

Ontogeny of South African intertidal oribatid mite species (Acari, Oribatida, Ameronothroidea) and supplements to adult morphology.

Elizabeth A. Hugo-Coetzee ^{a,b}, Julia Baumann ^c, Jan-Andries Neethling ^a, Iris Bardel-Kahr^c, Tobias Pfingstl ^c

^a Terrestrial Invertebrate Department, National Museum, PO Box 266, Bloemfontein 9300, South Africa.

^b Department of Zoology and Entomology, University of the Free State, Bloemfontein, South Africa.

^c Institute of Biology, Karl-Franzens University of Graz, Universitaetsplatz 2, 8010 Graz, Austria.

Original research

ABSTRACT

Information about larva and nymphal stages as well as additional descriptions of adults of four littoral species of the families Fortuyniidae, Selenoribatidae and Podacaridae found around the coast of South Africa are provided. Juveniles of *Fortuynia elamellata micromorpha* are well in accordance with the morphology of other known juveniles of *Fortuynia*, but the larva of the former shows distinctly barbed rostral setae, a trait which lacks in all the other species. Adults of the South African *Selenoribates divergens* are similar in morphology to the Egyptian specimens, except for the presence of small rostral humps, anterior notogastral tubercles and the position of lyrifissure *ih*. These differences are presently considered to be only geographic variation. Juveniles of *Sel. divergens* can be easily distinguished from juveniles of other known *Selenoribates* species by the presence of a spinose clavate bothridial seta and branched notogastral setae in deuto- and tritonymph. Due to the loss of type specimens of *Schusteria ugraseni*, a neotype was designated. The juveniles of this species are very similar to those of *Schusteria littorea* and *Schusteria melanomerus*, but differ in amongst others the ano-adanal and leg setation. Adults of *Halozetes capensis* show strong variation in the length of dorsal setae and juveniles of this species differ significantly from others in the number of prodorsal and gastronomic porose sclerites. Finally, a table is provided listing all ameronothroid species with known juvenile stages.

Keywords development; nymphs; littoral; Fortuyniidae; Selenoribatidae; Podacaridae

Introduction

The marine intertidal oribatid mites of the superfamily Ameronothroidea are air-breathing animals living on the edge of the constant fluctuating cycle of low tide and high tide, of submersion and emersion and variable temperatures. Consequently, they have adapted to this environment in their morphology, behavior, reproduction, respiration and physiology (Bücking *et al.* 1998; Pfingstl 2013a, 2017). Ameronothroid mites live in the littoral zone in algae mats, rock crevices, on boulders, in barnacles and tubeworms, and man-made structures (Marshall and Pugh 2002; Pfingstl 2013a, 2017) or in estuaries and mangrove forests (Pfingstl *et al.* 2014). They feed mainly on algae, but also on lichens and cyanobacteria (Luxton 1966; Pugh and King 1985; Bücking *et al.* 1998; Pfingstl 2013a).

Ameronothroidea consists of four families namely, Ameronothridae, which occurs in the northern polar and cold temperate regions, the Podacaridae of the southern polar and cold

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Corresponding author

Elizabeth A. Hugo-Coetzee 
lhugo@nasmus.co.za

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temperate regions and the Fortuyniidae and Selenoribatidae of the subtropics and tropics (Procheş and Marshall 2001; Pfingstl and Schuster 2014; Pfingstl 2017; Norton and Franklin 2018). Four species from three families of Ameronothroidea have been recorded along the South African coast (Procheş and Marshall 2002; Pfingstl *et al.* 2021a). There was a record of a fifth species, namely *Ameronothrus bilineatus*, which was found in a salt marsh near Port Alfred (Weigmann 1975), but this occurrence was suggested to be introduced (Procheş and Marshall 2001) and since then there have been no further records of this species. However, the distribution of the four native species follows the general trend where Fortuyniidae and Selenoribatidae are limited to the subtropical regions of the east coast and the Podacaridae to the warm- to cold-temperate regions of the south coast (Procheş and Marshall 2002; Pfingstl 2016; Pfingstl *et al.* 2021a). *Fortuynia elamellata micromorpha* Marshall & Pugh, 2002 (Fortuyniidae) and *Schusteria ugraseni* Marshall & Pugh, 2000 (Selenoribatidae), were described from samples of 1998 and 1999 from barnacles, oyster shells and shale deposits on the mid- to upper rocky shores from Park Rynie, KwaZulu-Natal on the east coast of South Africa; *Selenoribates divergens* Pfingstl, 2015c (Selenoribatidae) was originally described from Egypt, and therefore the occurrence of this species along the sub-tropical east coast of South Africa (Pfingstl *et al.* 2021a) needs further investigation. Procheş and Marshall (2002) reported a *Schusteria* species (*Schusteria* sp. 2), from St. Lucia, which may refer to *Sel. divergens*, however since that material is lost, and the exact sample location unknown, the identity is assumed, but not confirmed. *Halozetes capensis* Coetzee & Marshall, 2003 (Podacaridae) was described from samples taken in November 2000 from finely-branched algae in the mid- and upper eulittoral zone from Kommetjie on the south-western coast and Nature's Valley on the southern coast. The *Halozetes* sp. reported in Procheş and Marshall (2002) supposedly refers to *H. capensis*. The descriptions of the adults of these species were sufficient, only omitting information or drawings of legs and the gnathosoma in some species. With the exception of the tritonymph of *H. capensis*, the juveniles of these species are unknown.

The description of oribatid juvenile morphology is often neglected. This can be attributed to several reasons such as the difficulty in associating juveniles with the adult in samples or museum collections (this association is even more difficult in high diversity groups such as the Oppioidea or Oripodoidea), or the small size and cryptic or endophagous behavior of juveniles (Norton and Ermilov 2014). Despite the scarcity of information of juveniles, it is an important aspect contributing to knowledge of ecology, systematic and phylogeny and even to homology and applications of nomenclature with regard to body and leg setation (Norton 1977; Norton and Ermilov 2014; Zhang 2018). Interestingly, juveniles of mites associated with aquatic and semi-aquatic or intertidal environments are the best known among the brachypylina oribatids, with juveniles of more than half of the Ameronothroidea known or partly known. Possible reasons include the medium to large size of species, the distinctive setae or sclerites on the juveniles (Norton and Ermilov 2014), excellent historic studies so that the general habitus of juveniles of these mites are well known (e.g., Grandjean 1955, 1966, 1968; Hammen 1963; Schuster 1963; Luxton 1967; Behan-Pelletier 1997) and the recent interest in littoral mites. Adults and juveniles of littoral mites are also often collected together because of their aggregation behavior facilitating the adult-juvenile association (Bücking *et al.* 1998; Krisper and Schuster 2008; Pfingstl 2013a). Currently, information of juvenile morphology is known for 69% of Fortuyniidae, 37% of Selenoribatidae, 59% of Podacaridae and 63% of Ameronothridae species (see Appendix 1).

During a comprehensive project examining the biodiversity and distribution of intertidal mites along the South African coast, juvenile stages of all four species were collected. The main aim of the paper is to give supplementary descriptions of the adults and descriptions of all juvenile stages of *F. elamellata micromorpha*, *Sel. divergens*, *Sch. ugraseni* and *H. capensis* and to compare the juveniles with other known juveniles of the respective genus.

Material and methods

Sample collection

This study forms part of a larger study in which samples were taken at different locations along the coastline of South Africa (Pfingstl *et al.* 2021a). Fresh specimens for this study originated from Sheffield Beach, Umkomaas, Umdloti, St. Lucia (all KwaZulu-Natal), East London (Eastern Cape) and Nature's Valley (Western Cape) sampled in 2019 and 2020. In addition, previously collected specimens of *F. e. micromorpha* (collected in 1998-1999) and *H. capensis* (2000), housed at the National Museum, Bloemfontein, were used (these included holotypes, paratypes and juveniles). Localities and sample details are given in the respective species descriptions under: Material examined. Samples (app. 10 cm³) of littoral algae, barnacle and mussel shells were scraped off rocks with a knife or a small shovel and then put in Berlese-Tullgren funnels for 12 to 24 hours to extract mites. Most mites extract within 24 hours from these rather small samples with rare occurrences after this extraction time. Specimens were collected alive in small plastic containers with plaster of Paris, sorted with a fine brush and preserved in ethanol (100%) for morphological investigation. Juveniles were assigned to a specific species only if adults of a single species were contained in the respective sample. Specimens are stored in the Acarology collection of the National Museum, Bloemfontein, South Africa (abbreviated as NMB) and in the collection of the Senckenberg Museum für Naturkunde Görlitz.

Preparation and visual documentation

Specimens were mounted in lactic acid on temporary cavity slides for measurement and illustration. Body length was measured in lateral view, from the tip of the rostrum to the posterior edge of the notogaster. Notogastral width refers to the maximum width in dorsal view. Lengths of body setae were measured in the aspect they could be best observed. All body measurements are presented in micrometers. In most instances the range of sizes are given, but for body measurements the range is given followed by the mean in brackets. Drawings were made with a camera lucida using a Nikon transmission light microscope "Nikon Eclipse 50i". Drawings were made with software CorelDraw 2021. For photographic documentation, specimens were air-dried and photographed with a Keyence VHX-5000 digital microscope using automated image stacking.

Morphological terminology used in this paper follows Grandjean (1966, 1968) and Norton and Behan-Pelletier (2009); Norton (1977) for setal nomenclature; Norton and Franklin (2018) for notation of epimeral setae (e.g. Remark 15, setae are named according to their relative position and not to their ontogenetic appearance).

Abbreviations

The following abbreviations are used in the text, figures and tables: prodorsum: *ro*, *le*, *in*, *bs*, *ex* - rostral, lamellar, interlamellar, bothridial and exobothridial setae, respectively; notogaster: *c*, *da*, *dm*, *dp*, *la*, *lm*, *lp*, *h*, *p* - notogastral setae; *ia*, *im*, *ip*, *ih*, *ips* - lyrifissures; *gla* - opisthonotal gland opening; gnathosoma: *a*, *m*, *h* - subcapitular setae; *cha*, *chb* - cheliceral setae, *Tg* - Trägårdh's organ; epimeral and lateral podosomal regions: *1a*, *1b*, *1c*, *2a*, *3a*, *3b*, *3c*, *4a*, *4b* - epimeral setae; *PdI*, *PdII* - pedotecta I and II respectively; *ce*, *ci* - prodorsal canals of van der Hammen's organ; *dis* - discidium; *Cl* - Claparède's organ; *s₁*, *s₂* - enanthiophyses; anogenital region: *g*, *ag*, *an*, *ad* - genital, aggenital, anal, and adanal setae, respectively; *iad* - adanal lyrifissure; β - tendon β ; legs: *Tr*, *Fe*, *Ge*, *Ti*, *Ta* - leg trochanter, femur, genu, tibia, and tarsus, respectively; *pa* - leg porose area; ω , σ , ϕ - leg solenidia; ϵ - leg famulus; *d*, *l*, *v*, *ev*, *bv*, *ft*, *tc*, *it*, *p*, *u*, *a*, *s*, *pv*, *pl* - leg setae.

Results

Family Fortuyniidae Hammen, 1963

Genus *Fortuynia* Hammen, 1960

Fortuynia elamellata Luxton, 1967

Fortuynia elamellata micromorpha Marshall & Pugh, 2002

Adults

Measurements: females (n=2) length 399-414 (407), width 202-218 (210), males (n=5) length 392-408 (399), width 201-220 (211); holotype (female) length 397, width 190, paratypes (females) (n=3) length 398-408 (403), width 202-209 (206); body sizes in range of the specimens of the original description, females (n=7) length 380-404, width 206-215.

Integument (Figures 1 and 2): brown to dark brown, genital plate slightly darker, legs with slight darkening of proximal part of tarsi, distal part of tibiae, distal two thirds of femora and entire genua and trochanters; body surface finely punctate, lighter areas around insertions of notogastral setae; granulate in acetabular regions; chelicerae punctate.

Prodorsum (Figures 1A, C): rostrum broadly rounded, slightly flattened apex in dorsal view; no lamellar ridges; *ro* (35-41), *le* (26-35), smooth, *in*, *ex* represented by alveoli; *bs* (30-36) smooth, medially incurving, with clavate head; bothridium cup-like; transverse line developed posterior to insertion of alveoli of *ro*.

Gnathosoma (Figure 2E): Setae *a*, *m*, *h* thin, smooth; pedipalp setation 0-2-1-3-9(+ ω), ω on tarsus erect, not associated with eupathidium *acm*; femur with large porose area; chelicera with teeth, smooth seta *chb* shorter than barbed seta *cha*.

Notogaster (Figures 1A, C): elongate oval in dorsal view; lenticulus anteriorly with irregular border; 14 pairs of smooth, setiform notogastral setae, relatively long, *h*₂ longest, *c*₂, *p*₃ shortest (*c*₁ 60-73, *c*₂ 32-40, *da*, *dm*, *dp* 47-67, *la*, *lm*, *lp* 43-70, *h*₁ 35-50, *h*₂ 81-104, *h*₃ 50-67, *p*₁ 58-85, *p*₂ 34-53, *p*₃ 30-37), *c*₃ absent; five pairs of distinct lyrifissures present, *ia* postero-lateral to *c*₂, *im* between *lm* and *lp*, *ih* far lateral to *h*₃, *ip* and *ips* lateral to *p*₂; *gla* lateral to *im*.

Lateral aspect (Figure 1C): *PdI* round, small; cuticular canals of van der Hammen's organ present, canal *ce* very short, reaching posterior border of bothridium, canal *ci* absent.

Ventral (Figures 1B, C): all epimeral setae setiform, smooth, setation 3-1-3-2, seta *1b* (22-32) slightly longer than others (13-23); discidium rounded; five pairs of genital (*g*₁ 19-23, *g*₂₋₅ 16-19), one pair of aggenital (*ag* 15-19), two pairs of anal (*an*₁ 26-35, *an*₂ 20-31) and three pairs of adanal (*ad*₁ 40-54, *ad*₂ 27-36, *ad*₃ 22-27) setae thin, smooth; lyrifissure *iad* medially to *ad*₂, slightly obliquely orientated; anal plates slightly triangular (length 81-86, width 29-33), preanal organ triangular; genital plates trapezoid, large (length 65-80, width 38-49, no distinct difference in size between males and females but plates in females by trend slightly larger).

Legs (Figures 2A-D): monodactylous, long hook-like claws with small teeth dorsally; porose areas *pa* on Fe I-IV and Tr III, IV distinct; tarsi with proximal lyrifissure; famulus short, straight, weakly blunt-ended; all solenidia long, setiform; for leg setation and solenidia see Table 1.

