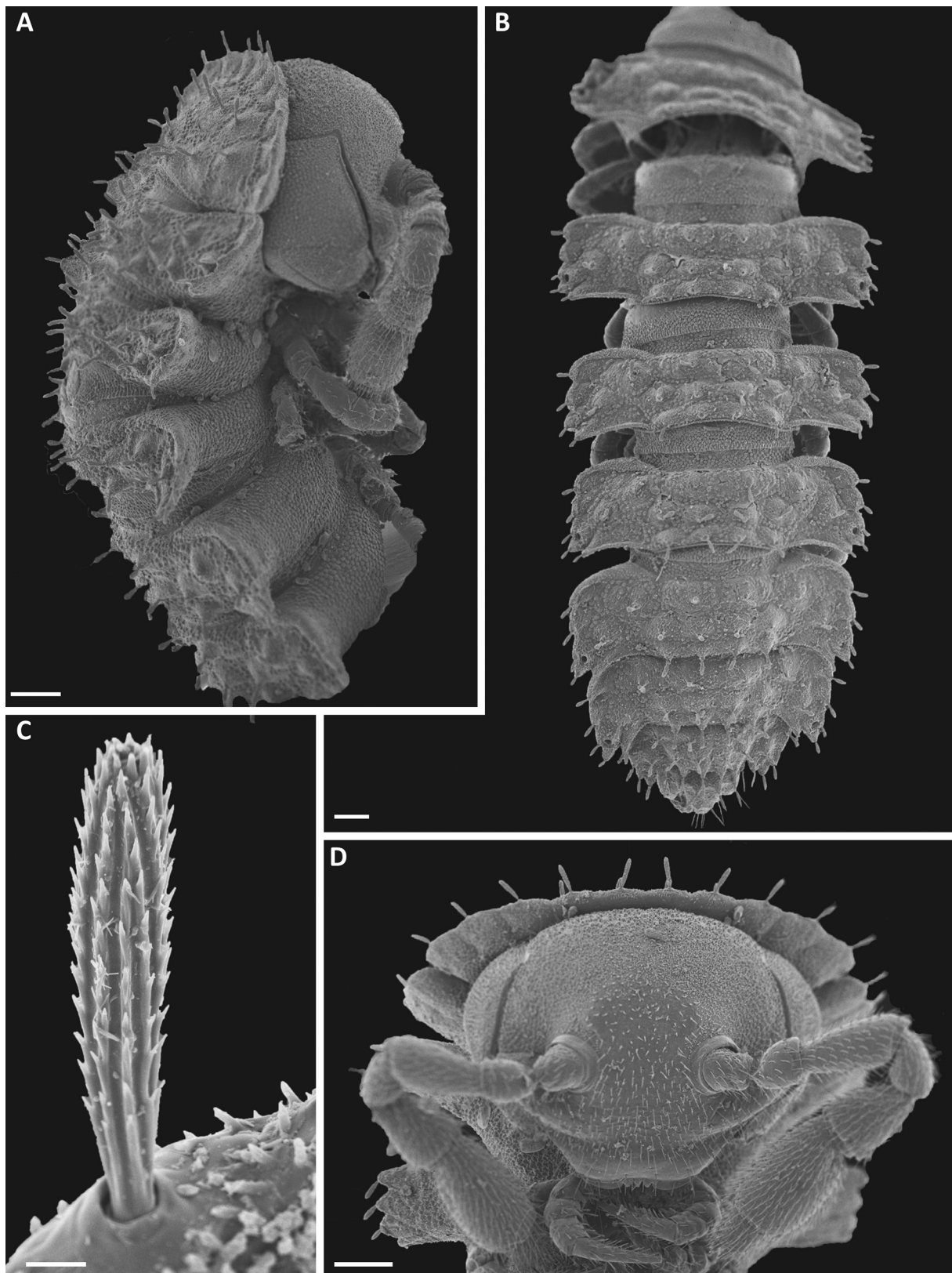


Fig. 8. *Cryptocorypha cactifer* sp. nov., paratype (NHMD 621836), ♂, from Mito Mitatu. **A.** Head and rings 1–6, lateral view. **B.** Rings 12–18 and telson, dorsal view. **C.** Tergal seta. **D.** Head and collum, frontal view. Scale bars: A–B, D = 0.1 mm; C = 0.005 mm.

Further differs from *C. geminiramus* by the smooth part of head capsule extending well above antennal sockets (Fig. 8D, compare with Fig. 2A), by having the gonopod coxa (*cx*) more regularly hemispherical

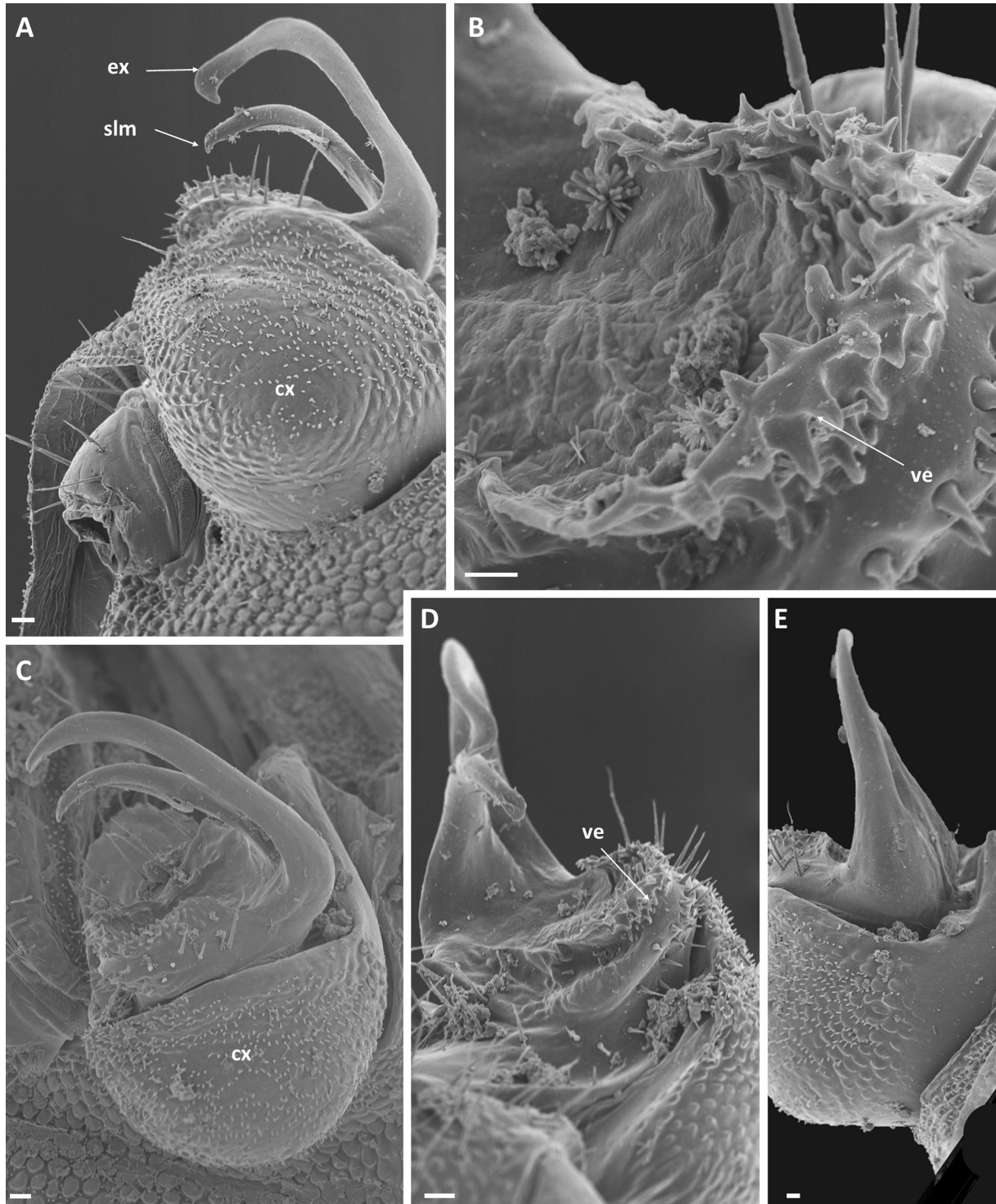


Fig. 9. *Cryptocorypha cactifer* sp. nov., paratype (NHMD 621836), ♂, from Mito Mitatu, left gonopod. **A.** Lateral view. **B.** Basal part of telopodite, showing jagged ?velum. **C.** (Sub)ventral view. **D.** Posterior view. **E.** Anterior view. Abbreviations: *cx* = coxa; *ex* = exomere; *slm* = solenomere; *ve* = velum? Scale bars: A, C–E = 0.01 mm; B = 0.005 mm.

(Fig. 9A, C) and by having a jagged semicircular ridge (velum?, *ve*) on the basal part of the gonopod telopodite (Fig. 9B, D).

Etymology

The species epithet (noun in apposition) means ‘bearer of cacti’ and refers to the some cactus-shaped metazonal setae.

Material examined (3 ♂♂, 1 ♀, 3 subadult ♀♀)

Holotype

TANZANIA • ♂; Morogoro Region, Udzungwa Mountains Natl Park, Kidatu; 07°40′45.5″ S, 36°55′06.9″ E; 1448 m a.s.l.; 21 Oct. 2014; J. Malumbres-Olarte leg.; pitfall trap, Plot 5; NHMD 621833.

