Zootaxa 5156 (1): 001–238
https://www.mapress.com/zt/

Monograph

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5156.1.1
http://zoobank.org/urn:lsid:zoobank.org:pub:A69EB824-6FF3-42CE-8C28-EB93503053BE

ZOOTAXA

5156

Echiniscidae (Heterotardigrada) of South Africa

PIOTR GĄSIOREK[1*], KATARZYNA VONČINA[1,2], MARCIN BOCHNAK[1,3], BARTŁOMIEJ SURMACZ[1,4], WITOLD MOREK[1,5] & ŁUKASZ MICHALCZYK[1‡]

[1]*Department of Invertebrate Evolution, Institute of Zoology and Biomedical Research, Faculty of Biology, Jagiellonian University, Gronostajowa 9, 30-387 Kraków, Poland*
[2] *kat.von@onet.eu; https://orcid.org/0000-0002-3210-0407*
[3] *bochnakmarcinxyz@gmail.com*
[4] *bartek9865@gmail.com; https://orcid.org/0000-0002-1593-6552*
[5] *wmorek@op.pl; https://orcid.org/0000-0003-3547-9755*
[*]*Corresponding author.* *piotr.lukas.gasiorek@gmail.com; https://orcid.org/0000-0002-2814-8117*
[‡]*Senior author.* *LM@tardigrada.net; https://orcid.org/0000-0002-2912-4870*

Magnolia Press
Auckland, New Zealand

Accepted by S. McInnes: 8 Apr. 2022; published: 27 Jun. 2022

PIOTR GĄSIORek, KATARZYNA VONČINA, MARCIN BOCHNAK, BARTŁOMIEJ SURMACZ, WITOLD MOREK & ŁUKASZ MICHALCZYK
Echiniscidae (Heterotardigrada) of South Africa
(*Zootaxa* 5156)

238 pp.; 30 cm.

27 Jun. 2022

ISBN 978-1-77688-546-6 (paperback)

ISBN 978-1-77688-547-3 (Online edition)

FIRST PUBLISHED IN 2022 BY

Magnolia Press

P.O. Box 41-383

Auckland 1041

New Zealand

e-mail: magnolia@mapress.com

https://www.mapress.com/zt

ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

Table of Contents

Abstract

The first publications on the Afrotropical tardigrade fauna date back to the beginning of the 20th century. However, the knowledge on the faunal composition, diversity and evolution of African tardigrades, including the speciose family Echiniscidae, is still fragmentary. Here, we present an extensive systematic, biogeographic, and ecological survey of echiniscid fauna of the southernmost part of the Afrotropical realm. Sampling was conducted in several biodiverse regions of South Africa: South African Woodlands and Savannahs, Cape evergreen sclerophyllous forests and scrubs, semi-desert Karoo, and the Afromontane Drakensberg and Swartberg ranges. The application of tools of integrative taxonomy allowed for the identification of 36 distinct echiniscid species grouped in five genera. Among these, as many as 19 species representing three genera, are described here as new to science: *Echiniscus attenboroughi* **sp. nov.**, *E. capensis* **sp. nov.**, *E. dentatus* **sp. nov.**, *E. draconis* **sp. nov.**, *E. gracilis* **sp. nov.**, *E. imitans* **sp. nov.**, *E. intricatus* **sp. nov.**, *E. irroratus* **sp. nov.**, *E. latruncularis* **sp. nov.**, *E. oreas* **sp. nov.**, *E. regularis* **sp. nov.**, *E. scabrocirrosus* **sp. nov.**, *E. setaceus* **sp. nov.**, *E. similaris* **sp. nov.**, *E. tetraspinosus* **sp. nov.**, *Hypechiniscus africanus* **sp. nov.** (the *exarmatus* group), *Pseudechiniscus* (*Pseudechiniscus*) *aquatilis* **sp. nov.**, *P.* (*P.*) *linnaei* **sp. nov.**, and *P.* (*Meridioniscus*) *wallacei* **sp. nov.** Moreover, *E. longispinosus* Murray, 1907 and *E. perarmatus* Murray, 1907 are formally re-described and their neotypes are established. Amendments to outdated descriptions of *E. africanus* Murray, 1907 and *E. crassispinosus* Murray, 1907 are also provided. Species descriptions and redescriptions contain detailed data on ecological preferences of species, their ontogenetic variability, sex ratios in gonochoristic/dioecious populations (males are recorded in African *Echiniscus* spp. for the first time), and, finally, on their phylogenetic relationships. The study reveals a diverse echiniscid assemblage, dominated by *Echiniscus*, that overlaps with the hotspots of Cape Floristic Region, Succulent Karoo, and Maputaland-Pondoland-Albany. According to our phylogenetic analyses, the great majority of South African *Echiniscus* species are endemics and they evolved from several species that colonised the region after the genus had originated (in contrast to earlier hypotheses, our work suggests that *Echiniscus* has the Laurasian rather than the Gondwanan origin). The remaining echiniscids found in South Africa represent pantropical or cosmopolitan species.