Juvenile stages

Common features – apherodermous; dark brown in colour, integument plicate and soft except for the more sclerotised centrodorsal plate, median posterior of centrodorsal plate with a less sclerotised area forming a narrow inverted 'v' (except in larva where the plate is uniform in sclerotisation); body finely granulate, with more distinct granulation around insertions of dorsal gastronal setae and in furrows and acetabular regions, granulation on prodorsum more distinct in the larva and deutonymph; prodorsum triangular, hysterosoma oval in dorsal view; rostrum broadly rounded; *le* setiform, short, smooth, *in* represented by alveoli; bothridia small, cup-like, *bs* with short stalk and smooth head clavate in lateral view, globose in dorsal view; ventral side with specific pattern of folds i.e., folds between epimeres 2 and 3, anterior and posterior of

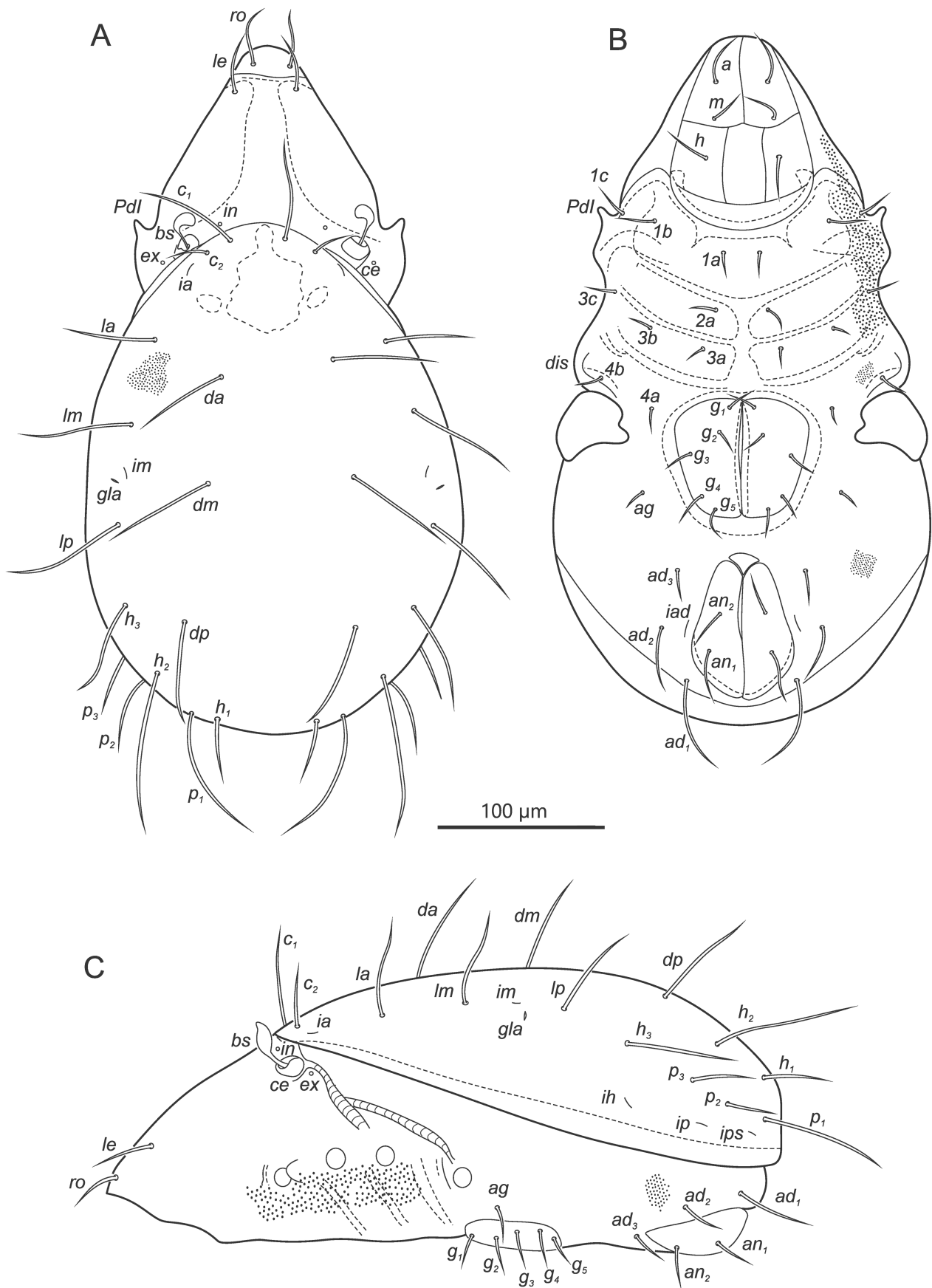


Figure 1 *Fortuynia elamellata micromorpha* Marshall & Pugh, 2002, Sheffield Beach. Adult. A. dorsal view (legs omitted), B. ventral view (only trochanter IV shown), C. lateral view (legs and epimeral setae omitted).

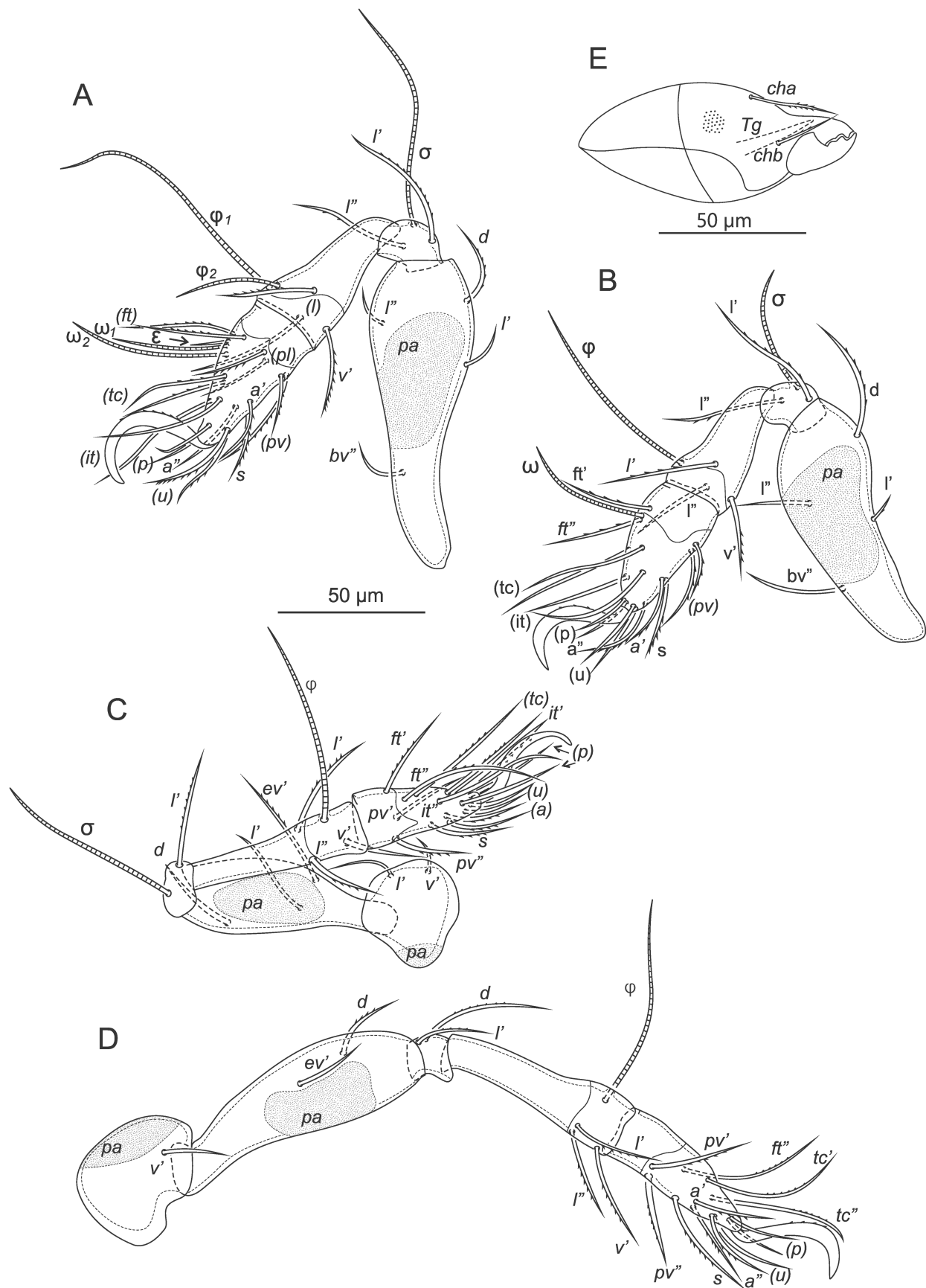


Figure 2 *Fortuynia elamellata micromorpha* Marshall & Pugh, 2002, Sheffield Beach. Adult legs A. leg I, right, paraxial view, B. leg II, right, paraxial view, C. leg III, left, paraxial view, D. leg IV, left, antiaxial view, E. chelicera.

genital area and lateral to anal orifice, with pores within these folds leading into tracheal tubes; legs monodactylous with large hook like claws, with small teeth dorsally; porose areas on legs as in adults; for leg setation and solenidia see Table 1.

Larva – (Figures 3A, B) (n=7) length: 175-224 (201), width: 103-139 (118).

Gastronotic region: *ro* setiform, short, barbed, *ex* minute; 11 pairs of gastronotal setae (*c*₁₋₃, *da*, *dm*, *dp*, *la*, *lm*, *lp*, *h*₁₋₂) setiform, barbed, except smooth seta *h*₂; *h*₂ lateral to anal folds on ventral side.

Ventral region of idiosoma: epimeral setation 2-1-2 (*la*, *lb*, *2a*, *3a*, *3b*), setiform, smooth, small; Claparède's organ present, no protective seta observed.

Protonymph – (Figures 3C, D) (n=9) length 234-273 (255), width 112-147 (131).

Gastronotic region: *ro* setiform, smooth, curved, *ex* represented by alveolus; 15 pairs of gastronotal setae (*h*₃, *p*₁₋₃ added), setiform, finely barbed (except *p*₂₋₃ smooth), *p*₂₋₃ lateral to anal opening; seta *c*₁ longer than other setae.

Ventral region of idiosoma: epimeral setation: 3-1-2-1 (*lc*, *4b* added), setae setiform, short, one pair of short genital setae; cupule *ip* anterior to anal valves distinct.

Deutonymph – (Figures 4A, B) (n=13) length 291-327 (313), width 134-176 (157).

Gastronotic region: *ro* setiform, smooth, *ex* represented by alveolus; 15 pairs of setiform, roughened gastronotal setae, except *p*₂₋₃ smooth, *p*₂₋₃ lateral to posterior part of anal folds, *h*₂ longest.

Ventral region of idiosoma: epimeral setation: 3-1-2-2 (*4a* added); two pairs of short genital setae, one pair of aggenital setae, three pairs adanal setae lateral to anal opening, *ad*₁ longest, two vestigial pairs of anal setae; cupule *iad* anterior to anal opening.

Tritonymph – (Figures 4C, D, supplementary figure 1) (n=4) length 381-400 (391) width 177-215 (198).

Gastronotic region: *ro* setiform, smooth, *ex* represented by alveolus; 15 pairs of setiform, smooth gastronotal setae, *c*₁, *h*₂ longest, *p*₂₋₃ ventrally, distanced from anal orifice.

Table 1 *Fortuynia elamellata micromorpha* Marshall & Pugh, 2002. Chaetome and solenidia from larva to adult. First development of setae and their homologies indicated by letters. () pairs of setae, - no change with regard to preceding stage.

	Instars	Trochanter	Femur	Genu	Tibia	Tarsus	Chaetome	Solenidia
Leg I	Larva	-	<i>d</i> , <i>bv</i> ''	(<i>l</i>), σ	(<i>l</i>), v' , φ_1	(<i>pl</i>), (<i>pv</i>), <i>s</i> , (<i>a</i>), (<i>u</i>), (<i>p</i>), (<i>tc</i>), (<i>ft</i>), ε , ω_1	0-2-2-3-16	1-1-1
	Protonymph	-	-	-	-	ω_2	0-2-2-3-16	1-1-2
	Deutonymph	-	<i>l</i> '	-	φ_2	-	0-3-2-3-16	1-2-2
	Tritonymph	-	<i>l</i> ''	-	-	(<i>it</i>)	0-4-2-3-18	1-2-2
	Adult	<i>l</i> '	-	-	-	-	1-4-2-3-18	1-2-2
Leg II	Larva	-	<i>d</i> , <i>bv</i> '	(<i>l</i>), σ	<i>l</i> ', v' , φ	(<i>pv</i>), <i>s</i> , (<i>a</i>), (<i>u</i>), (<i>p</i>), (<i>tc</i>), (<i>ft</i>), ω	0-2-2-2-13	1-1-1
	Protonymph	-	-	-	-	-	0-2-2-2-13	1-1-1
	Deutonymph	-	(<i>l</i>)	-	-	-	0-4-2-2-13	1-1-1
	Tritonymph	-	-	-	-	(<i>it</i>)	0-4-2-2-15	1-1-1
	Adult	<i>l</i> '	-	-	<i>l</i> ''	-	1-4-2-3-15	1-1-1
Leg III	Larva	-	<i>d</i> , <i>ev</i> '	<i>l</i> ', σ	v' , φ	(<i>pv</i>), <i>s</i> , (<i>a</i>), (<i>u</i>), (<i>p</i>), (<i>tc</i>), (<i>ft</i>)	0-2-1-1-13	1-1-0
	Protonymph	-	-	-	-	-	0-2-1-1-13	1-1-0
	Deutonymph	v'	-	-	-	-	1-2-1-1-13	1-1-0
	Tritonymph	-	<i>l</i> '	-	<i>l</i> '	(<i>it</i>)	1-3-1-2-15	1-1-0
	Adult	<i>l</i> '	-	-	<i>l</i> ''	-	2-3-1-3-15	1-1-0
Leg IV	Protonymph	-	-	-	-	(<i>pv</i>), (<i>u</i>), (<i>p</i>), <i>ft</i> ''	0-0-0-0-7	0-0-0
	Deutonymph	-	<i>d</i> , <i>ev</i> '	<i>d</i> , <i>l</i> '	v' , φ	<i>s</i> , (<i>a</i>), (<i>tc</i>)	0-2-2-1-12	0-1-0
	Tritonymph	v'	-	-	<i>l</i> '	-	1-2-2-2-12	0-1-0
	Adult	-	-	-	<i>l</i> ''	-	1-2-2-3-12	0-1-0

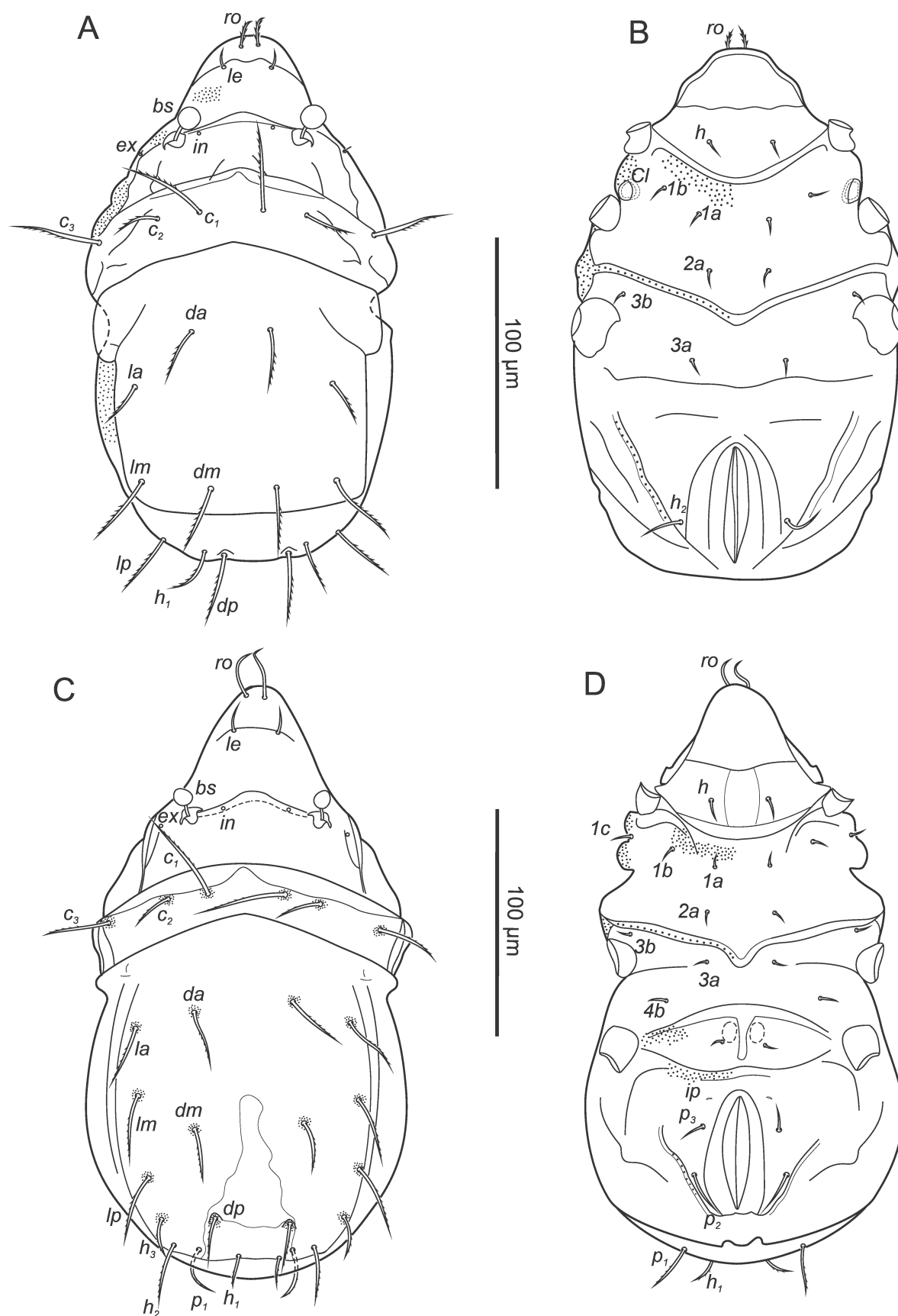


Figure 3 *Fortuynia elamellata micromorpha* Marshall & Pugh, 2002, Sheffield Beach, A. larva, dorsal view, B. larva, ventral view, C. protonymph, dorsal view, D. protonymph, ventral view.