Paratypes

TANZANIA • 2 subadult ♀♀; same collection data as for holotype; summed catch from 2 pitfall traps; NHMD 621834 • 1 ♀; same collection data as for holotype; 07°40′42.1″ S, 36°55′06.8″ E; 1482 m a.s.l.; pitfall trap, Plot 6; NHMD 621835 • 1 ♂; same collection data as for holotype; Mito Mitatu; 07°49′39.8″ S, 36°50′26.0″ E; 1552 m a.s.l.; 27 Oct. 2014; pitfall trap, Plot 15; NHMD 621836 • 1 ♂; Morogoro Region, Udzungwa Mountains Natl Park, above Mito Mitatu; 07°49.012′ S, 36°50.401′ E; 1643 m a.s.l.; 27 Dec. 2017; R. Lowassary, T. Pape and N. Scharff leg.; pitfall trap nr. 5, Acc. No.2017-EN-002; NHMD 621837 • 1 subadult ♀; Morogoro Region, Udzungwa Mountains, Mwanihana Forest Reserve; 1800–1850 m a.s.l.; 28–29 Sep., 1984; N. Scharff leg.; litter in montane rain forest; NHMD 621838.

Referred specimen, not a type

TANZANIA • 1 ♀; Udzungwa Mountains, Iringa Region, Udzungwa Scarp Forest Reserve, above Chita Village; 1600–1650 m a.s.l.; 8–13 Nov. 1984; N. Scharff leg.; montane forest, litter; NHMD 621839.

Description

SIZE. Males: Length 5.3–5.5 mm; maximal body width (across metazona) 0.91–0.92 mm; 17 podous + 1 apodous ring + telson. Female: Length 7.7 mm; maximal body width (across metazona) 1.19 mm; 18 podous + 1 apodous ring + telson.

OTHER CHARACTERS. Virtually identical to the smaller *C. geminiramus* sp. nov. with the following exceptions: All level 1 tubercles and all lateral paratergal lobes on podous and apodous rings with a club-shaped, ornamented club-shaped, somewhat cactus-like seta (Fig. 8C); smooth part of head capsule extending well above antennal sockets (Fig. 8D); gonopod coxa (*cx*) more regularly hemispherical (Fig. 9A, C); basal part of gonopod telopodite with a jagged semicircular ridge (velum?, *ve*), on the basal part of the gonopod telopodite (Fig. 9B, D).

Remarks

Almost all specimens of *C. cactifer* sp. nov. were found in mixed samples with *C. geminiramus* sp. nov. The single female from Udzungwa Scarp Forest Reserve fully matches the females from Udzungwa Mountains National Park, but in the light of the considerable geographical distance, combined with the absence of a male, the specimen from Udzungwa Scarp Forest Reserve is not included in the type series.

If the Afrotropical alternative in the first couplet of the key provided by Golovatch (2019) is chosen, *C. cactifer* sp. nov. runs to *C. diffusa* (Brolemann, 1920) from which it differs by several characters, especially by strongly different gonopods and hairy tergites. If the Asian alternative in the first couplet is chosen, *C. cactifer* sp. nov. runs to couplet 17(18) where it fits neither alternative.

Cryptocorypha exovo sp. nov.

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Figs 10–11

Diagnosis

Differs from all congeneric species by the unique shape of the ‘snakelike’ gonopod telopodite. Agrees with *C. geminiramus* sp. nov. in non-gonopodal characters.

Etymology

The species epithet means ‘out of the egg’ and refers to the shape of the gonopod which somewhat resembles a snake (telopodite) hatching from the egg (coxa).

Material examined

Holotype

TANZANIA • ♂; Morogoro Region, Udzungwa Mountains Natl Park, Mito Mitatu; 07°50'14.3" S, 36°50'46.8" E; 1207 m a.s.l.; 16 Dec. 2013; T. Pape and N. Scharff leg.; pitfall trap, Plot MM1; NHMD 621840.

Description

SIZE. Male: Length 5.3 mm; maximal body width (across metazona) 0.78 mm; 17 podous + 1 apodous ring + telson. Female: unknown.

OTHER NON-GONOPODAL CHARACTERS (Fig. 10). Virtually identical to *C. geminiramus* sp. nov.

GONOPODS (Fig. 11). Coxa (*cx*) moderately globose, its surface scaly and with scattered level 3 spherules, mesally forming a shallow gonocoel. Cannula (Fig. 11C, E: *ca*, not seen in the other two species) with a few tiny denticles (*de*). Telopodite projecting strongly from gonocoel, very evident in lateral and ventral views. Basal (‘prefemoral’) part of telopodite (*bt*) massive, with several distolateral setae, giving rise to a very long, sinuous shaft which slightly beyond its midlength divides into a slightly curved branch, probably corresponding to an exomere (*ex*), and a strongly S-shaped branch, probably the solenomere (*slm*). A velum is not evident.

Remarks

A male of *C. geminiramus* sp. nov. was found in the same pitfall trap as the unique holotype of *C. exovo* sp. nov.

If the Afrotropical alternative in the first couplet of the key provided by Golovatch (2019) is chosen, *C. exovo* sp. nov. runs to *C. diffusa* (Brolemann, 1920) from which it differs by several characters, especially by strongly different gonopods. If the Asian alternative in the first couplet is chosen, *C. exovo* sp. nov. runs to couplet 17(18) where it fits neither alternative.

Cryptocorypha (?) sp.

Material examined (7 ♀♀, 2 subad. ♀)

TANZANIA • 1 ♀; Iringa Region, Iringa District, New Dabaga/Ulangambi Forest Reserve, trapsite Kinyonga; 08°00'26.6" S, 35°56'06.1" E; 1910 m a.s.l.; Oct. 2000; Frontier Tanzania leg.; scrub/thicket; NHMD 621841 • 2 ♀♀; same collection data as for preceding; plot Kinyonga; 24 Oct. 2000; montane forest; NHMD 621842 • 1 ♀; same collection data as for preceding; 1904 m a.s.l.; 20 Oct. 2000; scrub/thicket/bush; NHMD 621843 • 2 ♀♀, 1 subad. ♀; same collection data as for preceding;

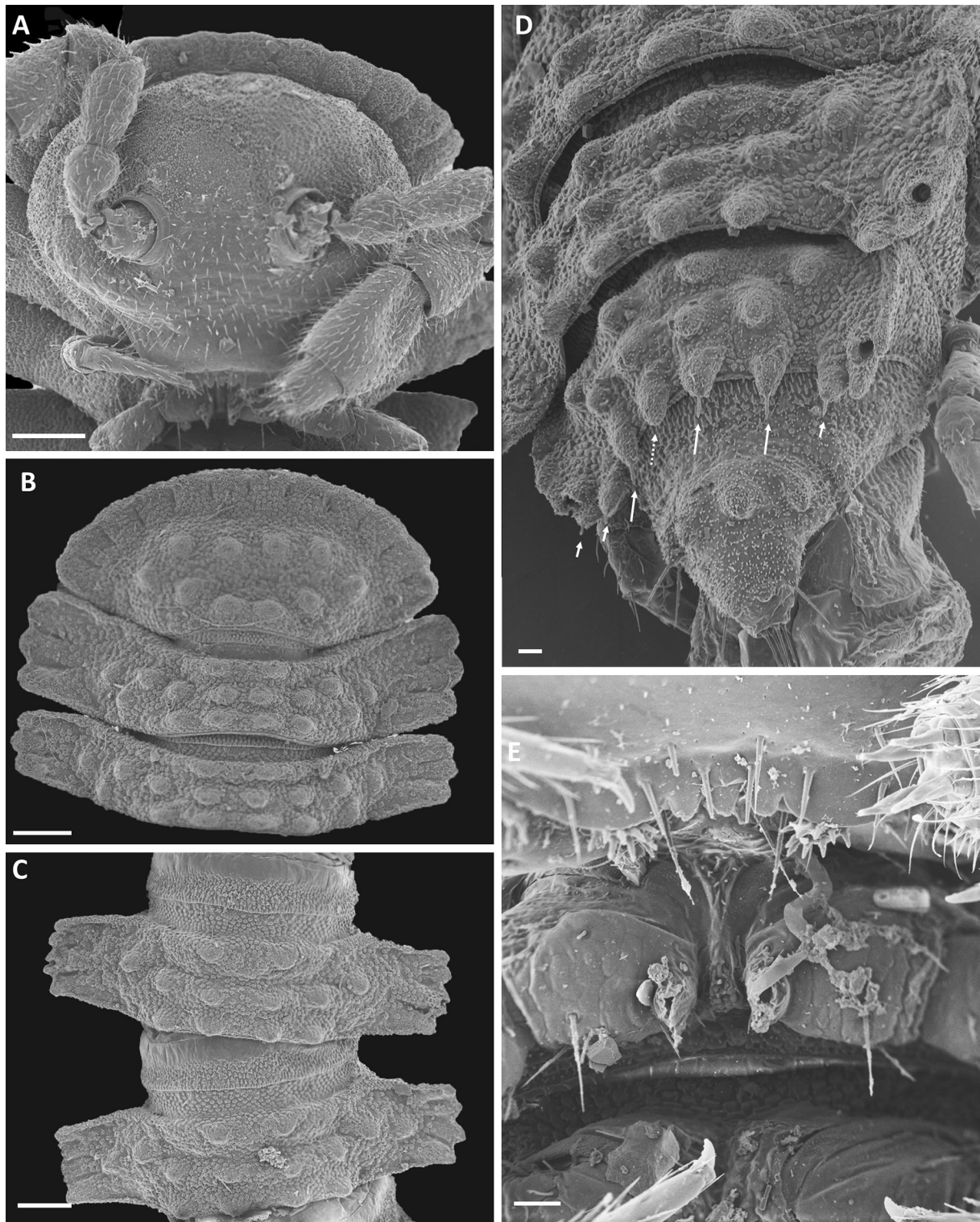


Fig. 10. *Cryptocorypha exovo* sp. nov., holotype (NHMD 621840), ♂. **A.** Head, frontal view. **B.** Collum and rings 2–3, dorsal view. **C.** Rings 2–3, dorsal view. **D.** Rings 16 (part), 17, 18 (apodous) and telson, oblique dorsal view, showing setae (long arrows) and a probably abraded seta (long stippled arrow) on posterior row of tubercles on apodous ring, and setae (short arrows) on paranota of apodous ring. **E.** Labrum and second coxae. Scale bars: A–C = 0.1 mm; D–E = 0.02 mm.