Key words: Afrotropical realm, biodiversity, biogeography, Echiniscoidea, limnoterrestrial, Tardigrada, taxonomy

Introduction

The southern part of Africa is remarkable because of a wide variety of ecoregions that were often evolving in separation from the rest of the continent, retaining the Gondwanan heritage of some plant and animal lineages (Gheerbrant & Rage 2006). The biogeographic distinctiveness of South Africa (Linder *et al*. 2012) evinces both in frequent cryptic speciation events that took place in isolation from the rest of the continent (Daniels *et al*. 2009) and in the presence of relictual endemic lineages in many organisms (Picker & Samways 1996), which is the reason why South Africa is recognised as a global biodiversity hotspot and why conservation of its fauna and flora has been prioritised (Cowling *et al*. 2003; Janion-Scheepers *et al*. 2016). Many of residual animal lineages co-evolved with the diversified plant assemblages that radiated exuberantly in Miocene (Linder 2003; Helme & Trinder-Smith 2006; Matenaar *et al*. 2018). Numerous ecoregions, such as Afromontane forests (*e.g*. Knysna-Amatole woods), although being small in area, are conservationally invaluable due to the stunning species richness (McDonald & Daniels 2012). Especially places characterised by great topographical heterogeneity, such as the Cape Peninsula (Cowling *et al*. 1996) harbour exceptional α-diversity, but more homogeneous savannahs, which constitute the largest biome in this part of the continent, also contribute to the total animal species richness (Foord *et al*. 2011).

Janion-Scheepers *et al*. (2016) underlined both the scarcity of studies on many animal taxa occurring in South Africa, and the generally high levels of endemism characterising groups that have already been subjected to more thorough systematic research. For example, well above 50% of Collembola, Ephemeroptera, Oribatida, and Trichoptera are recognised as endemic to South Africa (Barnard 1932, 1934; Niedbała 2006; Janion-Scheepers *et al*. 2015). Also, most likely, the vast majority of post-Gondwanan Peripatopsidae (Onychophora) found there are of ancient origin and do not exist elsewhere in the world (Daniels *et al*. 2016). However, the uniqueness of South African microfauna assemblages is usually much less evident, but also less studied. For example, a significant number of African rotifer species are cosmopolitan, thus resulting in a weak biogeographic differentiation of this continent (once called the "African anomaly", see Dumont 1983), and notably well below 50% of the South African representatives of the classes Bdelloidea and Monogononta are endemic (Sartory 1981; De Ridder 1987). This pattern is consistent with freshwater Cladocera (Branchiopoda), of which below 10% are limited to this part of Africa (Smirnov 2008). Thus, these figures stand in contrast to some animal clades characterised by a glaring 100% endemicity in South Africa (*e.g*. Tolley *et al*. 2004; Moussalli *et al*. 2009; Plisko 2012).