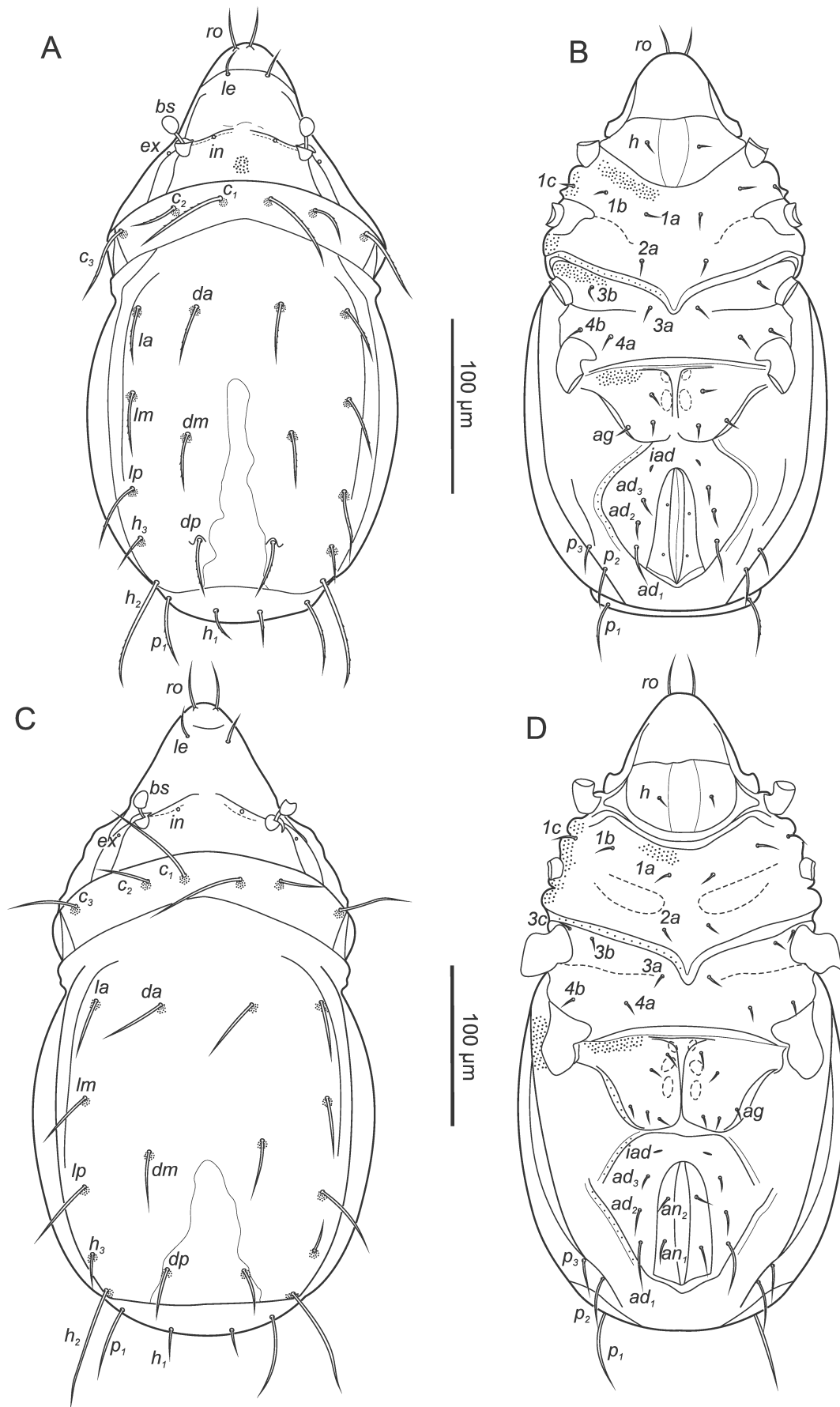


Figure 4 *Fortuynia elamellata micromorpha* Marshall & Pugh, 2002, Sheffield Beach, A. deutonymph, dorsal view, B. deutonymph, ventral view, C. tritonymph, dorsal view, D. tritonymph, ventral view.

Ventral region of idiosoma: Epimeral setation: 3-1-3-2 (3c added), four pairs of setiform genital, one pair of aggenital, three pairs of adanal, two pairs of anal setae; cupule *iad* anterior to anal valves.

Material examined

Holotype (NMB 4734.1.1) and three paratypes (NMB 4734.1.2) from Park Rynie, KwaZulu-Natal, South Africa, 30°21'S, 30°43'E, from barnacles, oyster shells and shale deposits, mid to upper rocky shore, 1998-1999, collected by D.J. Marshall and K. Ugrasen (in the original description the holotype should have been deposited elsewhere, but was instead recently sent to NMB); six adults, four larvae, seven protonymphs, six deutonymphs, one tritonymph from Sheffield Beach, KwaZulu-Natal, South Africa, 29°29.737'S, 32°15.127'E, from *Bostrychia* sp. algae from rock, upper eulittoral zone, 27 Feb. 2020, collected by T. Pfingstl (NMB 4717.1); one adult, one larva, four deutonymphs, two tritonymphs from Umkomaas, KwaZulu-Natal, 30°12.672'S, 30°48.00'E, from *Gelidum* sp. algae from tubeworms and rock in the lower eulittoral zone, 02 Mar. 2020, collected by T. Pfingstl (NMB 4720.1, NMB 4721.1); two larvae, two protonymphs, three deutonymphs and one tritonymph from Umdloti, KwaZulu-Natal, 29°40.560'S, 31°6.957'E, from *Gelidum* sp. algae on rock, barnacles, mussels, lower to median eulittoral zone, 29 Feb. 2020, collected by T. Pfingstl (NMB 4719.2).

Remarks

The original description of the adult by Marshall and Pugh (2002) provides good morphological information and the drawings are detailed, but there are no drawings of the lateral side of the body or the legs. Also, canal *ce* is present, but *ci* is absent, whereas the authors stated both are absent. The adults of the other locations match the adults of Park Rynie of the original description.

Some or all juvenile stages of several species of *Fortuynia* are known, namely *F. arabica* Bayartogtokh *et al.*, 2009, *F. atlantica* Krisper & Schuster, 2008, *F. churaumi* Pfingstl *et al.*, 2019, *F. dimorpha* Pfingstl, 2015, *F. elamellata elamellata* Luxton, 1967, *F. maledivensis* Pfingstl, 2015, *F. longiseta* Pfingstl, 2015, *F. rotunda* Marshall & Pugh, 2002, *F. shibai* Aoki, 1974, *F. smiti* Ermilov *et al.*, 2013, *F. taiwanica* Bayartogtokh *et al.*, 2009 and *F. yunkerii* Hammen, 1963 (see Appendix 1).

The morphology of most *Fortuynia* juveniles is similar in habitus and development of setation, except for the juveniles of *F. arabica* and *F. taiwanica* (Bayartogtokh *et al.* 2009), which may be attributed to several factors (see Pfingstl *et al.* 2021b). For the other 10 species, the main differences lie in the length and morphology of setae (Pfingstl and Schuster 2012a) and other minor characteristics such as ontogeny of certain leg setae, especially on the femora. One characteristic of the larva of *F. elamellata micromorpha* that is distinctly different is the strongly barbed rostral setae. The juveniles of *F. elamellata elamellata* are not very well described (Luxton 1967), but in general terms, besides the larger sizes they seem to be similar to *F. elamellata micromorpha*. The only difference is in the placement of the lamellar setae in the larva which is very close together in the nominate species and further from each other in the subspecies. However, only one badly damaged larva specimen was used for the description of *F. elamellata elamellata*.

Family: Selenoribatidae

Genus: *Selenoribates* Strenzke, 1961

Selenoribates divergens Pfingstl, 2015

Adult

Measurements: females (n=2): length 285-293 (289), width 157-175 (166), males (n=8): length 269-284 (279), width 162-174 (166); measurements in the original description of specimens from Egypt within range of South African specimens, mean length 273, mean width 164.

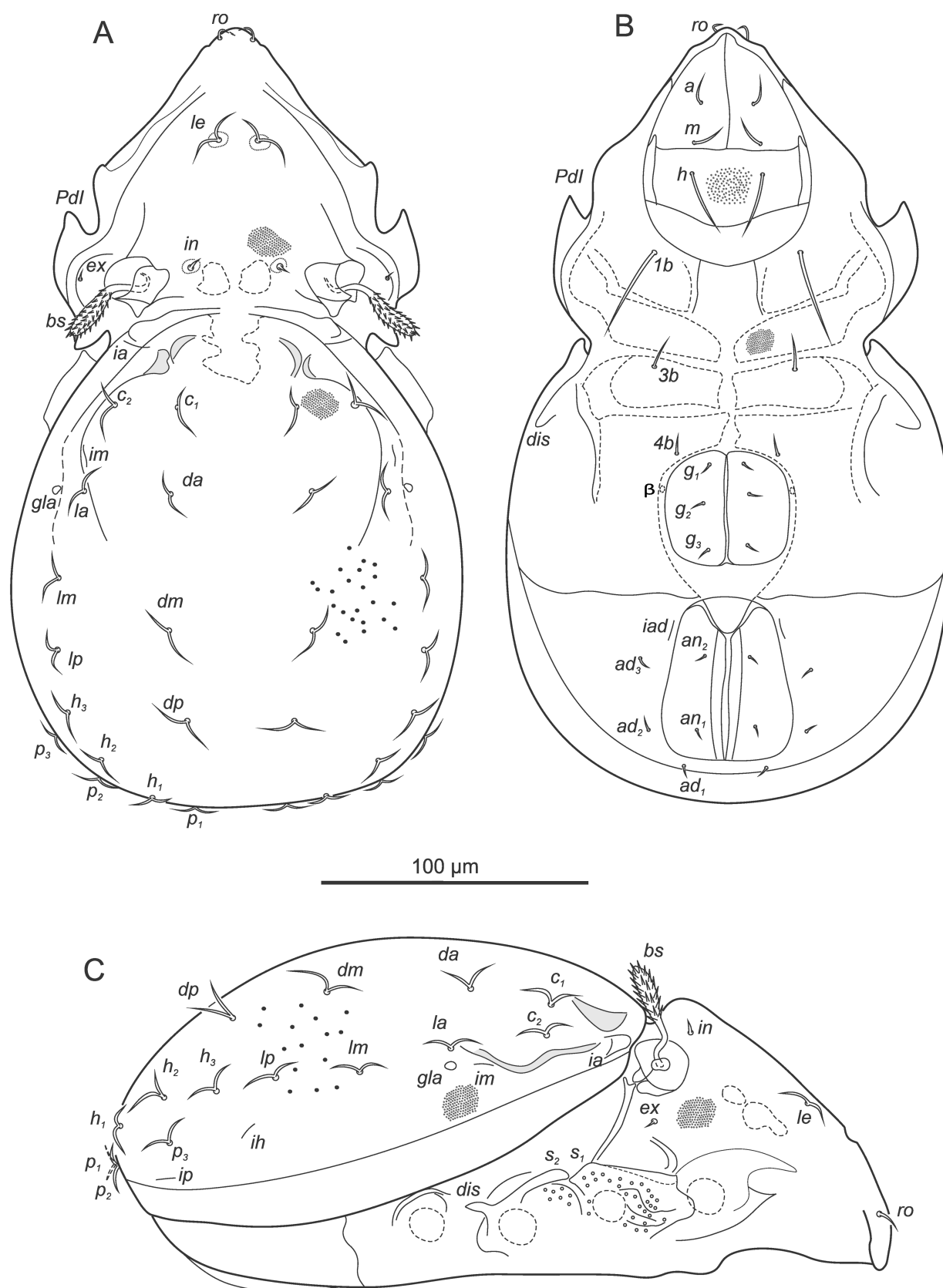


Figure 5 *Selenoribates divergens* Pfingstl, 2015. Adult. A. dorsal view (legs omitted), B. ventral view (legs omitted), C. lateral view (legs and ventral setae omitted).

Integument (Figure 5): brown in colour, antero-medial notogaster with lighter area, ventrally area posterior to genital plates darker than anterior to this area, genital and anal plates same colour as this posterior area, trochanters III and IV of legs darker than rest of legs; body densely granulate, larger granules irregularly sparsely distributed, denser bigger granules in acetabular region, legs with small dense granules.

Prodorsum (Figures 5A, C): rostrum with small lateral humps and rounded median apex; lamellar ridge absent; short line extending from bothridium anteriorly; *ro* (8-9), *in*, *ex* (3-4) short, simple, *le* branched in two sub-equal parts (10-16); bothridium large cups opening laterally, with postbothridial tubercle; *bs* with medium long stem and clavate, spinose head (30-41).

Gnathosoma: same as in Pfingstl (2015c).

Notogaster (Figures 5A, C): oval in dorsal view; dorsosejugal furrow incomplete; tubercle present antero-laterally, posterior to bothridial tubercle; two x-shaped ridges antero-laterally, slightly anterior of seta *c*₁; 14 pairs of notogastral setae (*c*₁₋₂, *da*, *dm*, *dp*, *la*, *lm*, *lp*, *h*₁₋₃, *p*₁₋₃), branched basally, branches sub-equal in length (10-20), *c*₃ absent; five pairs of lyrifissures distinct: *ia* in humeral region, *im* anterior to *la*, *ih* lateral to *lp* and *h*₃, *ip* lateral to *p*₃ close to lateroventral border of notogastral plate, *ips* laterally to *p*₂ and *p*₃; *gla* lateral to *la*.

Lateral aspect (Figure 5C): *PdI* directed anteriorly, rounded; discidium pointed; laterosejugal furrow developed as a groove, extending from *s*₁ to bothridium; enantiophyses (*s*₁, *s*₂) present as strong opposite triangular projections.