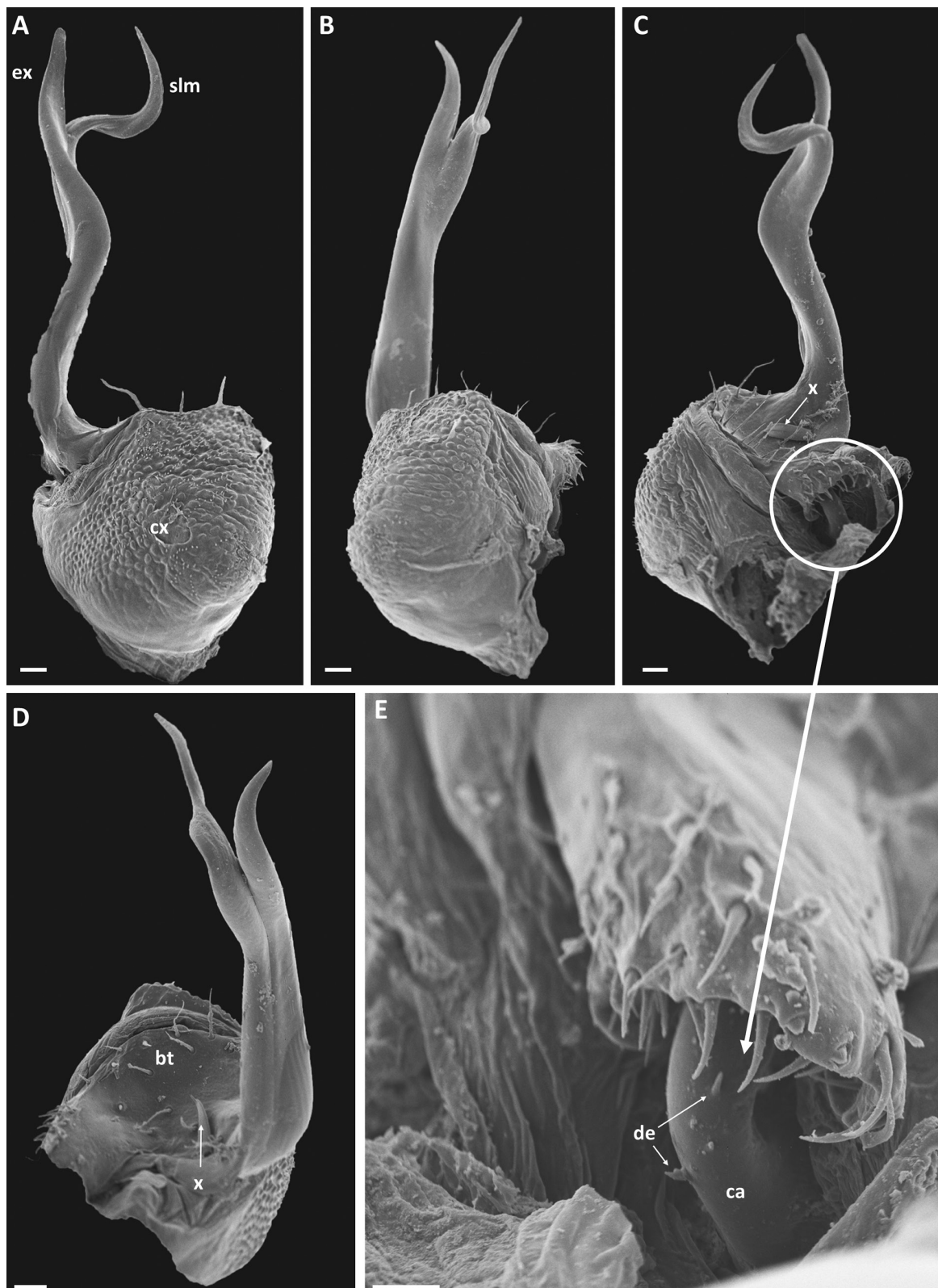


Fig. 11. *Cryptocorypha exovo* sp. nov., holotype (NHMD 621840), ♂, right gonopod. **A.** Lateral view. **B.** Posterior view. **C.** Mesal view. **D.** Anterior view. **E.** Close-up of circled area in D, showing cannula. Abbreviations: *bt* = basal part of telopodite; *ca* = cannula; *cx* = coxa; *de* = denticles; *ex* = exomere; *slm* = solenomere; *x* = 'dirt', not part of the gonopod. Scale bars: A–D = 0.02 mm; E = 0.01 mm.

plot Black Wattle; 08°03'59.2" S, 35°54'01.3" E; 2000–2025 m a.s.l.; plantation; NHMD 621844 • 1 subad. ♀; same collection data as preceding; plot 16; 08°05'34.5" S, 35°55'31.33" E; 1800–1900 m a.s.l.; 15–16 Nov. 2000; montane; NHMD 621845 • 1 ♀; Iringa Region, Iringa District, West Kilombero Scarp Forest Reserve, Nyati Camp; 07°48'39.0" S, 36°28'23.0" E; 1500 m a.s.l.; 6 Aug. 2000; Frontier Tanzania leg.; montane forest; NHMD 621846.

Descriptive notes

SIZE. Females: Length 6.5–7.4 mm; maximum body width 1.15–1.30 mm. 18 podous + 1 apodous ring + telson.

OTHER CHARACTERS. AS in the three species of *Cryptocorypha* described above. Notably, some of the specimens have metatergal setae, like *C. cactifer* sp. nov. (but the setae are smaller and less numerous), whereas others seem to lack such setae.

Remarks

In the absence of males, these specimens, which come from an area where none of the described species have been collected, are not associated with any species. In body size they best match *C. cactifer* sp. nov., with which some of them also share the metazonal setation.

Genus? species?

Material examined

TANZANIA • 1 ♀; Morogoro Region, Udzungwa Mountains Natl Park, Mito Mitatu; 07°50'29.1" S, 36°51'33.0" E; 1006 m a.s.l.; 26 Sep. 2014; J. Malumbres-Olarte leg.; Plot 14, pitfall trap; NHMD 621847.

Descriptive notes

SIZE. Female: Length 5.8 mm; maximal body width (across metazona) 0.80 mm; 18 podous + 1 apodous ring + telson.

OTHER CHARACTERS. A “stylodesmiform” pyrgodesmid sensu Mauriès & Maurin (1981), with deep-set horizontal, non-lobed paraterga and rows of large tubercles/crests on metazonae; not incrustated.

Remarks

In the absence of a male this specimen cannot even be referred to a genus. *Cryptocorypha geminiramus* sp. nov. was found in the same pitfall trap.

Genus? species?

Material examined

TANZANIA • 1 fragment; Udzungwa Mtrs, Iringa Region, Udzungwa Scarp Forest Reserve, above Chita Village; 1600–1650 m a.s.l.; 8–12 Nov. 1984; N. Scharff leg.; montane rain forest; NHMD 621848.

Descriptive notes

SIZE. Fragment (9 podous + 1 apodous ring + telson); maximal body width (across metazona) 1.03 mm.

OTHER CHARACTERS. A “stylodesmiform” pyrgodesmid sensu Mauriès & Maurin (1981), with strongly declivent paraterga and 2+2 large tubercles on metazonae; moderately incrustated.

Remarks

In the absence of a male this specimen cannot even be referred to a genus.

Family Cryptodesmidae Karsch, 1879
Subfamily Thelydesminae Cook, 1896

Genus *Elythesmus* Hoffman, 1978

Type species

Elythesmus enghoffi Hoffman, 1978, by original designation and monotypy.

Other included species

None.

Diagnosis

A genus of Thelydesminae Cook, 1896 in which the prefemora are unmodified in both sexes and the surface of the metaterga is covered by a dark secretion.

Elythesmus enghoffi Hoffman, 1978
Figs 12–17

Material examined (124 ♂♂, 1 subad. ♂, 48 ♀♀, 10 subad. ♀, 1 juv. ♀)

Holotype

TANZANIA • ♂; East Usambara Mountains, Amani, Monga; 1000 m a.s.l.; 4 Feb. 1972; H. Enghoff, O. Lomholdt and O. Martin leg.; under fallen leaves; ZMUC 0010126.

Paratypes

TANZANIA • 1 ♂, 1 ♀; same collection data as for holotype; NHMD 621777.

New material

TANZANIA – **Udzungwa Mountains** • 11 ♂♂; Morogoro Region, Udzungwa Mountains Natl Park, Kidatu; 07°41'13.5" S, 36°56'28.6" E; 650 m a.s.l.; 24 Oct. 2014; J. Malumbres-Olarte leg.; Plot 1, summed catch from five pitfall traps; NHMD 621778 • 6 ♂♂, 1 ♀; same collection data as for preceding; 07°41'14.9" S, 36°56'24.7" E; Plot 2, summed catch from five pitfall traps; NHMD 621779 • 23 ♂♂, 2 ♀♀, 3 subad. ♀♀; same collection data as for preceding; 07°41'02.4" S, 36°55'49.3" E; 1005 m a.s.l.; 14 Sep. 2014; Plot 3, summed catch from ten pitfall traps; NHMD 621780 • 10 ♂♂, 1 ♀; same collection data as for preceding; 07°41'05.2" S, 36°55'48.4" E; 993 m a.s.l.; 15 Oct. 2014; Plot 4, summed catch from eight pitfall traps; NHMD 621781 • 7 ♂♂, 1 ♀; same collection data as for preceding; 07°40'45.5" S, 36°55'06.9" E; 1448 m a.s.l.; 21 Oct. 2014; Plot 5, summed catch from five pitfall traps; NHMD 621786 • 7 ♂♂, 2 ♀♀, 1 subad. ♀; same collection data as for preceding; 07°40'42.1" S, 36°55'06.8" E; 1482 m a.s.l.; 21 Oct. 2014; Plot 6, summed catch from four pitfall traps; NHMD 621787 • 13 ♂♂; same collection data as for preceding; 07°41'23.4" S, 36°56'00.7" E; 708 m a.s.l.; 24 Oct. 2014; Plot 7, summed catch from six pitfall traps; NHMD 521788 • 10 ♂♂, 1 ♀; same collection data as for preceding; 07°41'12.9" S, 36°55'39.2" E; 978 m a.s.l.; 14 Sep. 2014; Plot 8, summed catch from seven pitfall traps; NHMD 621789 • 4 ♂♂; same collection data as for preceding; 07°41'06.2" S, 36°54'52.4" E; 1527 m a.s.l.; 14 Sep. 2014; Plot 9, summed catch from four pitfall traps; NHMD 621690 • 1 ♂; Morogoro Region, Udzungwa Mountains Natl Park, above Kidatu; 7°40'34.5" S, 36°55'07.0" E; 1589 m a.s.l.; 3 Sep. 2016; R. Lowassary, T. Pape and N. Scharff leg.; pitfall trap,



Fig. 12. *Elythemus enghoffi* Hoffman, 1978, specimens from Uluguru Mts, at Bunduki Village. **A.** 2 ♂♂ (NHMD 621814), dorsal view. **B.** ♂ (NHMD 621814), ventral view. **C.** ♀ (NHMD 621814), lateral view. Scale bars = 1 mm. Photo: S.G. Selvantharan.