Tardigrades, the closest relatives of onychophorans and arthropods, belong to a group of poorly studied microinvertebrates in South Africa, which is not startling given the insufficient sampling in most parts of the continent (Jørgensen 2001; Middleton 2003; McInnes *et al*. 2017). The first observations of the phylum in this region of the World were provided by Murray (1907a, 1913), who described seven species from the British Cape Colony. Substantial contributions were made also by Dastych (1980, 1992, 1993, 2009), who erected two new genera (*Calcarobiotus* and *Paradiphascon*), and described *Ramazzottius szeptycki*, the first ramazzottiid species known to exhibit dorsolateral gibbosities. Other studies dealt with single species found in Tsitsikamma Mountains (Binda 1984; Pilato *et al*. 1991), Drakensberg (Kaczmarek *et al*. 2006), the Table Mountain (Tumanov 2020a), or KwaZulu-Natal and Swaziland regions (Meyer & Hinton 2009; Meyer *et al*. 2018). Most recently, a preliminary analysis of apochelan tardigrades extracted from the same South African samples as analysed in the present study indicated the presence of at least *ca.* 24 *Milnesium* species, including 18 potentially endemic (75%), in the region (Morek *et al.* 2021). In other words, no comprehensive survey of tardigrade fauna has been conducted in South Africa, rendering the discovery of new species in this region almost certain.

Therefore, we extensively sampled (*ca*. 550 moss and lichen samples) several ecoregions in South Africa in search of heterotardigrades to perform a diversity survey along the lines of Dastych (1988). Our study reveals a total of 36 heterotardigrade species, representing five genera, from South Africa, of which more than a half (20 spp.) are also new to science. New species are described by means of integrative taxonomy and the data are also used to elucidate echiniscid phylogeny and geographic distribution, including niche modelling for some of the analysed species. Finally, new genetic data provided novel clues aiding the resolution of relationships within *Echiniscus*, *Hypechiniscus* and *Pseudechiniscus*, and they shed some light on the geographic origin of the genus *Echiniscus*. The study illustrates the grave lack of basic knowledge about diversity of tardigrades inhabiting tropical and subtropical areas of the world.

Materials and methods

Sample collection and specimen preparation

Tardigrades were extracted from samples collected in 42 localities distributed throughout the Republic of South Africa, specifically in three provinces: Western Cape, Eastern Cape, and KwaZulu-Natal (see Fig. 1 for exemplary sampled locales, Fig. 120A for sampling results, and Supplementary Material 1 for collection details). Additional, extra-African samples with *Echiniscus perarmatus* are also listed in SM1. The air-dried samples, stored in paper envelopes, were rehydrated in water for 6–12 hours, and the obtained sediment was poured into Petri dishes to search for microfauna under a stereomicroscope with dark field illumination. Individuals isolated from the samples were used for the following analyses: imaging under light contrast microscopy (LCM: morphology and morphometry), imaging under scanning electron microscopy (SEM), DNA sequencing (integrative species delineation and molecular phylogenetics). If a sample contained hundreds of echiniscids, they were frozen in a vial and kept in freezer for further investigation. Type and neotype series were divided between four tardigrade collections: at the Jagiellonian University (Poland), University of Catania (Italy), Natural History Museum of Denmark (accession numbers: NHMD921535–65), and the South African Museum (Cape Town, RSA).

Microscopy and imaging

Individuals for light microscopy and morphometry were either first air-dried on microscope slides, and then mounted in a small drop of Hoyer's medium (for medium-sized and large echiniscids, *i.e*. >200 μm in body length), or directly mounted in Hoyer's medium and slightly diluted in distilled water (for small echiniscids, *i.e*. <200 μm in body length) to achieve an optimal relaxation of animals, and then examined under an Olympus BX53 light microscope with phase (PCM) and Nomarski contrasts (NCM), associated with an Olympus DP74 digital camera. For the purpose of SEM observations, living animals were relaxed in a hot water bath in a glass cube, dehydrated *via* ethanol/acetone series, then subjected to CO_2 critical point drying, and finally sputter coated with a thin layer of gold. Specimens were examined under high vacuum in a Versa 3D DualBeam scanning electron microscope at the ATOMIN facility of the Jagiellonian University, Kraków, Poland. All figures were assembled in Corel Photo-Paint X7. For deep structures that could not be fully focused in a single light microscope photograph, a series of 2–12 images was taken every *ca*. 0.1 μm and then assembled into a single deep-focus image.