Ventral region (Figure 5B): median sternal cavity on epimeron I demarcated by a ridge; all setae smooth, simple; epimeral setation 1-0-1-1, seta *lb* very long (33-38) > *3b* (12-14) > *4b* (7-9); three pairs of genital (5-7), two pairs of anal and three pairs of adanal setae (6-9); genital plate (length 32-40, width 19-23) and anal plate (length 56-63, width 20-24) large; pre-anal organ triangularly rounded in ventral view; lyrifissure *iad* parallel and adjacent to anterior lateral border of anal plate.

Legs: see drawings in Pfingstl (2015c); monodactylous, long hook-like claws with proximo-ventral tooth; femora with ventral carinae; porose areas absent; solenidion ϕ_1 on Ti I long, but not necessarily curving backwards; for setation and solenidia see Table 2.

Juvenile stages

Common features – apherodermous; light brown in colour, integument strongly plicate and soft, except for the more sclerotised centrodorsal plate; body finely granulate (less distinct in larva), with more distinct granulation in the acetabular regions; prodorsum triangular, hysterosoma oval in dorsal view; rostrum with weak lateral humps and rounded apex; *le*, *ro* setiform, short, smooth, simple; *in* and *ex* very short; bothridia small, cup-like, *bs* with medium stalk and clavate spinose head; plicate centrodorsal shield bearing central dorsal setae, *da*, *dm*, *dp* on small apophyses; no cupules discernable; folds lateral to anal orifice; epimeral seta *lb* very long; legs monodactylous with hook like claws, small tooth proximo-ventrally on each claw; leg porose areas not visible; for leg setation and solenidia see Table 2.

Larva – (Figures 6A, B) (n=1) length: 170, width: 109.

Gastronotic region: 11 pairs of simple gastronotal setae (*c*₁₋₃, *da*, *dm*, *dp*, *la*, *lm*, *lp*, *h*₁₋₂), setae *da*, *dm*, *dp* setiform, thickened, barbed, setae *h*₁, *h*₂ slightly thickened, other setae thin setiform, smooth; *h*₂ lateral to anal folds on ventral side.

Ventral region of idiosoma: epimeral setation 1-0-1-0 (*lb*, *3b*), setiform, smooth, *3b* short; Claperède's organ present, not covered by protective seta.

Protonymph – (Figures 6C, D) (n=9) length 163-199 (178), width 87-108 (100).

Gastronotic region: 15 pairs of simple gastronotal setae (*h*₃, *p*₁₋₃ added), setiform, smooth, seta *h*₂ of similar length as setae *da*, *dm*, *dp*; *p*₂₋₃ lateral to anal folds.

Ventral region of idiosoma: Epimeral setation: 1-0-1-0, seta setiform; one pair of short genital setae.

Deutonymph – (Figures 7A, B) (n=1) length 235, width 138.

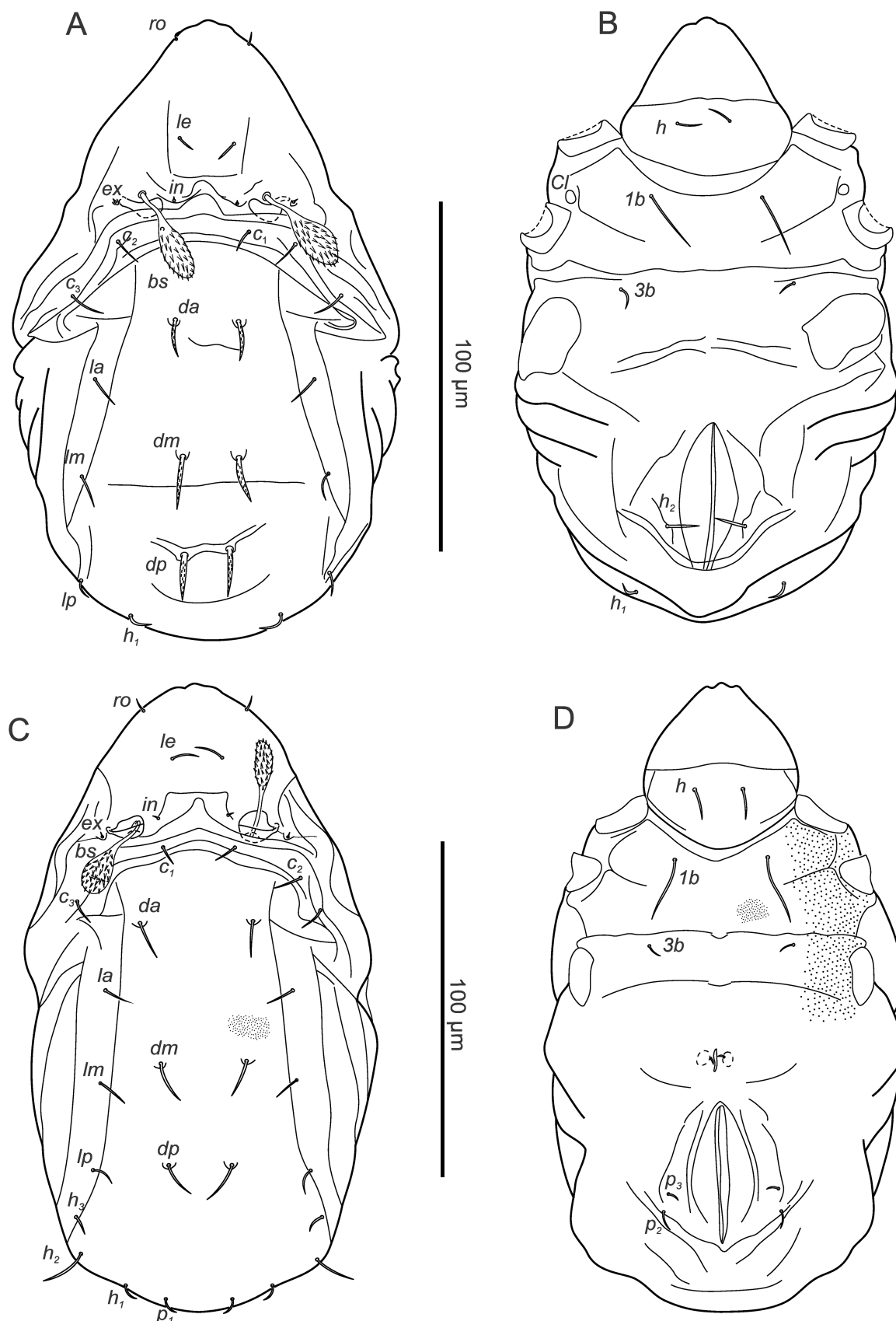


Figure 6 *Selenoribates divergens* Pfingstl, 2015. A. larva, dorsal view, B. larva, ventral view, C. protonymph, dorsal view, D. protonymph, ventral view.

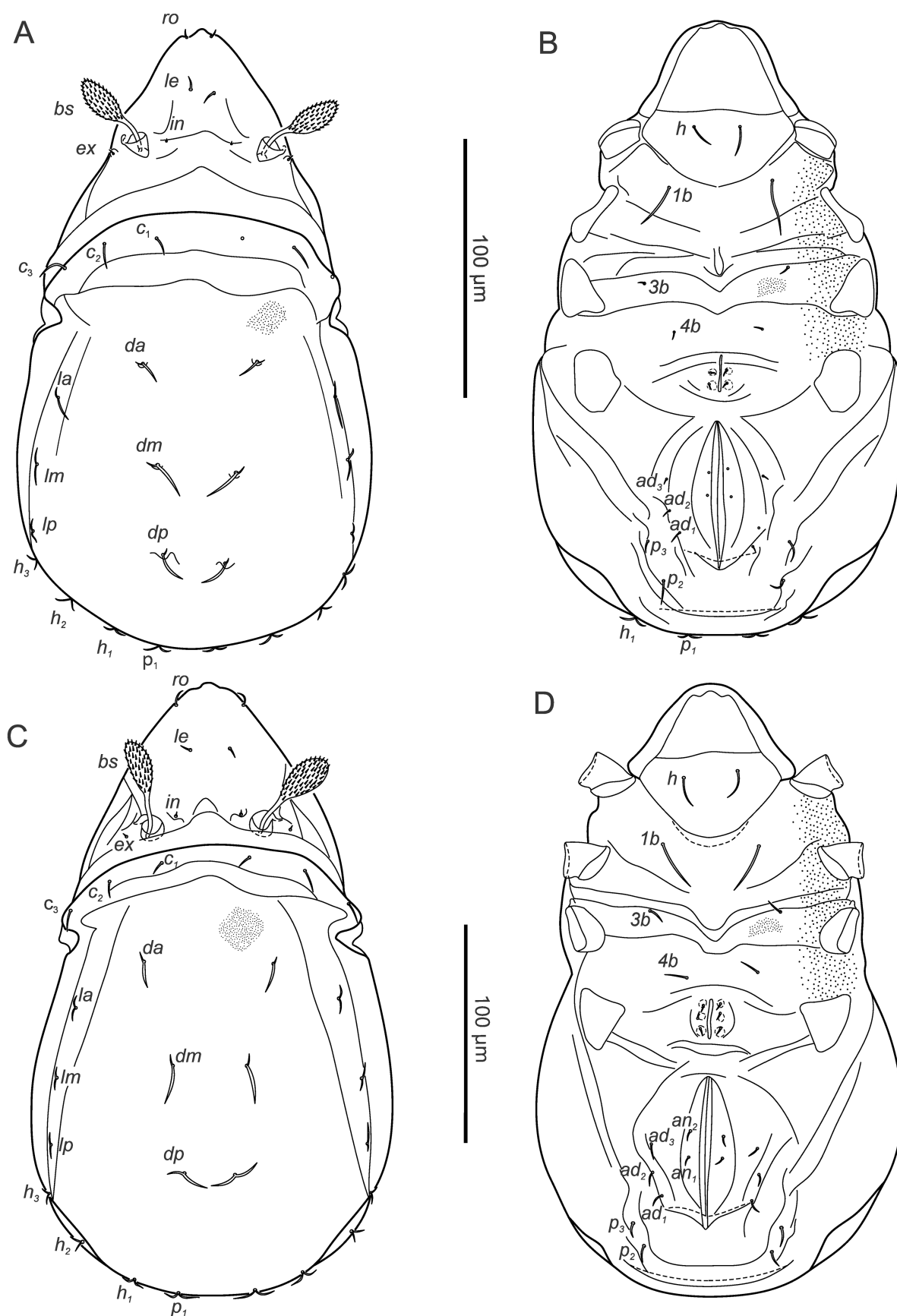


Figure 7 *Selenoribates divergens* Pfingstl, 2015. A. deutonymph, dorsal view, B. deutonymph, ventral view, C. tritonymph, dorsal view, D. tritonymph, ventral view.

Gastronotic region: 15 pairs of gastronotal setae, smooth, setae *da*, *dm*, *dp* branched with one small and one larger branch, setae *la*, *lm*, *lp*, *h*₁₋₃, *p*₁ branched into sub- equal branches, setae *c*₁₋₃, *p*₂₋₃ simple setiform, *p*₂₋₃ ventrally, posterior to anal folds.

Ventral region of idiosoma: epimeral setation: 1-0-1-1 (*4b* added); two pairs of short genital setae, three pairs of short setiform adanal setae lateral to anal valves, two vestigial pairs of anal setae.

Tritonymph – (Figures 7C, D, supplementary figure 2) (n=8) length 245-268 (257), width 139-159 (148).

Gastronotic region: 15 pairs of gastronotal setae (as in deutonymph).

Ventral region of idiosoma: epimeral setation as in deutonymph; three pairs of setiform genital, three pairs of adanal, two pairs of anal setae.

Material examined

Ten adults and 19 juveniles from Mission Rocks, iSimangaliso Wetland Park, St. Lucia, KwaZulu-Natal, South Africa, 28°16.708'S, 32°29.143'E, from *Bostrychia* sp. algae, median eulittoral zone, 3 Mar. 2020, collected by T. Pfingstl (NMB 2722.1).

Remarks

The original description of this species with material from Egypt provides very good morphological information and drawings of all aspects including the legs (Pfingstl 2015c). The South African specimens are similar in morphology to the Egyptian specimens, except for the presence of small lateral humps on the rostrum, the small tubercle antero-laterally on the notogaster and lyrifissure *ih* not located on the lateroventral border of the notogaster. Considering the large geographic distance between Egypt and South Africa, there is a possibility that these differences are indicative of a closely related but genetically distinct new species. However, the differences are very subtle and could also be a result of geographic variation. Without genetic

Table 2 *Selenoribates divergens* Pfingstl, 2015. Chaetome and solenidia from larva to adult. First development of setae and their homologies indicated by letters. () pairs of setae, - no change with regard to preceding stage.

	Instars	Trochanter	Femur	Genu	Tibia	Tarsus	Chaetome	Solenidia
Leg I	Larva	-	<i>d</i> , <i>bv</i> ''	(<i>l</i>), σ	<i>l</i> ', <i>v</i> ', φ ₁	(<i>pl</i>), (<i>pv</i>), <i>s</i> , (<i>a</i>), (<i>u</i>), (<i>p</i>), (<i>tc</i>), (<i>ft</i>), ε , ω ₁	0-2-2-2-16	1-1-1
	Protonymph	-	<i>l</i> '	-	<i>l</i> ''	ω ₂	0-3-2-3-16	1-1-2
	Deutonymph	-	-	-	φ ₂	-	0-3-2-3-16	1-2-2
	Tritonymph	-	-	-	-	(<i>it</i>)	0-3-2-3-18	1-2-2
	Adult	-	-	-	-	-	0-3-2-3-18	1-2-2
Leg II	Larva	-	<i>d</i> , <i>bv</i> ''	(<i>l</i>), σ	<i>l</i> ', <i>v</i> ', φ	(<i>pv</i>), <i>s</i> , (<i>a</i>), (<i>u</i>), (<i>p</i>), (<i>tc</i>), (<i>ft</i>), ω	0-2-2-2-13	1-1-1
	Protonymph	-	<i>l</i> '	-	-	-	0-3-2-2-13	1-1-1
	Deutonymph	-	-	-	-	-	0-3-2-2-13	1-1-1
	Tritonymph	-	-	-	-	(<i>it</i>)	0-3-2-2-15	1-1-1
	Adult	-	-	-	<i>l</i> ''	-	0-3-2-3-15	1-1-1
Leg III	Larva	-	<i>d</i> , <i>ev</i> '	<i>l</i> ', σ	<i>l</i> ', φ	(<i>pv</i>), <i>s</i> , (<i>a</i>), (<i>u</i>), (<i>p</i>), (<i>tc</i>), (<i>ft</i>)	0-2-1-1-13	1-1-1
	Protonymph	-	-	-	-	-	0-2-1-1-13	1-1-1
	Deutonymph	-	-	-	-	-	0-2-1-1-13	1-1-1
	Tritonymph	-	-	-	-	-	0-2-1-1-13	1-1-1
	Adult	<i>v</i> '	-	-	<i>v</i> ''	-	1-2-1-2-13	1-1-1
Leg IV	Protonymph	-	-	-	-	(<i>pv</i>), (<i>u</i>), (<i>p</i>), <i>ft</i> ''	0-0-0-0-7	0-0-0
	Deutonymph	-	<i>d</i> , <i>ev</i> '	<i>l</i> '	<i>l</i> ', φ	<i>s</i> , (<i>a</i>), (<i>tc</i>)	0-2-1-1-12	0-1-0
	Tritonymph	-	-	-	<i>v</i> ''	-	0-2-1-2-12	0-1-0
	Adult	<i>v</i> '	-	-	<i>v</i> '	-	1-2-1-3-12	0-1-0

data, we cannot conclude that the South African specimens represent a new species.