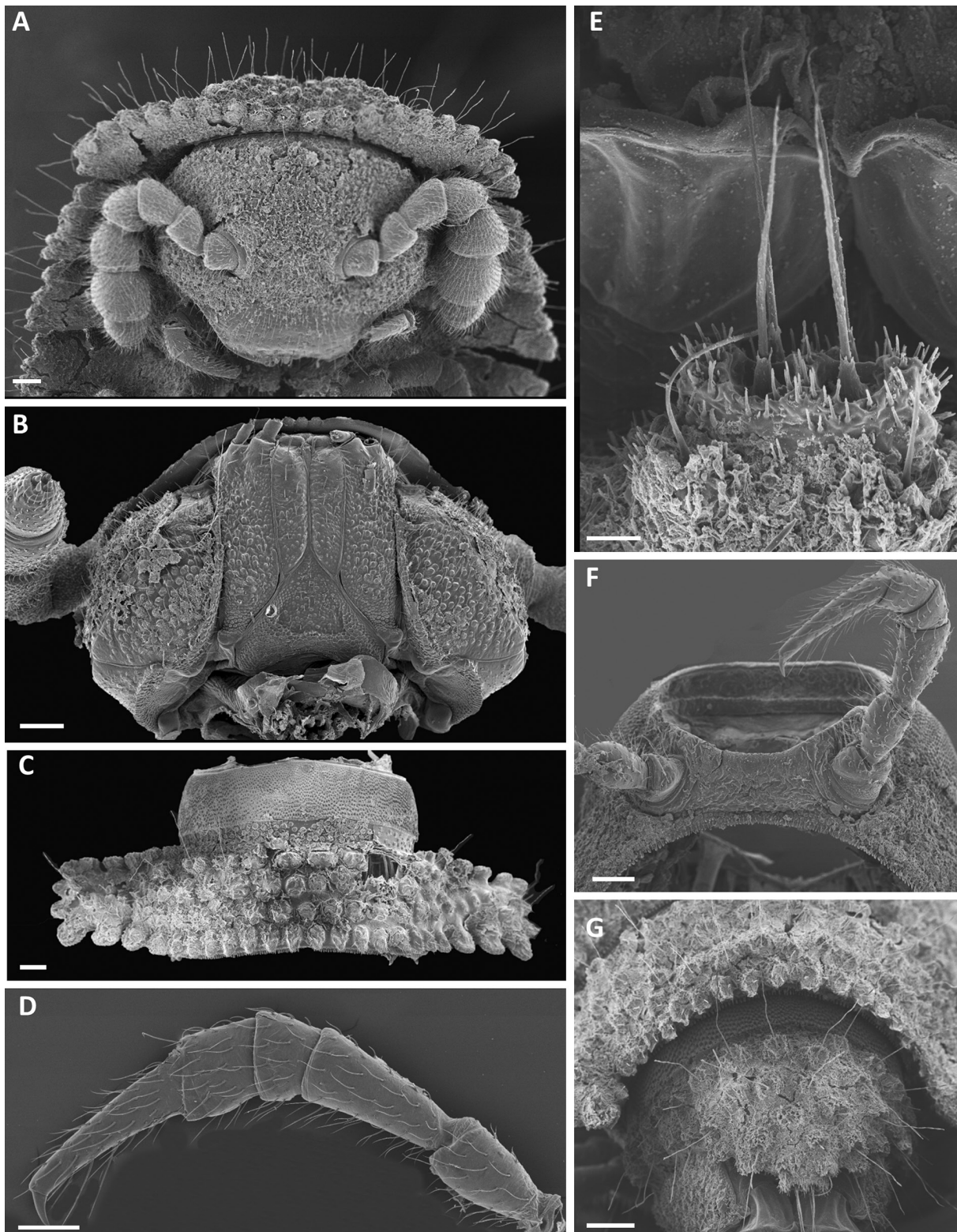


Fig. 13. *Elythesmus enghoffi* Hoffman, 1978, ♂♂, from Kidatu. **A, E–G.** ♂ (NHMD 621778). **B–D.** ♂ (NHMD 621779). **A.** Head and collum, frontal view. **B.** Gnathochilarium and mandibles, ventral view. **C.** Ring 9, treated with ultrasound. **D.** Midbody leg. **E.** Spinnerets on telson. **F.** Gonopodal aperture, posterior-ventral view. **G.** Apodous ring and telson, posterior view. Scale bars: A–D, F–G = 0.1 mm; E = 0.02 mm.

Acc. No. 2015-EN-001; NHMD 521691 • 1 ♂; Morogoro Region, Udzungwa Mountains Natl Park, Mito Mitatu; 07°50'26.1" S, 36°51'33.0" E; 1006 m a.s.l.; 26 Oct. 2014; J. Malumbres-Olarte leg.; Plot 14, pitfall trap; NHMD 621792 • 2 ♂♂; same collection data as for preceding; 07°49'39.8" S, 36°50'26.0" E; 1552 m a.s.l.; 27 Oct. 2014; Plot 15, summed catch from two pitfall traps; NHMD 621793 • 1 ♀; Morogoro Region, Udzungwa Mountains Natl Park, Sanje Chini Camp; 7°46'24.6" S, 36°53'47.7" E; 598 m a.s.l.; 17–19 Jan. 2014; T. Pape and N. Scharff leg.; hand collected; NHMD 621794 • 2 ♂♂; Morogoro Region, Udzungwa Mountains Natl Park, trail to Mizimu Camp; 250 m a.s.l.; 3 Sep. 2012; T. Pape and N. Scharff leg.; hand collected; NHMD 621795 • 1 ♂, 1 subad. ♂; Udzungwa Mountains, Mwanihana Forest above Sanje; 1700 m a.s.l.; 15 Aug. 1982; M. Stoltze and N. Scharff leg.; NHMD 621796 • 1 ♂; same collection data as for preceding; 1250 m a.s.l.; 25 Jul. 1982; in litter; NHMD 621797 • 1 subad. ♀; same collection data as for preceding; 1000 m a.s.l.; 1 Aug. 1982; in litter; NHMD 621798 • 1 ♂; same collection data as for preceding; 1000 m a.s.l.; 1 Aug. 1982; pitfall trap; NHMD 621810 • 2 ♀♀; Udzungwa Mountains, Morogoro Region, Mwanihana Forest Res.; 1000–1100 m a.s.l.; 10–24 Sep. 1984; N. Scharff leg.; intermediate rain forest; NHMD 621799 • 1 ♂; same collection data as for preceding; 700 m a.s.l.; 8–16 Sep. 1984; pitfall trap in lowland rain forest; NHMD 621800 • 3 ♂♂; Morogoro Region, Udzungwa Scarp Catchment Forest Reserve, Chita; 08°30'13.4" S, 35°55'08.9" E; 659 m a.s.l.; 31 Oct. 2014; J. Malumbres-Olarte leg.; Plot 16, summed catch from three pitfall traps; NHMD 621801 • 1 ♂; same collection data as for preceding; 08°29'59.1" S, 35°54'59.5" E; 908 m a.s.l.; 30 Oct. 2014; J. Malumbres-Olarte leg.; Plot 17, pitfall trap; NHMD 621802 • 2 ♂♂, 1 ♀, 1 subad. ♀; Udzungwa Mountains, Iringa Region, Udzungwa Scarp Forest Res., above Chita Village; 730–1050 m a.s.l.; 23 Oct.–14 Nov. 1984; N. Scharff leg.; lowland rain forest; NHMD 621803, NHMD 621804, NHMD 621805 • 1 ♂, 1 ♀; same collection data as for preceding; 1400 m a.s.l.; 4–5 Nov. 1984; pitfall traps in intermediate rain forest; NHMD 621806 • 1 ♀; same collection data as for preceding; 1500 m a.s.l.; 13 Nov. 1984; litter, montane rain forest; NHMD 621807 • 1 ♀; same collection data as for preceding; 1600–1650 m a.s.l.; 8–12 Nov. 1984; montane rain forest; NHMD 621808 • 1 ♂; same collection data as for preceding; 750 m a.s.l., 25–29 Oct. 1984; pitfall traps in lowland rain forest; NHMD 621809. – **Uluguru Mountains** • 1 ♂, 2 ♀♀; Lupanga, West; 1900 m a.s.l.; 1 Jul. 1981; M. Stoltze and N. Scharff leg.; litter; NHMD 621811 • 1 juv. ♀; Lupanga, East; 1300 m a.s.l.; 10 Jul. 1981; M. Stoltze and N. Scharff leg.; litter; NHMD 621812 • 1 ♂; Morogoro Region, Morogoro District, Kimboza Forest Reserve; 07°01' S. 37°48' E, Jan.–Mar. 1994; Frontier Tanzania leg.; NHMD 621813 • 11 ♂♂, 18 ♀♀; at Bunduki Village; 07°01'06" S. 37°39'45" E; 1569 m a.s.l.; 26 Nov. 2010; V. Grebennikov leg.; 'sifting 27'; NHMD 621814. – **Nguru (Kanga) Mountains** • 1 ♀; Morogoro Region, Kanga Mountains, Kanga Forest Reserve; 400–500 m a.s.l.; 22–25 Nov. 1984, N. Scharff leg.; lowland rain forest; NHMD 621815. – **East Usambara Mountains** • 1 ♂; Amani; 1000 m a.s.l.; 15 Jul. 1980; M. Stoltze and N. Scharff leg.; pitfall trap; NHMD 621816 • 1 subad. ♀; Sangarawe Forest; 5°6.5' S, 38°35.7' E; 990 m a.s.l.; 5–6 Nov. 1995; N. Scharff and C. Griswold leg.; sifting litter; NHMD 621817. – **West Usambara Mountains** • 1 subad. ♀; Mazumbai forest Reserve; 19–29 Sep. 1992; M. Andersen leg.; NHMD 621818 • 3 ♂♂, 1 subad. ♀; Mazumbai Forest; 4°49' S, 38°30' E; 1400–1600 m a.s.l.; 11–19 Nov. 1995; N. Scharff and C. Griswold leg.; NHMD 621819.