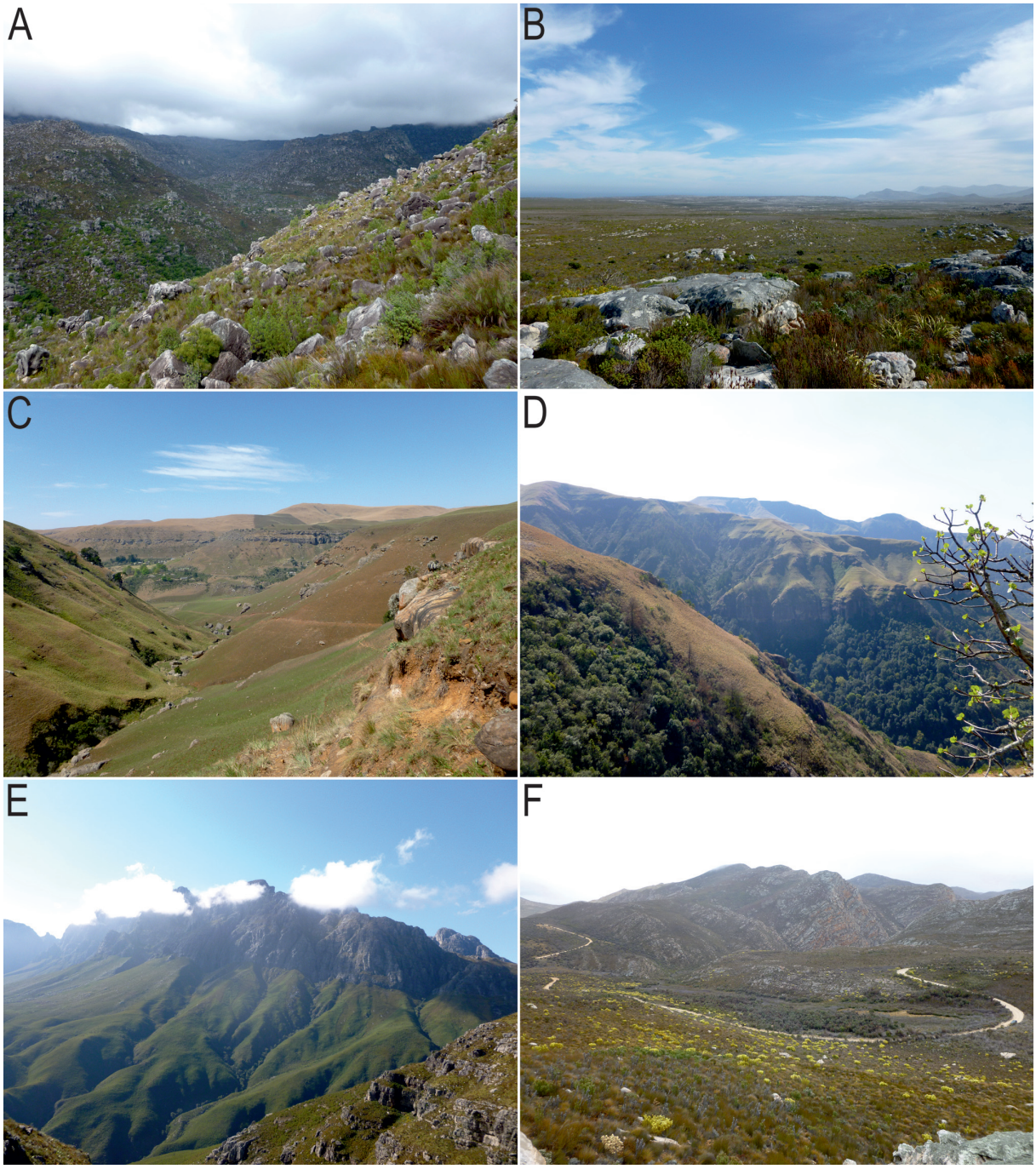

FIGURE 1. Exemplary collecting sites and type localities (echiniscid species found in given localities are listed in brackets): A—Bain's Kloof Pass (*E. attenboroughi* **sp. nov.**, *E. dentatus* **sp. nov.**, *E. draconis* **sp. nov.**, *E. gracilis* **sp. nov.**, *E. irroratus* **sp. nov.**, *E. lichenorum*, *E. longispinosus*, *E. setaceus* **sp. nov.**, *E. virginicus*), B—Cape of Good Hope (*E. capensis* **sp. nov.**, *E. dentatus* **sp. nov.**,), C—Garden Castle Nature Reserve, Drakensberg (*E. baius*, *E. blumi*, *E. cavagnaroi*, *E. imitans* **sp. nov.**, *E. longispinosus*, *E. oreas* **sp. nov.**, *E. pellucidus*, *E. regularis* **sp. nov.**, *E. scabrospinosus*, *E. virginicus*, *H. africanus* **sp. nov.**, *P. aquatilis* **sp. nov.**, *P.* cf. *ehrenbergi*, *P. wallacei* **sp. nov.**), D—Giants Castle Nature Reserve, Drakensberg (*C. madagascariensis*, *E. africanus*, *E. baius*, *E. blumi*, *E. draconis* **sp. nov.**, *E. imitans* **sp. nov.**, *E. intricatus* **sp. nov.**, *E. lichenorum*, *E. longispinosus*, *E. oreas* **sp. nov.**, *E. pellucidus*, *E. perarmatus*, *E. regularis* **sp. nov.**, *E. scabrospinosus*, *E. tetraspinosus* **sp. nov.**, *E. tristis*, *E. virginicus*, *P.* cf. *ehrenbergi*, *P. wallacei* **sp. nov.**), E—Jonkershoek Nature Reserve (*C. madagascariensis*, *E. dentatus* **sp. nov.**, *E. gracilis* **sp. nov.**, *E. irroratus* **sp. nov.**, *E. latruncularis* **sp. nov.**, *E. longispinosus*, *E. merokensis*, *E. scabrospinosus*, *E. setaceus* **sp. nov.**, *P.* cf. *ehrenbergi*, *P. wallacei* **sp. nov.**), F—Swartberg (*E. attenboroughi* **sp. nov.**, *E. dentatus* **sp. nov.**, *E. draconis* **sp. nov.**, *E. imitans* **sp. nov.**, *E. lichenorum*, *E. longispinosus*, *E. scabrocirrosus* **sp. nov.**, *E. setaceus* **sp. nov.**, *E. similaris* **sp. nov.**).

Morphometrics and terminology

All measurements are given in micrometres (μm) and were performed under PCM. Structures were measured only if they were not damaged and if their orientations were suitable. Body length was measured from the anterior to the posterior end of the body, excluding the hind legs. The *sp* ratio is the ratio of the length of a given structure to the length of