Some juvenile stages of three other species are known, namely *S. satanicus* Pfingstl, 2013 (larva), *S. quasimodo* Pfingstl, 2013 (proto- and tritonymph) and *S. mediterraneus* Grandjean, 1966 (deuto- and tritonymph) (Grandjean 1966; Pfingstl 2013b; see Appendix 1). The larvae of *S. divergens* and *S. satanicus* are similar in general habitus and morphology of setae and integument, but differ in the form of the bothridial seta which is with a medium long stem and clavate spinose head in the former and long, flagelliform in the latter (also different in adults).

The protonymph and tritonymph of *S. divergens* and *S. quasimodo* differ most noticeably by the number of gastronotal setae and many more gastronotal folds in the latter. The nymphs of *S. divergens* have 15 pairs of setae, whereas the protonymph of *S. quasimodo* has 24 pairs and the tritonymph 44 pairs stemming from a multiplication of certain setae. Furthermore, the setae in the tritonymph of *S. divergens* are branched, while the setae in *S. quasimodo* are setiform, with setae *da*, *dm*, *dp* thickened and serrated. Setae *ex* is minute in *S. divergens* and vestigial in *S. quasimodo*. There is only one difference on the leg setae in the number of setae on Fe II (*S. divergens* proto- and tritonymph: 3 setae, *S. quasimodo* protonymph: 2, tritonymph: 4). Other characteristics, which also differ in the adults, are the form of the bothridial setae (*S. divergens* head clavate, spinose, *S. quasimodo* flagelliform) and the number of adanal setae (*S. divergens* three pairs, *S. quasimodo* two pairs).

In general, the deuto- and tritonymph of *S. divergens* and *S. mediterraneus* look similar in habitus and gastronotal folds. An obvious difference is that *S. divergens* has branched gastronotal setae with setae *da*, *dm*, *dp* slightly thickened while *S. mediterraneus* has setiform setae and all setae are thin. There are differences on the leg setae in the number of setae on Fe I and II (*S. divergens*: 3 setae, *S. mediterraneus*: 4). Other characteristics, which also differ in the adults, is the form of the bothridial setae (*S. divergens*: head clavate, spinose, *S. mediterraneus*: spatuliform) and the number of adanal setae (*S. divergens*: three pairs, *S. mediterraneus*: two pairs).

Family: Selenoribatidae Schuster, 1963

Genus: *Schusteria* Grandjean, 1968

Schusteria ugraseni Marshall & Pugh, 2000

Adult

Measurements: females (n=9): length 368-389 (378), width 227-244 (227), males (n=9): length 351-394 (369), width 220-245 (229); neotype (female): length 384, width 236; no difference in size between individuals from the two locations (Sheffield Beach and Winterstrand); measurements in the original description are within close range, females: length 331, 334, width 205, 220.

Integument (Figures 8 and 9): brown in colour, antero-medial notogaster with lighter area, ventrally the area posterior to genital plates darker than the anterior area, genital and anal plates dark with small foveolae; legs lighter brown, except trochanter III and IV dark brown; femora distally with faint striae; body distinctly granulate with large granules interspersed with small granules, larger granules on *PdI*.

Prodorsum (Figures 8A, C): rostrum rounded in dorsal view; *ro*, *le*, *in* short (6-11), fine, smooth, *ex* as alveolus; bothridium, large, rectangular with small lateral incision and small opening for *bs*; *bs* with relative long stem and clavate, spinose head (38-55).

Gnathosoma: similar to *S. littorea* (see Grandjean 1968).

Notogaster (Figures 8A, C): oval in dorsal view; dorsosejugal furrow incomplete medially; 15 pairs (*c*₁₋₃, *da*, *dm*, *dp*, *la*, *lm*, *lp*, *h*₁₋₃, *p*₁₋₃) fine, short, smooth setae, all of similar length (10-18), *c*₃ not necessarily closer to *c*₁ than to *c*₂ as in original description, but indeed *c*₃ closer to lyrifissure *im* than to *ia*; five pairs of distinct lyrifissures: *ia* next to anterior lateral border of notogaster, *im* posterior to *c*₃, *ih* laterally to *lm* and *lp*, *ips* laterally to *p*₃, *ip* between *p*₂ and *p*₃; *gla* postero-laterally to *im*.

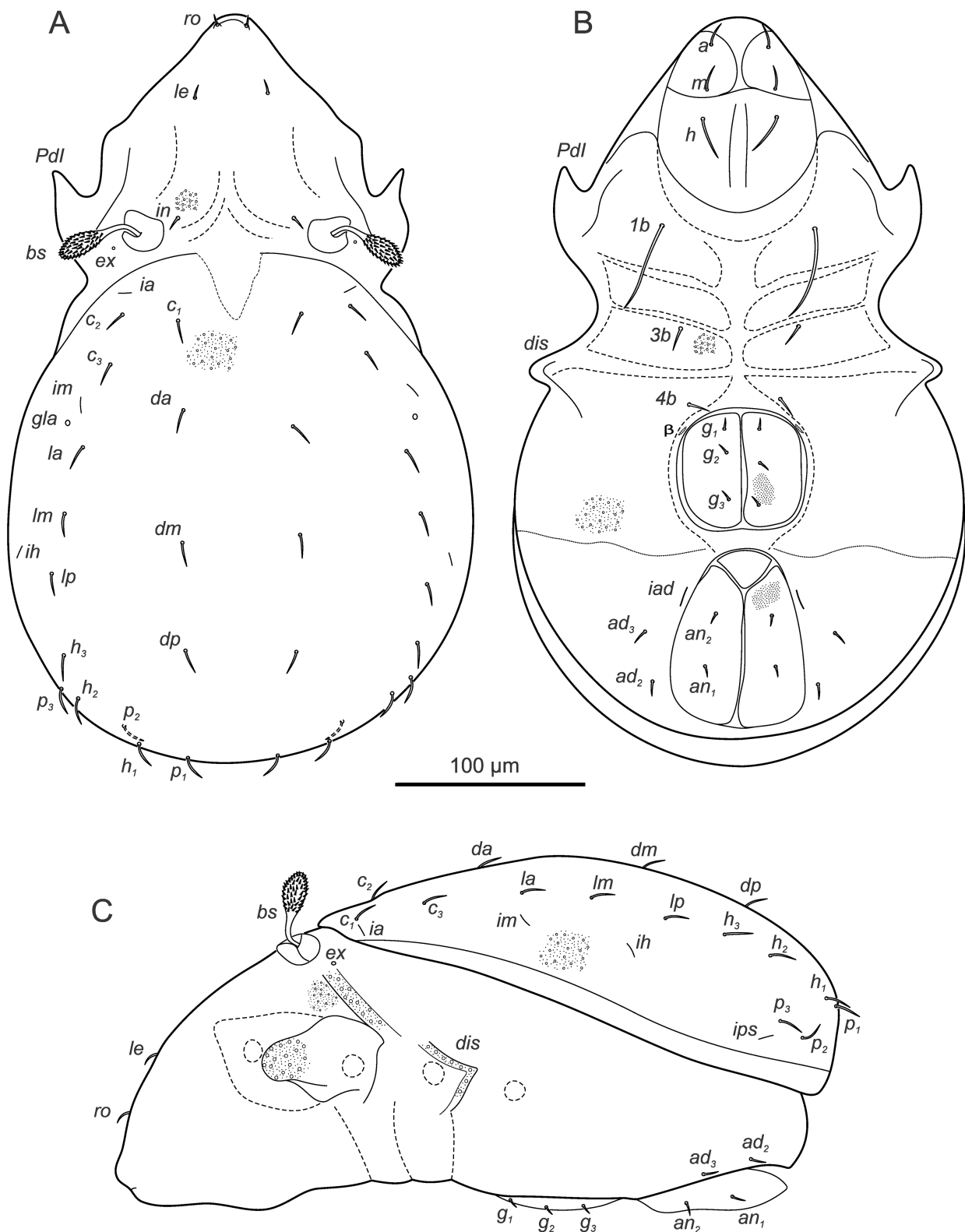
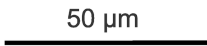


Figure 8 *Schusteria ugraseni* Marshall & Pugh, 2000. Neotype, adult, Sheffield Beach. A. dorsal view (legs omitted), B. ventral view (legs omitted), C. lateral view (legs and some ventral setae omitted).



Lateral aspect (Figure 8C): *PdI* directed anteriorly, rounded; discidium rounded triangularly.

Ventral (Figures 8B, C): all setae smooth, fine; epimeral setation 1-0-1-1, seta *lb* very long (43-56) > *3b* (8-11) > *4b* (6-8); three pairs of genital (5-7), two pairs of anal and two pairs of adanal (7-8) setae; lyrifissure *iad* parallel, antero-laterally to anal plates; setae *ad*₃ posterior to *iad*, *ad*₂ and *ad*₃ close together; genital plates (length 49-60, width 26-30) and anal plates (length 79-86, width 29-33) large; pre-anal organ triangular in ventral view.

Legs (Figures 9A-D): monodactylous, hooked claw with small tooth proximo-ventrally; most setae barbed, except thickened blunt antiaxial lateral seta on genua I-IV; Fe I, II with only three setae (as in *S. littorea*), on tarsi seta *u'* longer than *u''*; for setation and solenidia see Table 3.

Juvenile stages

Common features – apherodermous; light brown in colour, integument strongly plicate and soft, except for the more sclerotised centrodorsal plate; body strongly granulated; prodorsum triangular, hysterosoma oval in dorsal view; rostrum rounded; *ro*, *le*, *in* setiform, short, smooth, fine; bothridia small, cup-like; *bs* with medium stalk and clavate spinose head; plicate centrodorsal shield bearing central dorsal setae, *da*, *dm*, *dp* on very small apophyses; all gastronotal setae simple, fine, short; no cupules discernible; folds lateral to anal orifice; epimeral seta setiform, smooth, *lb* very long, seta *3b* shorter; legs monodactylous with hooked claw and small tooth proximo-ventrally; leg porose areas not visible; for setation and solenidia see Table 3.

Larva – (Figures 10A, B) (n=5) length 179-207 (194), width 102-124 (115).

Gastronotic region: *ex* similar to *in*; 11 pairs of gastronotal setae (*c*₁₋₃, *da*, *dm*, *dp*, *la*, *lm*, *lp*, *h*₁₋₂); *h*₂ lateral to anal opening on ventral side, slightly longer than other setae.

Ventral region of idiosoma: epimeral setation 1-0-1-0 (*lb*, *3b*); Claparède's organ present, no protective seta observed.

Protonymph – (Figures 10C, D) (n=4) length 219-246 (234), width 135-146 (140).

Gastronotic region: *ex* similar to *in*; 15 pairs of gastronotal setae (*h*₃, *p*₁₋₃ added), *p*₂₋₃ lateral to anal opening.

Table 3 *Schusteria ugraseni* Marshall & Pugh, 2000. Chaetome and solenidia from larva to adult. First development of setae and their homologies indicated by letters. () pairs of setae, - no change with regard to preceding stage.

	Instars	Trochanter	Femur	Genu	Tibia	Tarsus	Chaetome	Solenidia
Leg I	Larva	-	<i>d</i> , <i>bv''</i>	(<i>l</i>), σ	(<i>l</i>), <i>v'</i> , ϕ_1	(<i>pl</i>), (<i>pv</i>), <i>s</i> , (<i>a</i>), (<i>u</i>), (<i>p</i>), (<i>tc</i>), (<i>ft</i>), ϵ , ω_1	0-2-2-3-16	1-1-1
	Protonymph	-	<i>l'</i>	-	-	ω_2	0-3-2-3-16	1-1-2
	Deutonymph	-	<i>l''</i>	-	ϕ_2	-	0-4-2-3-16	1-2-2
	Tritonymph	-	-	-	-	(<i>it</i>)	0-4-2-3-18	1-2-2
	Adult	-	loose <i>l''</i>	-	-	-	0-3-2-3-18	1-2-2
Leg II	Larva	-	<i>d</i> , <i>bv''</i>	(<i>l</i>), σ	<i>l'</i> , <i>v'</i> , ϕ	(<i>pv</i>), <i>s</i> , (<i>a</i>), (<i>u</i>), (<i>p</i>), (<i>tc</i>), (<i>ft</i>), ω	0-2-2-2-13	1-1-1
	Protonymph	-	<i>l'</i>	-	-	-	0-3-2-2-13	1-1-1
	Deutonymph	-	<i>l''</i>	-	<i>l''</i>	-	0-4-2-3-13	1-1-1
	Tritonymph	-	-	-	-	(<i>it</i>)	0-4-2-3-15	1-1-1
	Adult	-	loose <i>l''</i>	-	-	-	0-3-2-3-15	1-1-1
Leg III	Larva	-	<i>d</i> , <i>ev'</i>	<i>l'</i> , σ	<i>v'</i> , ϕ	(<i>pv</i>), <i>s</i> , (<i>a</i>), (<i>u</i>), (<i>p</i>), (<i>tc</i>), (<i>ft</i>)	0-2-1-1-13	1-1-0
	Protonymph	-	-	-	-	-	0-2-1-1-13	1-1-0
	Deutonymph	-	-	-	-	-	0-2-1-1-13	1-1-0
	Tritonymph	-	-	-	-	-	0-2-1-1-13	1-1-0
	Adult	<i>v'</i>	-	-	<i>v''</i>	-	1-2-1-2-13	1-1-0
Leg IV	Protonymph	-	-	-	-	(<i>pv</i>), (<i>u</i>), (<i>p</i>), <i>ft''</i>	0-0-0-0-7	0-0-0
	Deutonymph	-	<i>d</i> , <i>ev'</i>	<i>l'</i>	<i>v'</i> , ϕ	<i>s</i> , (<i>a</i>), (<i>tc</i>)	0-2-1-1-12	0-1-0
	Tritonymph	-	-	-	<i>l'</i>	-	0-2-1-2-12	0-1-0
	Adult	<i>v'</i>	-	-	<i>v''</i>	-	1-2-1-3-12	0-1-0

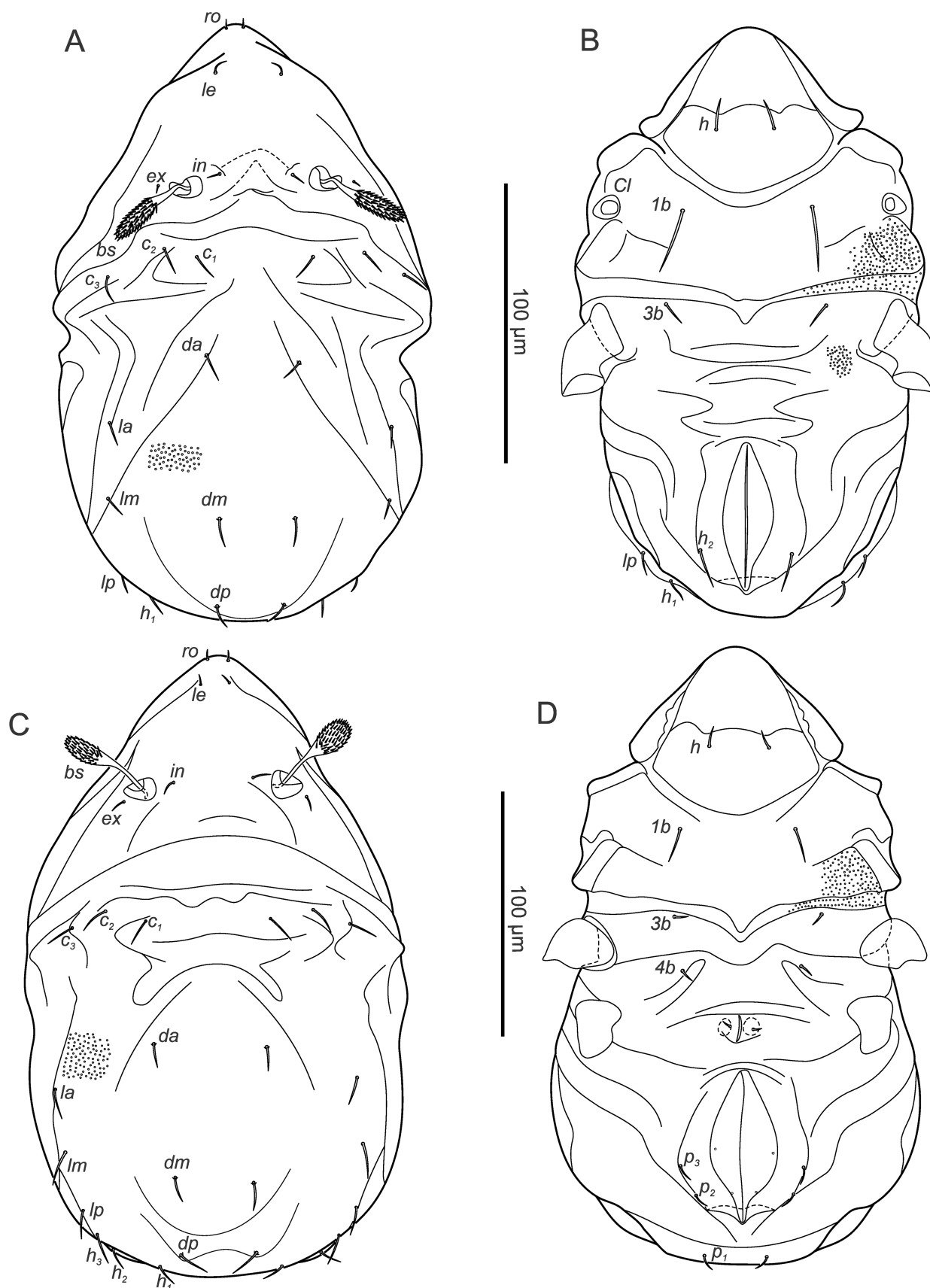


Figure 10 *Schusteria ugraseni* Marshall & Pugh, 2000, Winterstrand, A. larva, dorsal view, B. larva, ventral view, C. protonymph, dorsal view, D. protonymph, ventral view.