Descriptive notes

The original description (Hoffman 1978) is exhaustive. The large material studied here, including by scanning electron microscopy (SEM), allows some supplementary notes as well as an account of interspecific variation. See Figs 12–16.

SIZE. Males: Length 6.6–13.2 mm; maximal body width (across metazona) 1.32–2.35 mm; 17 or 18 podous rings + 1 apodous ring + telson. One male possible with only 16 podous rings, see remarks. Females: Length 9.6–16 mm, maximal body width (across metazona) 1.57–2.69 mm; 18 podous rings + 1 apodous ring + telson. The considerable size variation is in part geographical, specimens from the

East and West Usambara Mountains being larger than those from elsewhere. The very extensive material from the Udzungwa Mountains suggests a correlation between altitude and body size, cf. Remarks.

BODY RINGS. Prozonites divided into two zones (Figs 13C, 14C). The anterior ca $\frac{2}{3}$ is covered in a sculptural pattern consisting of tiny depressions delimited by fine walls, the caudal part of the walls being drawn out, each with ca five micro-ridges, each micro-ridge ending in a fine tooth (Fig. 14C). Posterior ca $\frac{1}{3}$ unevenly covered by circular ‘buttons’ (Akkari & Enghoff 2011: fig. 2) resembling the level 2 structural elements described for *Cryptocorypha*. Metazonites covered by a brown to blackish layer or secretion which can be removed partially using a needle, but which is resistant to ultrasonic cleaning as well as digestion with trypsin or commercial enzymatic detergent. Under the secretion, the metazonital tubercles are covered by rows of hairlike processes which presumably help to keep the secretion layer in place (Fig. 14A). The long setae of which each metazonital tubercle carries one are in high magnification seen to be segmented (Fig. 14D), their apical part is flattened (Fig. 14E). The limbus consists of tongue-shaped, apically sometimes finely serrate lobes, overlaid by a row of spines of ca the same length (Fig. 14B, see also Akkari & Enghoff 2011: fig. 26).

GONOPODS (Fig. 16). Exactly as described by Hoffman (1978) in all studied males, irrespective of geographical origin, body size or number of podous rings.

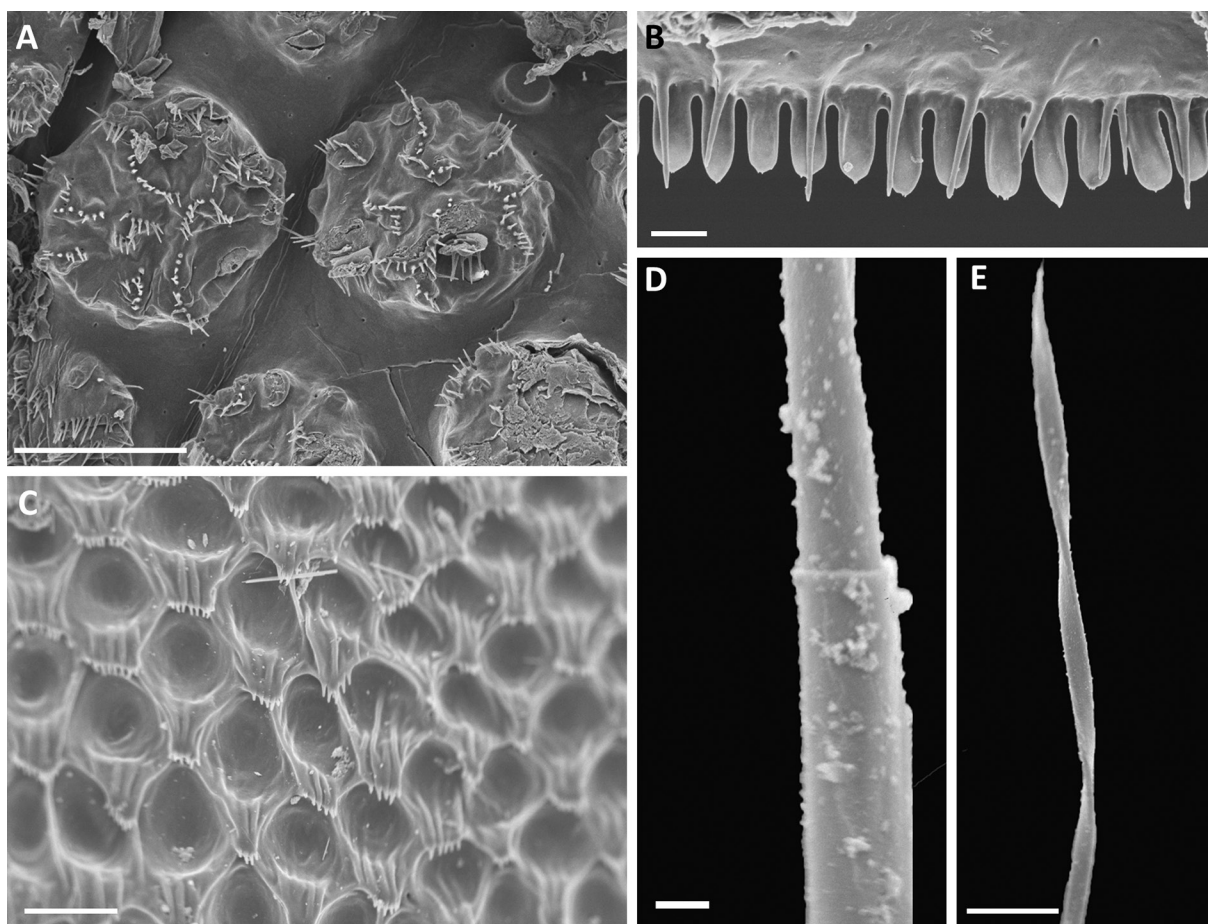


Fig. 14. *Elythesmus enghoffi* Hoffman, 1978, ♂♂ from Kidatu. **A–B.** ♂ (NHMD 621779). **C–E.** ♂ (NHMD 621778). **A.** Metazonital tubercles after mechanical removal of blackish secretion, showing rows of hair-like processes. **B.** Limbus. **C.** Microsculpture of anterior part of prozona. **D–E.** Metazonital setae showing articulation and flattened tip. Scale bars: A = 0.05 mm; B–C, E = 0.01 mm; D = 0.001 mm.

Table 1 (continued on next page). *Elythemus enghoffi* Hoffman, 1978. **A.** Ring numbers (N) and size. **B.** Sorted by altitude. In Udzungwa Scarp (Chita) all are 18+1+T. In Udz. Mts Natl Pk (everything else), 18+1+T is only found at 1482+ m a.s.l.

A.					
locality	plot no.	alt. in m a.s.l.	male ring nos	male width (mm)	N
UDZUNGWA: Kidatu	1	650	17+1+T	1.61–1.84	12
UDZUNGWA: Kidatu	2	650	17+1+T	1.90	6
UDZUNGWA: Kidatu	3	1005	17+1+T	1.90	13
UDZUNGWA: Kidatu	4	993	17+1+T	1.81	10
UDZUNGWA: Kidatu	5	1448	17+1+T	1.72–1.84	6
UDZUNGWA: Kidatu	6	1482	18+1+T	1.34	1
UDZUNGWA: Kidatu	6	1482	17+1+T	1.79	1
UDZUNGWA: Kidatu	7	708	17+1+T	1.50–1.95	1
UDZUNGWA: Kidatu	8	978	17+1+T	1.75–1.79	5
UDZUNGWA: Kidatu	9	1527	18+1+T	1.41	1
UDZUNGWA: Kidatu	9	1527	17?+1+T	1.34–1.43	2
UDZUNGWA: Kidatu	9	1527	16?+1+T	1.34	1
UDZUNGWA: above Kidatu	–	1589	18+1+T	1.39	1
UDZUNGWA: Mito Mitatu	14	1006	17+1+T	1.92	1
UDZUNGWA: Mito Mitatu	15	1552	18+1+T	1.61–1.71	2
UDZUNGWA: trail to Mizimu Camp	–	250	17+1+T	1.55–1.95	2
UDZUNGWA: above Sanje	–	1700	18+1+T	1.32	1
UDZUNGWA: above Sanje	–	1250	17+1+T	1.90	1
UDZUNGWA: above Sanje	–	700	17+1+T	1.95	1
UDZUNGWA: Chita	16	659	18+1+T	1.90–1.95	3
UDZUNGWA: Chita	17	908	18+1+T	1.99	1
UDZUNGWA: above Chita	–	730	18+1+T	2.04	1
UDZUNGWA: above Chita	–	1050	18+1+T	1.99	1
UDZUNGWA: above Chita	–	1400	18+1+T	1.46	1
EAST USAMBARA: Amani	–	1000	18+1+T	2.20–2.35	3
WEST USAMBARA: Mazumbai	–	1400–1600	18+1+T	2.24–2.28	2
ULUGURU: Lupanga West	–	1900	17+1+T	2.11	1
ULUGURU: Kimboza	–	?	17+1+T	2.24	1
ULUGURU: Bunduki	–	1569	18+1+T	1.55–1.86	8

B.					
locality	plot no.	alt. in m a.s.l.	male ring nos	male width (mm)	N
UDZUNGWA: trail to Mizimu Camp	–	250	17+1+T	1.55–1.95	2
UDZUNGWA: Kidatu	1	650	17+1+T	1.61–1.84	12
UDZUNGWA: Kidatu	2	650	17+1+T	1.90	6

Table 1. continued.