Ventral region of idiosoma: epimeral setation: 1-0-1-1 (*4b* added); one pair of short genital setae; two pairs of white spots on anal valves.

Deutonymph – (Figures 11A, B) (n=11) length 252-303 (281), width 153-194 (169).

Gastronotic region: *ex* similar to *in*; 15 pairs of gastronotal setae (as in protonymph), p_{2-3} ventrally, laterally to anal folds.

Ventral region of idiosoma: epimeral setation: 1-0-1-1; two pairs of short genital setae, two pairs of short setiform adanal setae lateral to anal folds, two vestigial pairs of anal setae on anal valves.

Tritonymph – (Figures 11C, D, supplementary figure 3) (n=8) length 320-366 (338), width 191-233 (207).

Gastronotic region: *ex* vestigial; 15 pairs of gastronotal setae (as in deutonymph), setae p_{2-3} postero-laterally to anal folds.

Ventral region of idiosoma: epimeral setation 1-0-1-1; three pairs of setiform genital, two pairs of adanal, two pairs of anal setae present.

Material examined

Four adults and 28 juveniles from Winterstrand, East London, Eastern Cape, South Africa, 33°5.67'S, 27°47.759'E, from algae in rock and tubeworms, eulittoral zone, 22 Oct. 2020, collected by J.A. Neethling (NMB 4707.1); six adults from Sheffield Beach, KwaZulu-Natal, South Africa, 29°29.737'S, 2°15.127'E, from *Bostrychia* sp. algae from rock, upper eulittoral zone, 27 Feb. 2020, collected by T. Pfingstl (NMB 4717.2).

Neotype designation

The holotype and paratype of *S. ugraseni* have been lost (Marshall, personal communication) and therefore a neotype should be selected. There is no material available from the type locality (Park Rynie). The specimens used here originate from Sheffield Beach (app. 116 km from Park Rynie) and Winterstrand (app. 612 km from Park Rynie). Due to the closer proximity, we selected a neotype from Sheffield Beach (NMB 4717.2.1) and five neo-paratypes from Sheffield Beach (NMB 4717.2.2) and four neo-paratypes from Winterstrand (NMB 4707.1.1) stored in the Acarology collection of NMB. Additional specimens will be stored in the Senckenberg Natural History Museum, Görlitz, Germany.

Remarks

The original description of Marshall and Pugh (2000) provides good morphological information and drawings of all aspects of the body, but not the legs. The adult specimens from Sheffield and Winterstrand match the description of the specimens from Park Rynie of the original description.

In general appearance the juveniles of *S. ugraseni* are very similar to those of the other two species of which juvenile stages are known: *S. littorea* Grandjean, 1968 (all stages) and *S. melanomerus* Marshall & Pugh, 2000 (protonymph) (Grandjean 1968; Pfingstl 2016). They have the same appearance and specific patterns of lateral and ventral folds. The protonymph of *S. ugraseni* differs from *S. melanomerus* in the presence of short *ex* (vestigial in *S. melanomerus*), two pairs of white spots on the anal valves (vs absent) and setae *l'* on Fe I and II (vs absent).

A distinct difference between the adults of *S. ugraseni* and *S. littorea* is the number of anal and adanal setae with two pairs of anal and two pairs of adanal setae in the former, but one pair of anal and two pairs of adanal setae in the latter species. This trait is also different in the juveniles of these two species: the deuto- and tritonymph of *S. ugraseni* with two pairs of adanal setae and *S. littorea* with one pair, deutonymph and tritonymph of *S. ugraseni* with two pairs of anal (vestigial in deutonymph) while *S. littorea* has one pair in deuto- and tritonymph (also vestigial in deutonymph); the anal valves of the protonymph of *S. ugraseni* has two pairs of white spots, but they are absent in *S. littorea*. There is also a difference in the leg setae with seta *l''* on Ti II present in the deuto- and tritonymphs, while it is only appearing in the adult of

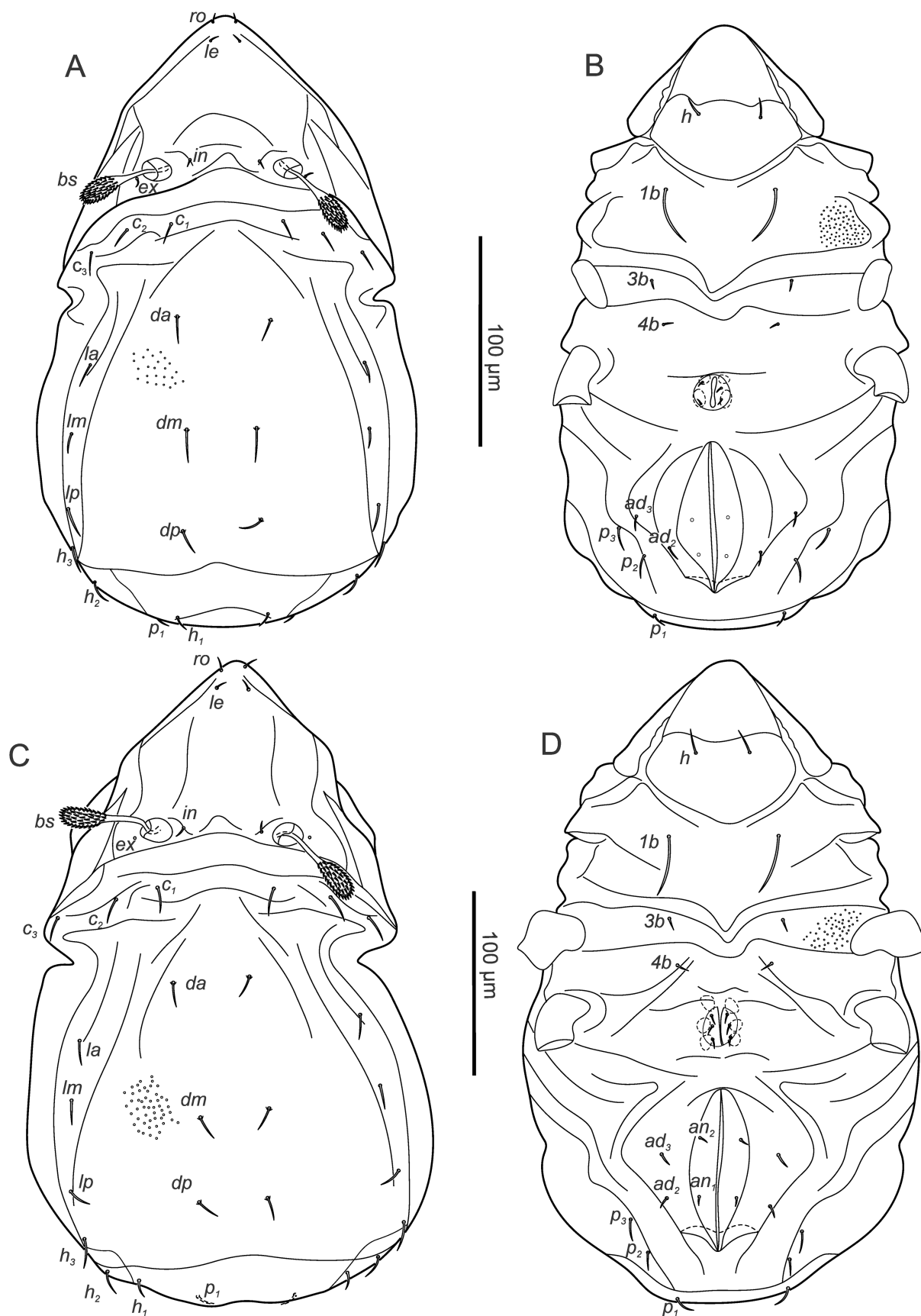


Figure 11 *Schusteria ugraseni* Marshall & Pugh, 2000, Winterstrand, A. deutonymph, dorsal view, B. deutonymph, ventral view, C. tritonymph, dorsal view, D. tritonymph, ventral view.

S. littorea. Another difference is the presence in *S. ugraseni* of a short *ex* seta in larva, proto- and deutonymphs and alveolus in tritonymph and adult, while a short *ex* seta is present in all stages of *S. littorea* and in the adult.

Family Podacaridae Grandjean, 1955

Genus: *Halozetes* Berlese, 1916

Halozetes capensis Coetzee & Marshall, 2003

Adult

Measurements: Adult body size: Kommetjie: holotype (female) length 637, width 351 (the scale bar in the drawing of the original description (Coetzee & Marshall 2003) is correct, but the sizes given in the text are incorrect and are rectified here), paratypes: female (n=1): length 662, width 374, males (n=4) length 565-595 (585), width 292-327 (314); Nature's Valley: females (n=2) length 590-617 (604), width 326-339 (333), males (n=3) length 571-586 (580), width 300-321 (311).

Integument (Figure 12): dark brown in colour; leg tarsi, tibiae lighter brown; dorsal side distinctly granulate with various sized granules, on prodorsum granules medially from anterior to posterior along hour-glass shape of *ro*, *le* and *in*, ventrally small area of granules between leg I and II, remainder of ventral side without granulation, legs with granules of various sizes; chelicera punctate.

Prodorsum (Figures 12A, D): rostrum rounded in dorsal view, slightly projected in lateral view; *ro* (20-31) smooth, *le* (35-69) roughened, *in* very long (150-181), roughened, directed upwards, *ex* short (8-13), smooth; bothridium cup-like with small opening for *bs*; *bs* with short stalk and clavate head (34-39).

Gnathosoma (Figure 12C): palp similar to that of *H. belgicae mickii* (Coetzee 2000), palp setation 0-2-1-3-9+1 ω , palp solenidion ω and eupathidium *acm* connected, forming double horn; cheliceral setae setiform, barbed, *chb* slightly shorter than *cha*.

Notogaster (Figures 12A, D): elongated oval in dorsal view; anterior margin projecting anteriorly, dorsosejugal furrow medially indistinct; 14 pairs of smooth, stout notogastral setae (*c*₁₋₂, *da*, *dm*, *dp*, *la*, *lm*, *lp*, *h*₁₋₃, *p*₁₋₃), *c*₃ absent, ranges in the lengths of the dorsal setae on the notogaster quite large within populations, in the holotype the lengths towards the lower ranges (see Figure 2 in Coetzee and Marshall 2003, Figure 12 here depicts longer setae), mostly seta *h*₂ longer than the others (*c*₁ 14-21, *c*₂ 18-25, *da*, *dm*, *dp* 12-28, *la* 10-27, *lm* 13-40, *lp* 16-47, *h*₁, *h*₃ 10-29, *h*₂ 27-59, *p*₁ 17-34, *p*₂₋₃ 14-46); five pairs of distinct lyrifissures, *ia* postero-laterally to *c*₂, *im* between *lm* and *lp*, *ih* lateral to *lp*, *ips* lateral to *ih* close to latero-ventral border of notogaster, *ip* anterior to *p*₁; *gla* posterior to *lp*.

Lateral aspect (Figure 12D): *PdI* small lamina, directed forward; discidium rounded.

Ventral (Figures 12B, D): all setae smooth; epimeral setation 3-1-2-2, seta *lb* (40-56) > *3b* (18-33) > *4a*, *4b* (13-24) > *1a*, *2a*, *1c*, *3a* (9-19); six pairs of genital (*g*₁ 15-19, *g*₂₋₆ 12-16), one pair of aggenital (22-39), two pairs of anal (17-29) and three pairs of adanal (*ad*₁ 14-18, *ad*₂₋₃ 17-25) setae present; anal plates large (length 114-141, width not measured due to distortion of plates in many specimens), genital plates larger in females than males (female: length 106-115, males 84-92; width not measured due to distortion of plates in many specimens), also genital plates of females with distinct posterior interlocking triangle, males with weaker triangle.

Legs: matching drawings in Coetzee and Marshall (2003); tridactylous, middle claw strong, long hook-like claws, weakly serrated dorsally; porose areas present; for setation and solenidia see Table 4.

Juvenile stages

Common features – apheredermous; dark brown in colour, integument strongly plicate and soft, body distinctly granulate; three oval sclerites in posterior region of prodorsum, three pairs of sclerites on notogaster laterally between setal rows of *l*-series and *d*-series, anterior pair

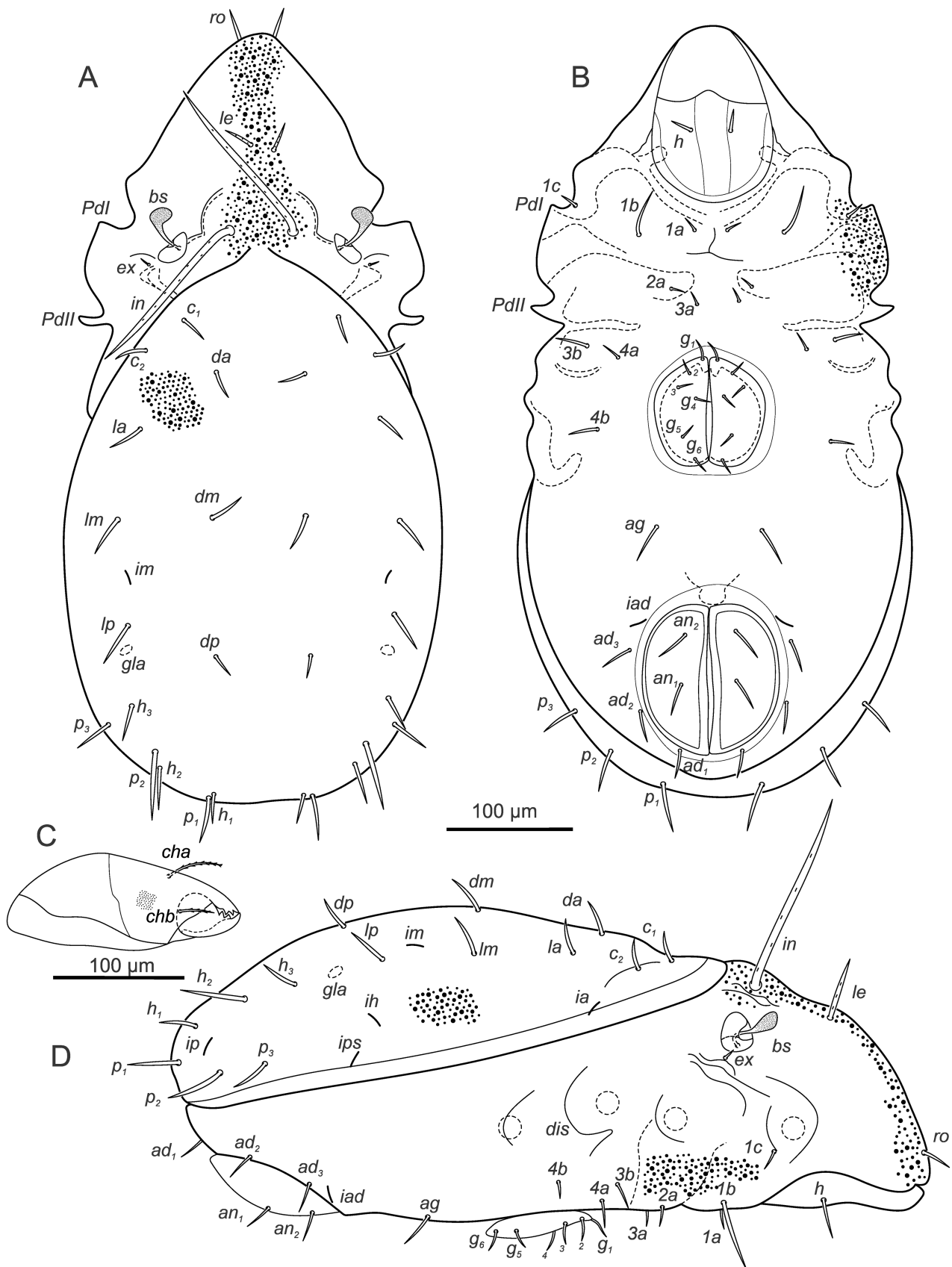


Figure 12 *Halozetes capensis* Coetzee & Marshall, 2003, Nature's Valley, Adult (legs omitted). A. dorsal view, B. ventral view, C. chelicera, D. lateral view.

irregular in shape, others rounded or oval; prodorsum triangular, hysterosoma oval in dorsal view; rostrum rounded; *ro* short, *le* of medium length, *in* very long, all three setae roughened, *ex* very short, smooth; bothridia small; gastronotal setae thickened, setiform, smooth or slightly roughened; no cupules discernible; folds lateral to anal opening; epimeral region with folds; legs monodactylous; leg porose areas visible; for setation and solenidia see Table 4.

Larva – (Figures 13A, B) (n=8) length 268-298 (282), width 143-169 (154).

Gastronotic region: *bs* not visible externally, 12 pairs of gastronotal setae (*c*₁₋₃, *da*, *dm*, *dp*, *la*, *lm*, *lp*, *h*₁₋₃), setae *lp* longest; *h*₂, *h*₃ lateral to anal opening on ventral side.

Ventral region of idiosoma: epimeral setation 3-1-2-0 (*la*, *lb*, *lc*, *2a*, *3a*, *3b*) short setiform, smooth, third seta of first epimere forms protective scale over respective Claparède's organ.

Protonymph – (Figures 13C, D) (n=8) length 321-397 (361), width 185-221 (204).

Gastronotic region: *bs* not visible externally; 15 pairs of gastronotal setae (*p*₁₋₃ added), seta *lm* slightly longer and *lp* and *h*₂ much longer than others, *p*₂₋₃ lateral and *p*₁ posterior to anal folds.

Ventral region of idiosoma: epimeral setation: 3-1-2-1 (*4b* added), setae smooth, setiform; one pair of short genital setae.

Deutonymph – (Figures 14A, B) (n=9) length 424-479 (439), width 230-254 (241).

Gastronotic region: *bs* not visible externally; 15 pairs of gastronotal setae, setae *lp* and *h*₂ longest, *p*₂₋₃, laterally to anal folds; some dorsal setae of specimens from Nature's Valley distinctly longer than specimens from Kommetjie (Nature's Valley *c*₁₋₂ 15-21, *c*₃ 24-27, *da*, *dm* 23-27, *dp* 11-16, *la*, 24-28, *lm* 31-34, *h*₁₋₃ 12-18, Kommetjie *c*₁₋₂ 8-10, *c*₃ 21-22, *da*, *dm* 8-14, *dp* 8-9, *la*, 14-16, *lm* 15-20, *h*₁₋₃ 8-13), other setae slightly shorter (Nature's Valley *lp* 40-47, *h*₂ 59-66, Kommetjie *lp* 47-59, *h*₂ 72-78).

Ventral region of idiosoma: epimeral setation: 3-1-2-2 (*4a* added); three pairs of short genital setae, three pairs of short setiform adanal setae lateral to anal opening, aggenital setae added.

Tritonymph – (Figures 14C, D) (n=11) length 492-636 (561) width 284-324 (307).

Gastronotic region: *bs* with short stalk and very small, rounded head; 15 pairs of gastronotal setae, setae *lp* and *h*₂ longest, *p*₁₋₃ ventrally, *p*₁₋₂ posterior to anal folds; some dorsal setae of

Table 4 *Halozetes capensis* Coetzee & Marshall, 2003. Chaetome and solenidia from larva to adult. First development of setae and their homologies indicated by letters. () pairs of setae, - no change with regard to preceding stage.

	Instars	Trochanter	Femur	Genu	Tibia	Tarsus	Chaetome	Solenidia
Leg I	Larva	-	<i>d</i> , <i>bv</i> ''	(<i>l</i>), σ	(<i>l</i>), <i>v</i> ', ϕ_1	(<i>pl</i>), (<i>pv</i>), <i>s</i> , (<i>a</i>), (<i>u</i>), (<i>p</i>), (<i>tc</i>), (<i>ft</i>), ω_1	0-2-2-3-15	1-1-1
	Protonymph	-	-	-	-	ω_2	0-2-2-3-15	1-1-2
	Deutonymph	-	(<i>l</i>)	-	ϕ_2	-	0-4-2-3-15	1-2-2
	Tritonymph	<i>v</i> '	-	-	-	(<i>it</i>)	1-4-2-3-17	1-2-2
	Adult	-	-	-	<i>v</i> ''	-	1-4-2-4-17	1-2-2
Leg II	Larva	-	<i>d</i> , <i>bv</i> ''	(<i>l</i>), σ	<i>l</i> ', <i>v</i> ', ϕ	(<i>pv</i>), <i>s</i> , (<i>a</i>), (<i>u</i>), (<i>p</i>), (<i>tc</i>), (<i>ft</i>), ω_1	0-2-2-2-13	1-1-1
	Protonymph	-	-	-	-	-	0-2-2-2-13	1-1-1
	Deutonymph	-	(<i>l</i>)	-	-	ω_2	0-4-2-2-13	1-1-2
	Tritonymph	<i>v</i> '	-	-	<i>l</i> ''	(<i>it</i>)	1-4-2-3-15	1-1-2
	Adult	-	-	-	<i>v</i> ''	-	1-4-2-4-15	1-1-2
Leg III	Larva	-	<i>d</i> , <i>ev</i> '	<i>l</i> ', σ	<i>v</i> ', ϕ	(<i>pv</i>), <i>s</i> , (<i>a</i>), (<i>u</i>), (<i>p</i>), (<i>tc</i>), (<i>ft</i>)	0-2-1-1-13	1-1-0
	Protonymph	<i>v</i> '	-	-	-	-	1-2-1-1-13	1-1-0
	Deutonymph	<i>l</i> '	<i>l</i> '	-	<i>l</i> '	-	2-3-1-2-13	1-1-0
	Tritonymph	-	-	-	-	(<i>it</i>)	2-3-1-2-15	1-1-0
	Adult	-	-	-	<i>v</i> ''	-	2-3-1-3-15	1-1-0
Leg IV	Protonymph	-	-	-	-	(<i>pv</i>), (<i>u</i>), (<i>p</i>), <i>ft</i> ''	0-0-0-0-7	0-0-0
	Deutonymph	-	<i>d</i> , <i>ev</i> '	<i>d</i>	<i>v</i> ', ϕ	<i>s</i> , (<i>a</i>), (<i>tc</i>)	0-2-1-1-12	0-1-0
	Tritonymph	<i>v</i> '	-	<i>l</i> '	<i>l</i> '	-	1-2-2-2-12	0-1-0
	Adult	-	-	-	<i>v</i> ''	-	1-2-2-3-12	0-1-0

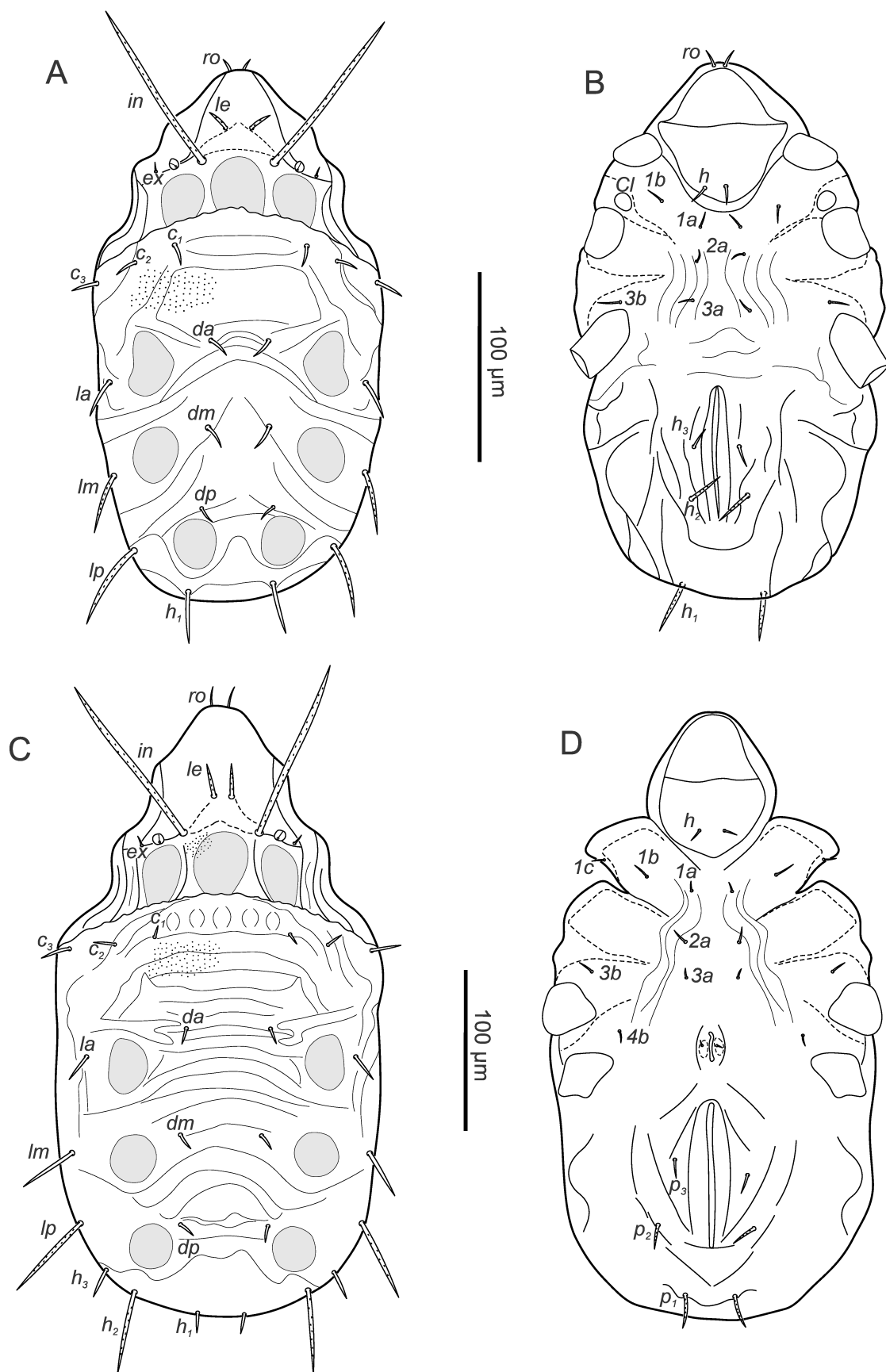


Figure 13 *Halozetes capensis* Coetzee & Marshall, 2003, Kommetjie, A. larva, dorsal view, B. larva, ventral view, C. protonymph, dorsal view, D. protonymph, ventral view.

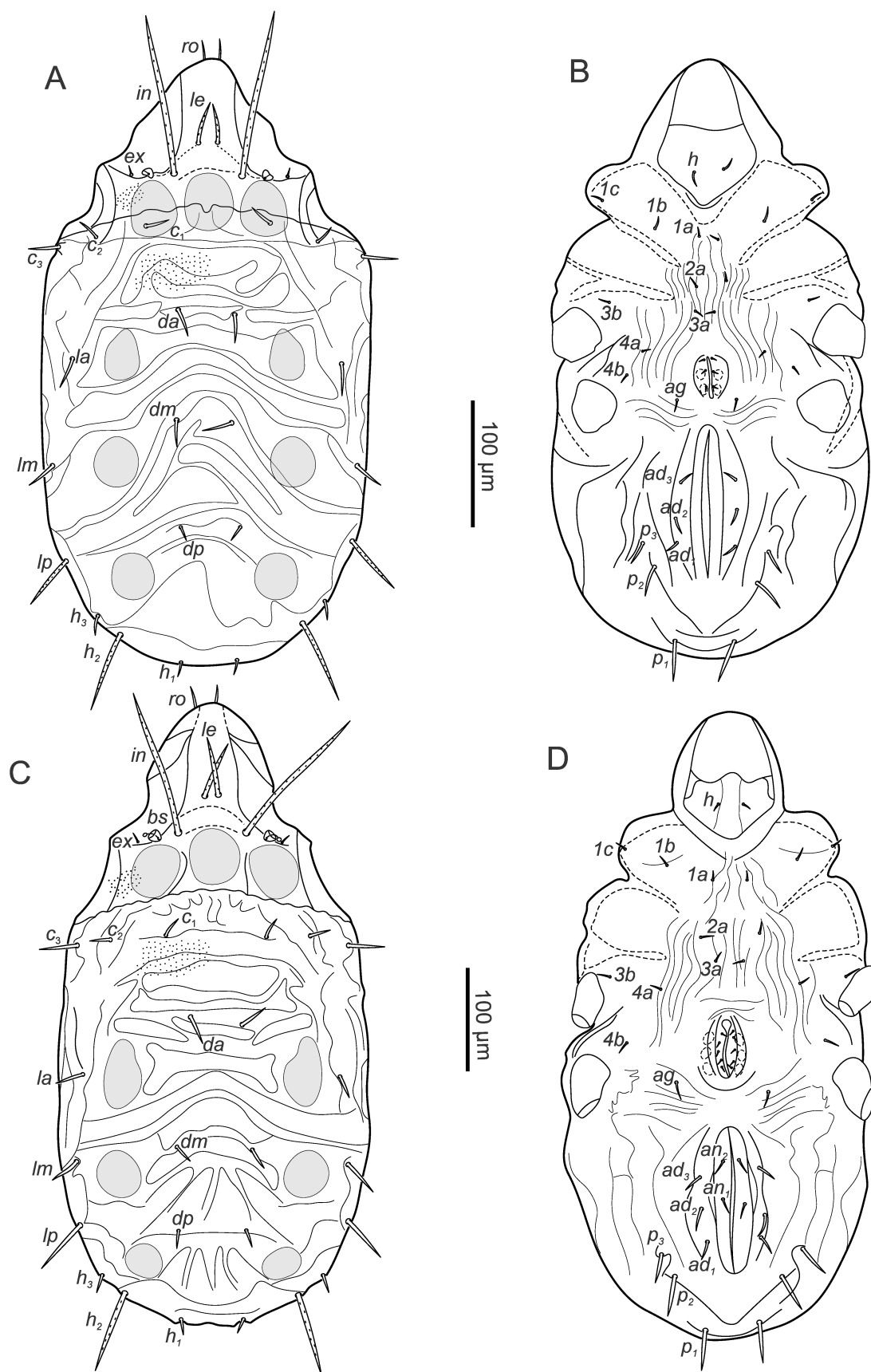


Figure 14 *Halozetes capensis* Coetzee & Marshall, 2003, Nature's Valley, A. deutonymph, dorsal view, B. deutonymph, ventral view, C. tritonymph, dorsal view, D. tritonymph, ventral view.

specimens from Nature's valley slightly longer or shorter than specimens from Kommetjie but not as distinct as in deutonymph (see difference in setal lengths in Figure 14 here compared to Figure 10 in Coetzee and Marshall (2003)).