B.					
locality	plot no.	alt. in m a.s.l.	male ring nos	male width (mm)	N
UDZUNGWA: above Sanje	–	700	17+1+T	1.95	1
UDZUNGWA: Kidatu	7	708	17+1+T	1.50–1.95	1
UDZUNGWA: above Chita	–	730	18+1+T	2.04	1
UDZUNGWA: Chita	17	908	18+1+T	1.99	1
UDZUNGWA: Kidatu	8	978	17+1+T	1.75–1.79	5
UDZUNGWA: Kidatu	4	993	17+1+T	1.81	10
UDZUNGWA: Kidatu	3	1005	17+1+T	1.90	13
UDZUNGWA: Mito Mitatu	14	1006	17+1+T	1.92	1
UDZUNGWA: above Chita	–	1050	18+1+T	1.99	1
UDZUNGWA: above Sanje	–	1250	17+1+T	1.90	1
UDZUNGWA: above Chita	–	1400	18+1+T	1.46	1
UDZUNGWA: Kidatu	5	1448	17+1+T	1.72–1.84	6
UDZUNGWA: Kidatu	6	1482	18+1+T	1.34	1
UDZUNGWA: Kidatu	6	1482	17+1+T	1.79	1
UDZUNGWA: Kidatu	9	1527	18+1+T	1.41	1
UDZUNGWA: Kidatu	9	1527	17+1+T	1.34–1.43	2
UDZUNGWA: Kidatu	9	1527	16+1+T	1.34	1
UDZUNGWA: Mito Mitatu	15	1552	18+1+T	1.61–1.71	2
UDZUNGWA: above Kidatu	–	1589	18+1+T	1.39	1
UDZUNGWA: above Sanje	–	1700	18+1+T	1.32	1

Remarks on variation

There is a considerable size variation in the large material of *E. enghoffi* studied. The width of adult males varies from 1.32 mm in the smallest male (from Udzungwa Mountains) to 2.35 mm in the largest males (from East Usambara Mountains). On the whole, specimens from the Udzungwa Mountains are smaller (male width 1.32–2.04 mm), compared to 2.20–2.35 mm in males from East and West Usambara Mountains and 1.55–2.11 mm in males from Uluguru Mountains (Table 1).

Even more remarkable is the variation in ring number in adult males. Whereas adult females always have 18 podous rings (plus one apodous ring plus telson, adding up to the traditional “20 segments”), adult males may have 18 or 17, possibly even 16 podous rings. In the Udzungwa Mountains there is a geographical pattern: all examined males from the SW part of the Udzungwa (Udzungwa Scarp Catchment Forest Reserve, 659–1400 m a.s.l.) have 18 podous rings. In contrast, among males from the NE part of the mountains (Udzungwa Mountains National Park), males with 18 podous rings were found only at 1482+ m a.s.l.; all males from lower altitudes (down to 250 m a.s.l.) had 17 podous rings, but such males also occurred at altitudes as high as 1527 m a.s.l.

The sample from Kidatu, plot 9 (NHMD 621790) is particularly intriguing: out of four males, one has 18 podous rings, two seem to have 17, and one seems to have only 16 podous rings. However, this apparent case of very local variation in ring number needs verification because the males were unfortunately dissected for gonopod study before the rings were counted, so although deemed improbable, it cannot be completely excluded that one or two rings have become lost.

Figure 17 shows the relationship between podous ring number, body width and altitude in the Udzungwa Mountains.

The much smaller material from the Usambara Mountains only includes males with 18 podous rings, whereas males with 17 and 18 podous rings are present in the also quite small material from the Uluguru Mountains.

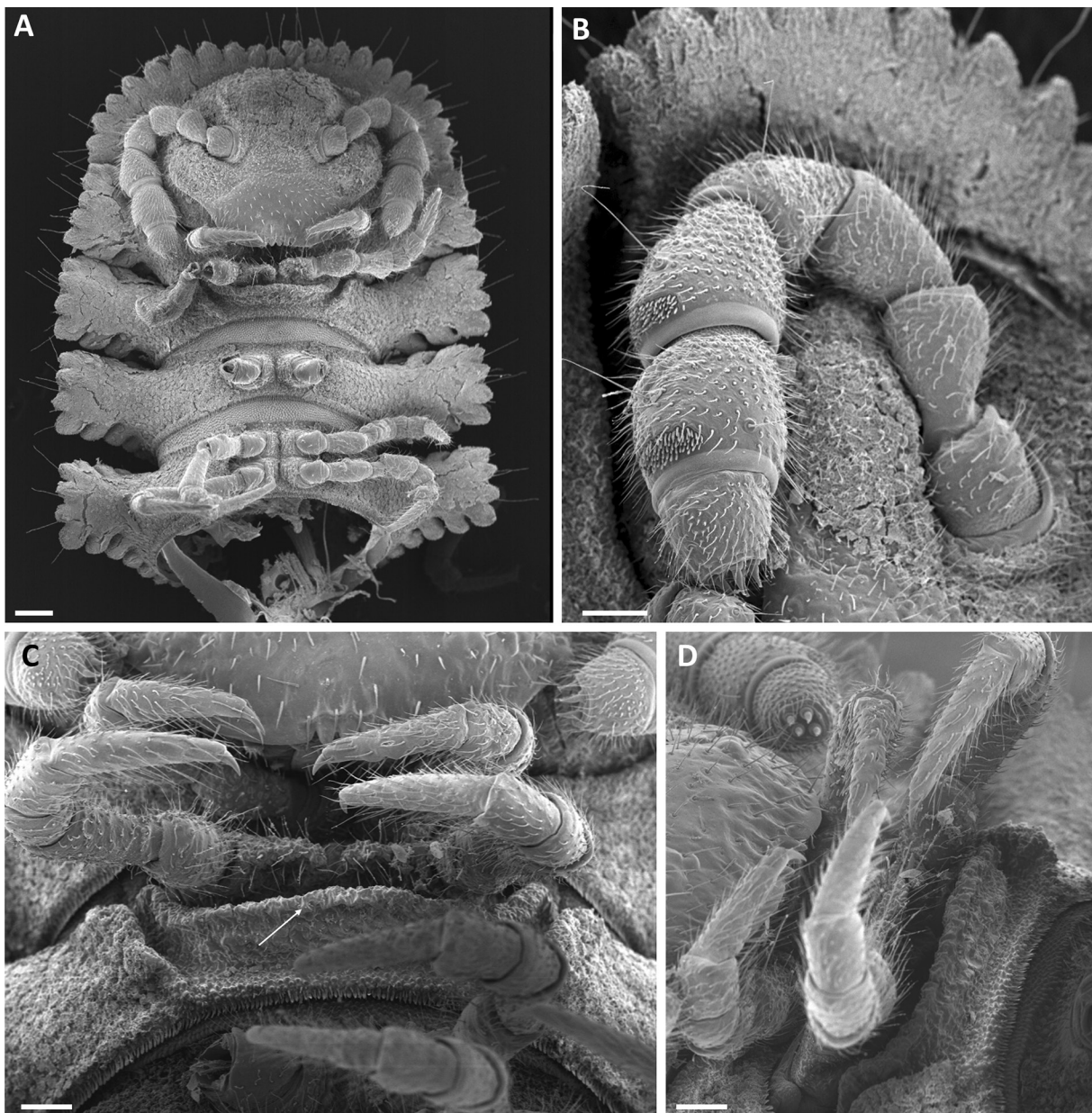


Fig. 15. *Elythesmus enghoffi* Hoffman, 1978, ♀ (NHMD 621780) from Kidatu. **A.** Head and rings 1–5, ventral view. **B.** Right antenna, ventro-lateral view. **C.** Leg pairs 1–2, plus left legs 3–4, and epigynal ridge (arrow), ventral view. **D.** Leg pairs 1–2 and epigynal ridge, ventro-lateral view. Scale bars: A = 0.2 mm; B–D = 0.1 mm.