Ventral region of idiosoma: epimeral setation as in deutonymph; five pairs of setiform genital, one pair of aggenital, three pairs of adanal, two pairs of anal setae.

Material examined

Five adults, one protonymph, nine deutonymphs, six tritonymphs from Nature's Valley, Western Cape, South Africa, 33°59.333'S, 23°32.796'E, from *Bostrychia intricata* algae on rocks, upper eulittoral zone, 23 Feb. 2019, collected by T. Pfingstl (NMB 4671.1); holotype (NMB 4150.1), five adult paratypes (the paratypes of the original description could not be identified, as they were within a vial of 59 individuals), eight larvae, seven protonymphs, four deutonymphs, five tritonymphs from Kommetjie, Western Cape, South Africa, 34°13'S, 18°32'E, from finely branched algae on rocks, middle and upper eulittoral zone, Oct. 2000, collected by D.J. Marshall (NMB 4150).

Remarks

The original description by Coetzee and Marshall (2003) of *H. capensis* provides very good morphological information and drawings of all aspects including legs. The adults from Nature's Valley of our samples do not differ from those of Kommetjie. The variation in the length of dorsal setae, even within a population, is noteworthy.

Some or all juvenile stages of several *Halozetes* species and subspecies are known, namely *H. belgicae belgicae* (Michael, 1903), *H. belgicae mickii* Coetzee, 2000, *H. capensis*, *H. crozetensis* (Richters, 1907), *H. intermedius* Wallwork, 1963, *H. litoralis* Wallwork, 1963, *H. marinus marinus* (Lohmann, 1907), *H. marinus devilliersi* Engelbrecht, 1974, *H. marinus minor* Wallwork, 1966, *H. marionensis* Engelbrecht, 1974, *H. macquariensis* (Delenius, 1958), *H. necrophagus* Wallwork, 1967 and *H. plumosus* Wallwork, 1966 (Norton & Ermilov 2014, also Appendix 1). Ermilov *et al.* (2012) provided very useful information and a key to the juveniles of the various species. The juveniles of *H. capensis* differ from other known juveniles mostly in the number of porose sclerites on the prodorsum and gastronomum, the distinctness of *bs*, length of setae *in* and *le* and in the morphology of gastronomotal setae (see Table 5 for a summary of the differences).

Table 5 Selective characteristics of known *Halozetes* species larval and nymphal stages.

Species and instars	No. of porose sclerites on prodorsum	No. of dorsal porose sclerites on gastronomum	Bothridial seta distinct	Length of <i>in</i> setae	Length of <i>le</i> relative to <i>ro</i>	Longest gastronotal setae	Morphology of gastronotal setae
<i>H. belgicae belgicae</i>							
Larva	5	0	yes	long	<i>le</i> slightly shorter than <i>ro</i>	c_3, h_1	barbed
Nymphs	5	0	yes	long	Similar in length	$c_1, c_3, h_{1-3}, p_{1-3}$	$c_{1-3}, h_{1-3}, p_{1-3}$ barbed, others very short, smooth
<i>H. belgicae mickii</i>							
Larva	5	0	yes	medium, not reaching <i>ro</i>	<i>le</i> much shorter than <i>ro</i>	h_1	barbed
Nymphs	5	0	yes	medium, not reaching <i>ro</i>	<i>le</i> much shorter than <i>ro</i>	proto: h_{1-3} , deuto, trito: h_1, h_2	barbed
<i>H. capensis</i>							
Larva	3	6	no	long	<i>le</i> longer than <i>ro</i>	lp	roughened
Nymphs	3	6	only in tritonymph	long	<i>le</i> longer than <i>ro</i>	lp, h_2	roughened
<i>H. crozetensis</i>							
Larva	0	0	yes	medium, not reaching <i>ro</i>	<i>le</i> longer than <i>ro</i>	h_1, h_2	barbed
Nymphs	0	0	yes	medium, not reaching <i>ro</i>	<i>le</i> longer than <i>ro</i>	h_{1-3}	barbed
<i>H. intermedius</i>							
Nymphs	5	13	yes	long	<i>le</i> longer than <i>ro</i>	p_1, h_{1-3}	barbed
<i>H. littoralis</i>							
Tritonymph	3	13	yes	medium, not reaching <i>ro</i>	similar in length	c_3, h_2, p_{1-3}	roughened
<i>H. marinus marinus</i>							
Tritonymph	5	13	yes	long	<i>le</i> longer than <i>ro</i>	h_2	smooth
<i>H. marinus devilliersi</i>							
Larva	5	9	no	long	<i>le</i> longer than <i>ro</i>	h_2	smooth
Nymphs	5	10	yes	long	<i>le</i> longer than <i>ro</i>	h_2	smooth, only h_2 roughened
<i>H. marinus minor</i>							
Nymph (unspecified)	1	11	no	long	<i>le</i> slightly longer than <i>ro</i>	h_2	smooth
<i>H. marionensis</i>							
Larva	0	0	no	long	<i>le</i> slightly longer than <i>ro</i>	h_2	barbed
Nymphs	0	0	yes	long	similar in length	proto: lm, lp, h_{2-3} ; deuto: la, lm, lp, h_{2-3} ; trito: h_2	barbed
<i>H. macquariensis</i>							
Nymph (unspecified)	0	10	yes	medium, not reaching <i>ro</i>	<i>le</i> shorter than <i>ro</i>	p_1, h_{1-2}	smooth
<i>H. necrophagus</i>							
Nymphs	5	13	no	long	<i>le</i> longer than <i>ro</i>	proto, deuto: c_3, h_2, p_2 ; trito: h_2	smooth
<i>H. plumosus</i>							
Nymph (unspecified)	1	13	yes	long	similar in length	h_{1-3}, p_1	barbed

Halozetes belgicae belgicae (Dalenius and Wilson 1958; Wallwork 1965, 1967; Dastych 1990), *H. belgicae mickii* (Coetzee 2000, and personal observation of material in NMB), *H. capensis* (Coetzee and Marshall 2003, this paper) *H. crozetensis* (Ermilov et al. 2012; although Wallwork 1962b also described the juveniles, it is debatable if the specimens were indeed *H. crozetensis*), *H. intermedius*, *H. marinus marinus* (Wallwork 1963), *H. littoralis* (Wallwork 1970), *H. marinus devilliersi* (Engelbrecht 1974, and personal observation of material in NMB), *H. marionensis* (Engelbrecht 1974), *H. marinus minor*, *H. macquariensis*, *H. plumosus* (Wallwork 1966), *H. necrophagus* (Wallwork 1967).

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ORCID

Elizabeth A. Hugo-Coetzee  <https://orcid.org/0000-0003-0525-9049>

Julia Baumann  <https://orcid.org/0000-0002-4486-4121>

Jan-Andries Neethling  <https://orcid.org/0000-0003-1702-9566>

Tobias Pfingstl  <https://orcid.org/0000-0002-0778-8051>

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Appendix

Species of the superfamily Ameronothroidea for which information on juveniles exist in the literature

Family and species	Information of juveniles	Family and species	Information of juveniles
<u>Ameronothridae</u>		<u>Fortuyniidae</u>	
<i>Ameronothrus bilineatus</i> (Michael, 1888)	Michael 1888; Schubart 1975	<i>Alismobates inexpectatus</i> Pflingstl & Schuster, 2012	Pflingstl and Schuster 2012a; Pflingstl and Krisper 2014
<i>A. lapponicus</i> Dalenius, 1963	Schubart 1975	<i>A. galapagoensis</i> Pflingstl & Schatz, 2017	Pflingstl and Schatz 2017
<i>A. lineatus</i> (Thorell, 1871)	Michael 1888; Schubart 1975; Ermilov et al. 2012	<i>A. keniaensis</i> Pflingstl, 2016	Pflingstl 2016
<i>A. maculatus</i> (Michael, 1882)	Michael 1882; Schubart 1975	<i>A. pseudoreticulatus</i> Pflingstl, 2015	Pflingstl 2015b
<i>A. marinus</i> (Banks, 1896)	Grandjean 1949; Schubart 1975	<i>A. reticulatus</i> Luxton, 1992	Pflingstl et al. 2021b
<i>A. schneideri</i> (Oudemans, 1903)	Schubart 1975	<i>Circellobates venustus</i> Luxton, 1992	Luxton 1992
<i>A. schusteri</i> Schubart, 1970	Schubart 1970; Sitnikova 1975	<i>Fortuynia arabica</i> Bayartogtokh, Chatterjee & Chan, 2009	Bayartogtokh et al. 2009
<i>A. yoichi</i> Pflingstl & Shimano, 2019	Pflingstl et al. 2019b	<i>F. atlantica</i> Krisper & Schuster, 2008	Pflingstl and Schuster 2012a; Pflingstl and Krisper 2014
<i>Aquanothrus montanus</i> Engelbrecht, 1975	Engelbrecht 1975; Norton and Franklin 2018	<i>F. churaumi</i> Pflingstl, Shimano & Hiruta, 2019	Pflingstl et al. 2021b
<i>Paraquanothrus grahami</i> Norton & Franklin, 2018	Norton & Franklin 2018	<i>F. elamellata elamellata</i> Luxton, 1967	Luxton 1967
<i>P. spooneri</i> Norton & Franklin, 2018	Norton & Franklin 2018	<i>F. dimorpha</i> Pflingstl, 2015	Pflingstl 2015a
<i>Chudalupia meridionalis</i> Wallwork, 1981	Wallwork 1981; Norton and Franklin 2018	<i>F. longiseta</i> Pflingstl, 2015	Pflingstl 2015b
<u>Podacaridae</u>		<i>F. maledivensis</i> Pflingstl, 2015	Pflingstl 2015b
<i>Alaskozetes antarcticus antarcticus</i> (Michael, 1903)	Michael 1903; Wallwork 1962a, 1965, 1967; Dastych 1990	<i>F. rotunda</i> Marshall & Pugh, 2002	Pflingstl et al. 2021b
<i>A. antarcticus intermedius</i> Wallwork, 1967	Ermilov et al. 2012	<i>F. shibai</i> Aoki, 1974	Pflingstl et al. 2021b
<i>Antarcticola meyeri</i> Wallwork, 1967	Wallwork 1967; Norton and Franklin 2018	<i>F. smiti</i> Ermilov, Tolstikov, Mary & Schatz, 2013	Pflingstl 2015b
<i>Halozetes belgicae belgicae</i> (Michael, 1903)	Michael 1903; Dalenius and Wilson 1958; Wallwork 1965, 1967; Sitnikova 1968; Dastych 1990	<i>F. taiwanica</i> Bayartogtokh, Chatterjee & Chan, 2009	Bayartogtokh et al. 2009
<i>H. belgicae mickii</i> Coetzee, 2000	Coetzee 2000; Norton and Franklin 2018	<i>F. yunkerii</i> Hammen van der, 1963	Hammen van der 1963
<i>H. capensis</i> Coetzee & Marshall, 2003	Coetzee and Marshall 2003	<i>Litoribates caelestis</i> Pflingstl & Schatz, 2017	Pflingstl and Schatz 2017
<i>H. crozetensis</i> (Richters, 1907)	Wallwork 1962b; Ermilov et al. 2012	<i>L. bonairensis</i> Pflingstl, Baumann, Lienhard & Schatz, 2017	Pflingstl et al. 2017
<i>H. intermedius</i> Wallwork, 1963	Wallwork 1963; Sitnikova 1968	<u>Selenoribatidae</u>	
<i>H. litoralis</i> Wallwork, 1970	Wallwork 1970	<i>Arotrobates granulatus</i> Luxton, 1992	Pflingstl et al. 2021b
<i>H. marinus marinus</i> (Lohman, 1907)	Dalenius and Wilson 1958; Wallwork 1963; Sitnikova 1968	<i>Carinozetes trifoveatus</i> Pflingstl & Schuster, 2012	Pflingstl and Schuster 2012b
<i>H. marinus devilliersi</i> Engelbrecht, 1974	Engelbrecht 1974; Norton and Franklin 2018	<i>C. bermudensis</i> Pflingstl & Schuster, 2012	Pflingstl and Schuster 2012b, Pflingstl and Krisper 2014
<i>H. marinus minor</i> Wallwork, 1966	Wallwork 1966	<i>Indopacifica iohanna</i> Resch & Pflingstl, 2019	Resch et al. 2019
<i>H. marionensis</i> Engelbrecht, 1974	Engelbrecht 1974	<i>I. taiyo</i> Pflingstl, Shimano & Hiruta, 2021	Pflingstl et al. 2021b
<i>H. macquariensis</i> (Dalenius, 1958)	Wallwork 1966	<i>I. tyda</i> Pflingstl, Shimano & Hiruta, 2021	Pflingstl et al. 2021b
<i>H. necrophagus</i> Wallwork, 1967	Wallwork 1967	<i>Schusteria littorea</i> Grandjean, 1968	Grandjean 1968
<i>H. plumosus</i> Wallwork, 1966	Wallwork 1966	<i>S. melanomerus</i> Marshall & Pugh, 2000	Pflingstl 2016
<i>Podacarus auberti auberti</i> Grandjean, 1955	Grandjean 1955	<i>Selenoribates mediterraneus</i> Grandjean, 1966	Grandjean 1966
<i>P. auberti occidentalis</i> Wallwork, 1966	Wallwork 1970	<i>S. quasimodo</i> Pflingstl, 2013	Pflingstl 2013b
<i>Pseudantarcticola georgia</i> Wallwork, 1970	Wallwork 1970; Ermilov et al. 2012	<i>S. satanicus</i> Pflingstl, 2013	Pflingstl 2013b
		<i>Thalassozetes tenuisetosus</i> Bayartogtokh & Chatterjee, 2010	Bayartogtokh and Chatterjee 2010
		<i>T. canariensis</i> Pflingstl, De La Paz, Hernández-Teixidor, 2020	Pflingstl et al. 2020
		<i>T. riparius</i> Schuster, 1963	Schuster 1963