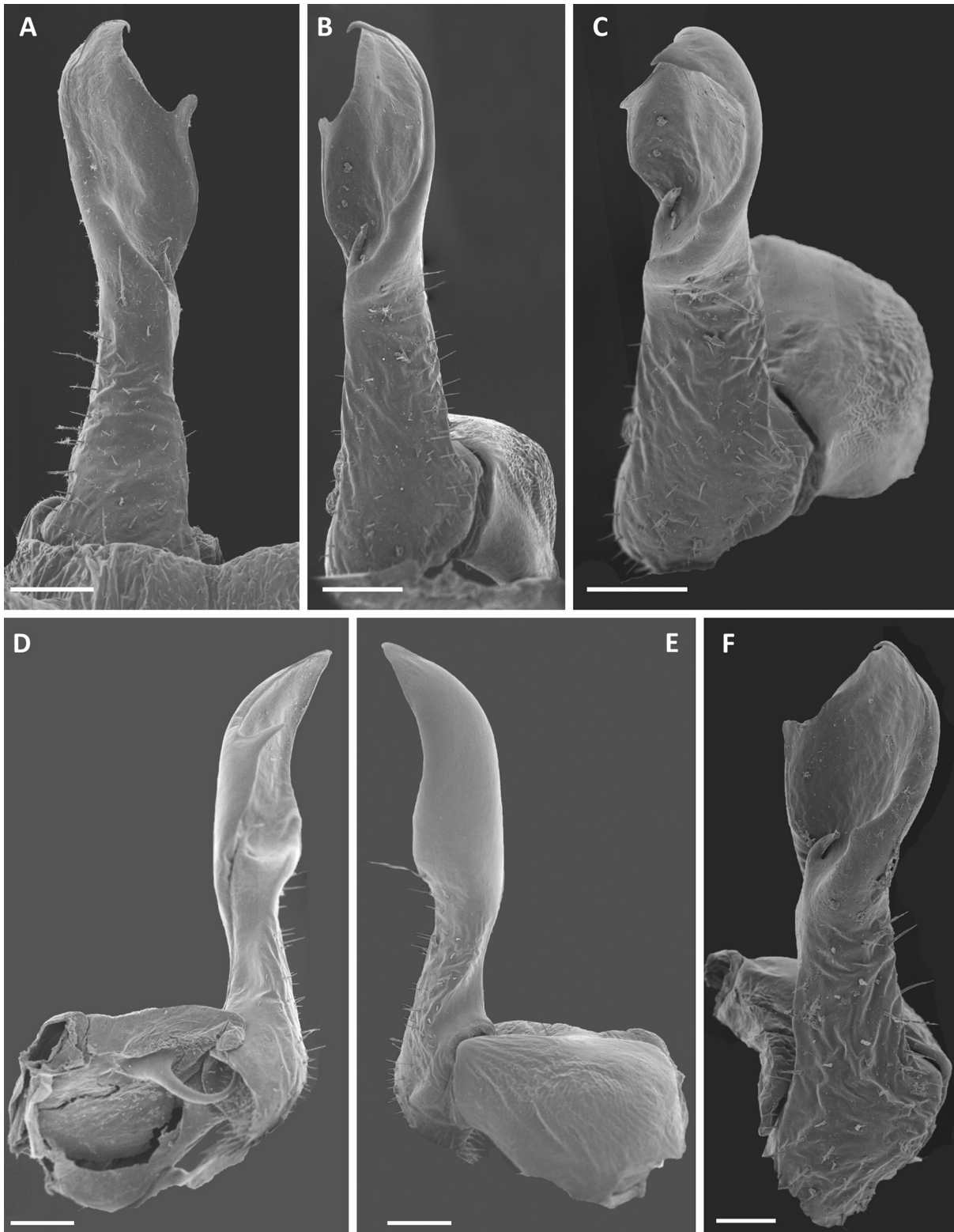


Fig. 16. *Elythesmus enghoffi* Hoffman, 1978, gonopods. **A.** Topotype, ♂, with 18 podous rings from Amani, East Usambara Mts (NHMD 621816), right gonopod, ventral view. **B–E.** ♂ (NHMD 621778) with 17 podous rings from Kidatu, left gonopod. **B.** Ventral view. **C.** Oblique (slightly apical) meso-ventral view. **D.** Mesal view. **E.** Lateral view. **F.** Specimen (NHMD 621787) with 18 podous rings from Kidatu, right gonopod, meso-ventral view. Scale bars: A–E = 0.1 mm; F = 0.05 mm.

?Elythesmus sp.

Material examined (2 ♀♀, 1 subad. ♀)

TANZANIA • 1 ♀; Iringa Region, Iringa District, West Kilombero Scarp Forest Reserve; 07°50'38.4" S, 36°22'17.6" E; 1400 m a.s.l.; Nov. 2000; Frontier Tanzania leg.; montane forest, trap site Paradise; NHMD 621820 • 1 ♀; same collection data as for preceding; 07°48'50.6" S, 36°25'26.2" E; 1586 m a.s.l.; 28 Aug. 2000; plot Firefly; NHMD 621821 • 1 subad. ♀; same collection data as for preceding; 07°48'34.0" S, 36°28'23.0" E; 1500 m a.s.l.; 6 Aug. 2000; Nyati-camp; NHMD 621822.

Remarks

These specimens are extremely similar to *Elythesmus enghoffi*, with one notable exception: the paranota are shining white, completely devoid of the dark layer which is so characteristic of *E. enghoffi*, and on the central part of the metazonae, there is only a faint brownish colouration. In the absence of males, the significance of this difference remains unclear.

Discussion

The Udzungwa species of *Cryptocorypha* Attems, 1907

The species of *Cryptocorypha* described here from the Udzungwa Mountains constitute a remarkable trio and highlight some general problems in pyrgodesmid/cryptodesmoid/polydesmidean taxonomy. All three species are tiny, and all share the same non-gonopodal morphology, except for the metatergal setation in *C. cactifer* sp. nov. The gonopods in *C. geminiramus* sp. nov. and *C. cactifer* sp. nov. are

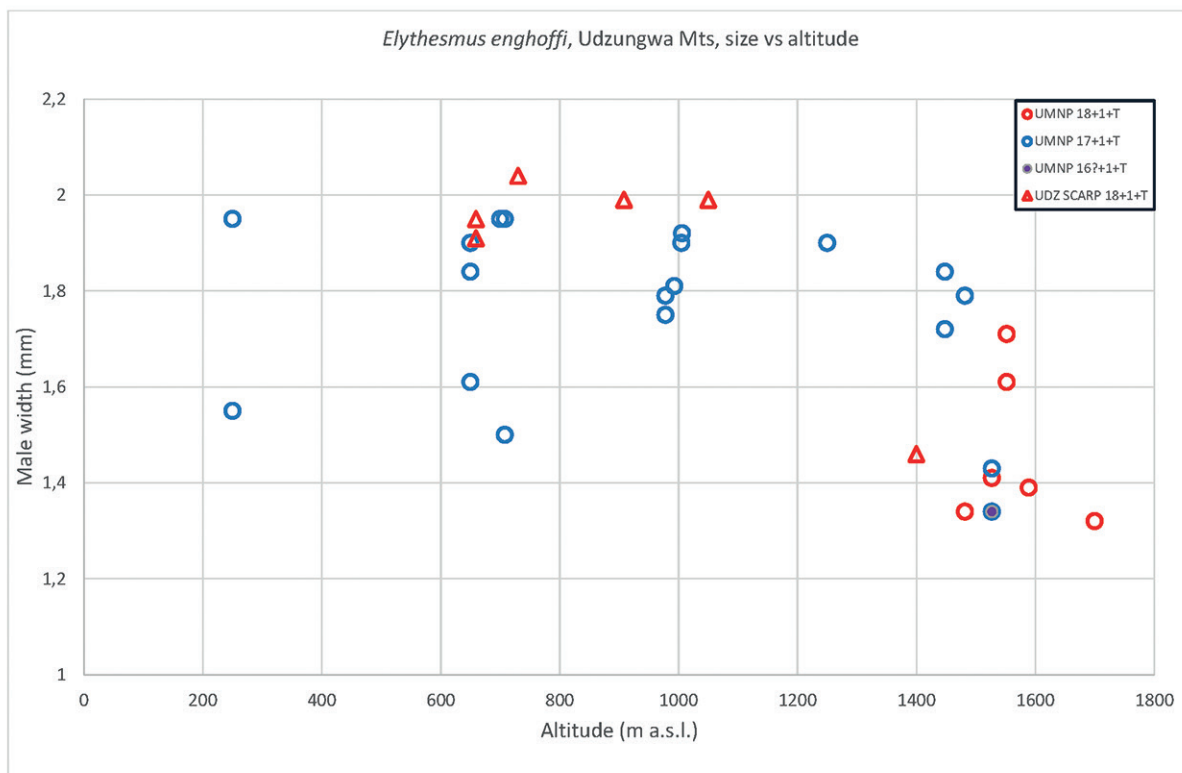


Fig. 17. *Elythesmus enghoffi* Hoffman, 1978, variation in body width and number of body rings of males from the Udzungwa Mts. Abbreviations: UDZ SCARP = Udzungwa Scarp Catchment Forest Reserve; UMNP = Udzungwa Mts National Park.

virtually identical (and differ significantly from those of all other known congeners), whereas the gonopods of *C. exovo* sp. nov. are radically different. Under a splitter approach, the gonopods of *C. exovo* sp. nov. would easily warrant the erection of a new genus, and the same might be said about the presence of metatergal setae on podous body rings in *C. cactifer* sp. nov.

According to the informal classification of Mauriès & Maurin (1981), *Cryptocorypha* belongs to the cryptodesmoid pyrgodesmids. However, *C. cactifer* sp. nov., might as well be grouped with the trichopolydesmid pyrgodesmids because of its extensive dorsal setation, cf. the treatment of the genus *Cachania* Schubart, 1955 by Golovatch & VandenSpiegel (2014). The absence of metatergal setae was part of the diagnosis of *Cryptocorypha* by Golovatch (2019) which therefore has been modified (see under the heading “Genus *Cryptocorypha* Attems, 1907”). To add to the confusion, *C. geminiramus* sp. nov. and *C. exovo* sp. nov. both have a few setae on the apodous ring in front of the telson, and the females here identified as *Cryptocorypha* (?) sp. also have metatergal setae on podous rings.

Prozonital surface sculpture

Akkari & Enghoff (2011) discussed possible phylogenetic implications of the differences in prozonital surface sculpture. The three species of *Cryptocorypha* described here share an identical elaborate prozonital surface sculpture (Fig. 3B–C). The prozona is clearly divided into three zones. The anterior zone is almost smooth, with an indistinct cover of low swellings; in the intermediate zone these swellings are replaced by triangular denticles, interspersed with level 3 spherules; the posterior zone is sharply demarcated from the intermediate zone, with a dense cover of level 2 buttons and level 3 spherules. A virtually identical pattern has been reported from *Cryptocorypha ornata* (Attems, 1938), *C. monomorpha* Golovatch *et al.* 2017, *C. chernovi*, *C. enghoffi* Likhitrakarn *et al.*, 2019, and probably also *C. perplexa* Golovatch & VandenSpiegel, 2015) (Akkari & Enghoff 2011: fig. 9; Likhitrakarn *et al.* 2019: fig. 3f; Golovatch & VandenSpiegel 2015: fig. 3a; Golovatch *et al.* 2013: fig. 2d; 2017: fig. 26l), but also from other pyrgodesmid genera, viz., *Cynedesmus* sp. (Akkari & Enghoff 2011: fig. 8) and *Nonnodesmus niger* (Attems, 1953) (Golovatch *et al.* 2017: fig. 1l). Still other genera of Pyrgodesmidae have somewhat different patterns, e.g., *Evurodesmus proximus* Golovatch *et al.*, 2010 (Golovatch *et al.* 2010: fig. 13), *Udodesmus harpago* Golovatch & VandenSpiegel 2014 (Golovatch & VandenSpiegel 2014: fig. 14l), *Myrmecodesmus hastatus* (Schubart, 1945) (Golovatch *et al.* 2016: fig. 11, and *Monachodesmus* spp. (Golovatch *et al.* 2015: fig. 6m; 2017: figs 10l, 12l, 13k, 15h, 21k).

The prozonital sculpture of *Elythesmus enghoffi* as described here is identical to that described for the same species by Akkari & Enghoff (2011). An almost identical pattern was found in *Thelydesmus dispar* Cook, 1896 (Fig. 18) belonging to the same subfamily, Thelydesminae Cook, 1896, as *Elythesmus*. The only difference between the two thelydesmines is that in *Thelydesmus* the caudal part of the walls separating the tiny depressions is not ridged, and the buttons on the posterior $\frac{1}{3}$ are somewhat larger. Of other cryptodesmids of which SEM images are available, *Aporodesmus* sp. (Pterodesminae) and *Astrolabius hoffmani* Golovatch *et al.* 2010 (Otodesminae), lack buttons on the posterior part of the prozonite while the micro-sculpture on the anterior part resembles that seen in *Thelydesmus* (Akkari & Enghoff 2011: fig. 52; Golovatch *et al.* 2010: fig. 36). *Trichopeltis* spp. (Otodesminae) do have the buttons, but the sculpture on the anterior $\frac{2}{3}$ is different (Golovatch *et al.* 2010: figs. 15, 33). (Also, the limbus of *T. dispar* is similar to that of *E. enghoffi*, see Fig. 18C)

Summarizing, our findings underline the ‘phylogenetic potential’ of the prozonital surface sculpture; however, the pattern is not at all clear-cut.

“Cerotegument” and “microvilli”

Likhitrakarn *et al.* (2019) described the tegument of *Cryptocorypha enghoffi* as “encrusted with a microspiculate cerotegument, dull, beset with microvilli”. A cerotegument is “a thick cement layer built

after moulting ... an additional layer of hardening secretion covering the epicuticle” (Wolff *et al.* 2017). The fine SEM images of Likhitrakarn *et al.* (2019) in my opinion show no indication of a cerotegument in this sense, and likewise, in the species of *Cryptocorypha* described here there is nothing that looks like a cerotegument. On the other hand, the dark layer covering the dorsal side of *Elythesmus enghoffi* might well be termed a cerotegument although Hoffman (1978) did not use this term.

The “microvilli” referred to by Likhitrakarn *et al.* (2019) would correspond to what I have called “level three spherules” (Fig. 3). Because “Microvilli are finger-like membrane protrusions, supported by the actin cytoskeleton, and found on almost all cell types” (Orbach & Su 2020), I would recommend not using this term for the minute cuticular outgrowths found on different arthropods, including the species of *Cryptocorypha* described here (Fig. 3A).

Intraspecific variation in body ring number, or several species of *Elythesmus*?

Elythesmus enghoffi is remarkable in including males with 18 and 17 podous rings (maybe even 16). Intraspecific variation on ring number is very rare in the order Polydesmida. Apart from the genus *Devillea* Silvestri, 1903 (family Xystodesmidae), in which the normally strict regulation of ring numbers has obviously become relaxed (see Enghoff *et al.* 1993), and some laboratory-induced cases (David & Geoffroy 2011), the only known examples are from the family Ammodesmidae where several species of the genus *Ammodesmus* Cook, 1896 may have 16 or 17 podous rings in both sexes (VandenSpiegel & Golovatch 2012, 2015). Although the number of studied females of *E. enghoffi* is modest, nothing

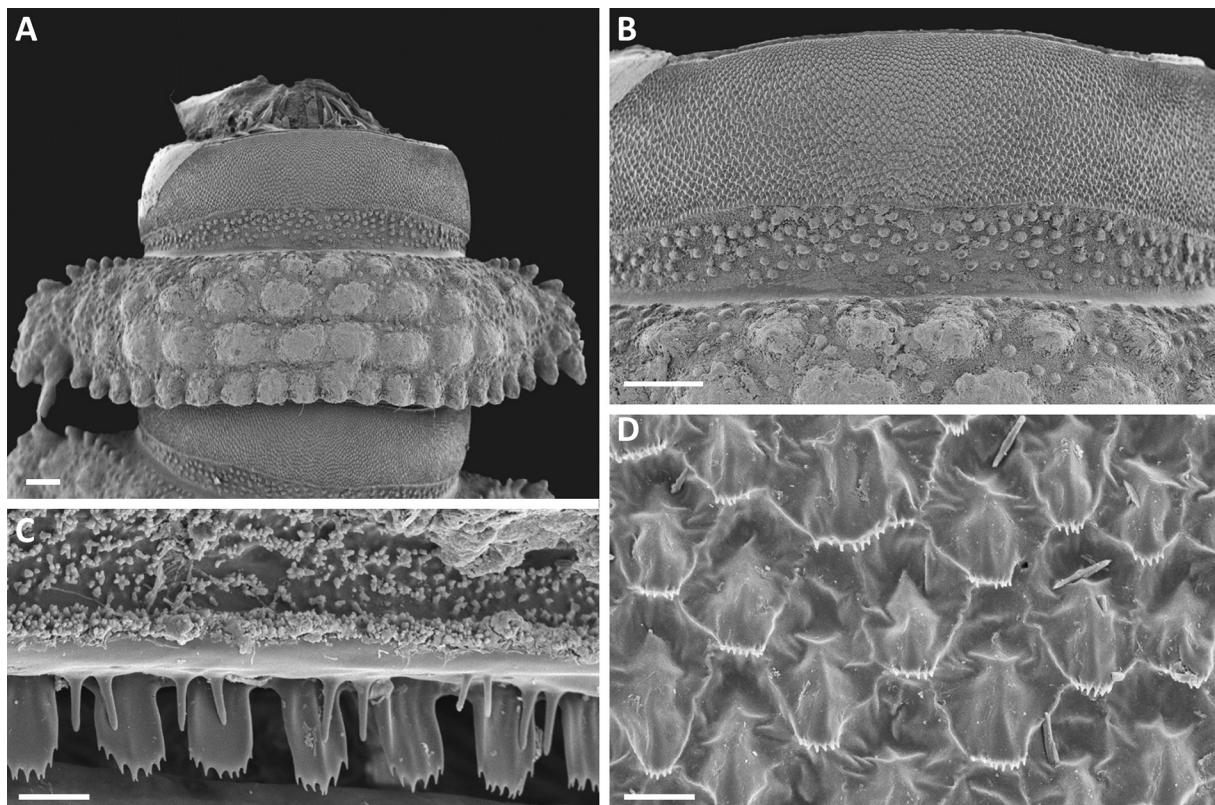


Fig. 18. *Thelydesmus dispar* Cook, 1896, ♀ (NHMD 621849) from Côte d’Ivoire, 12 km S of Lakota, 1965, V. Schiøtz leg. **A.** Ring 8, dorsal view. **B.** Ring 8, median part of prozona and anterior part of metazona. **C.** Ring 10, limbus. **D.** Ring 8, part of anterior $\frac{2}{3}$ of prozona. Scale bars: A–B = 0.2 mm; C–D = 0.01 mm.

suggests that females may have other than 18 podous rings, since only females with this ring number have an epigynal crest (Fig. 15C–D).

David & Geoffroy (2011) mentioned *Muyudesnus obliteratus* Kraus, 1960 (now placed in the genus *Poratia* Cook & Cook, 1894, family Pyrgodesmidae) as another example of intraspecific variation in ring number, but actually the two ‘morphs’ in this case are now regarded as representing different species (Golovatch & Sierwald 2000). The obvious question is, whether the variation described here for *E. enghoffi* might similarly be due to the existence of two or more species of *Elythesmus*. This may very well be the case, but the pattern of variation is rather complicated (see “remarks on variation” under *E. enghoffi*): 1) males with 17 and 18 podous rings exist at least in two mountain blocks, Udzungwa and Uluguru, 2) in the Udzungwas, males with 18 podous rings are known only from the NE part (Udzungwa Mountains National Park), 3) there is considerable size variation which seems in part to be correlated with altitude, 4) no variation in the gonopods could be observed. For the time being, all *Elythesmus* samples, except the few females from West Kilombero Scarp Forest Reserve (see above under ?*Elythesmus* sp.) are referred to *E. enghoffi*, but an in-depth analysis applying molecular methods might possibly change the picture.

Sex ratio and juveniles in samples

The vast majority of material for the present study was obtained by pitfall trapping. Pitfall traps catch animals that move actively and pitfall catches therefore show a bias towards more active life stages. It is in full agreement with this that the material of the two most abundant species show a very strong preponderance of adult males over adult females, and an even stronger preponderance of adults over juveniles. *Cryptocorypha geminiramus* sp. nov.: 159 adult ♂♂, 19 adult ♀♀, 3 subadult ♀♀, *Elythesmus enghoffi*: 124 adult ♂♂, 48 adult ♀♀, 10 subadults. These findings are in line with the general observation that adult millipedes are more active than juveniles and that male millipedes are more active than females. Examples of other studies on millipedes using pitfall trapping and showing ‘superabundance’ of adults, especially males, include Geoffroy & Célérier (1996) and Mesibov & Churchill (2003).

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