the scapular plate (Dastych 1999); presented in italics in the text. Claw height was measured from the middle of the claw base to the highest point of the branch curvature. Claw spur length was measured as the shortest line joining the tip of the spur and its base, i.e. in the medial point between the edges of the spur base. The position of claw spurs in relation to claw height was measured from the middle of the claw base to the medial point between edges of the spur base. Morphometric data were handled using the Echiniscoidea ver. 1.3 template available from the Tardigrada Register, www.tardigrada.net/register (Michalczyk & Kaczmarek 2013). The *t*-tests were computed for morphometric comparisons of the sexes only if morphometric ranges were overlapping. Measurements of adult females of *Pseudechiniscus* spp. were used in the formulation of differential diagnoses, if not specified otherwise. The terminology follows Kristensen (1987) and subsequent changes proposed in Gąsiorek *et al*. (2019a). Body and trunk appendage configuration is given according to Ramazzotti & Maucci (1983) and amendments by Gąsiorek *et al*. (2017). The term "plate faceting" describes the presence of clearly defined thickened epicuticular ridges that join distinct plate surfaces, which are positioned at different angles to each other. The classification of echiniscids follows Gąsiorek & Michalczyk (2020a).

Comparative material and redescriptions

During the prepration of differential diagnoses of new species and shortened descriptions of other species, the individuals of the following species were used for comparisons: *Bryodelphax parvulus* Thulin, 1928 (details in Gąsiorek *et al*. 2020), *Cornechiniscus madagascariensis* Maucci, 1993 (Gąsiorek & Michalczyk 2020a), *Hypechiniscus cataractus* Gąsiorek *et al*., 2021, *H. crassus* Gąsiorek *et al*., 2021, and *H. exarmatus* (Murray, 1907) (Gąsiorek *et al*. 2021b, d), *Pseudechiniscus suillus* (Ehrenberg, 1853) (Grobys *et al*. 2020). For the purpose of the phylogeny reconstruction, all *Echiniscus s.s*. spp. from Gąsiorek *et al*. (2019a) were provided with the both ITS and COI sequences. The detailed collection data/information for other *Echiniscus* spp. used for comparisons: (1) *E. lapponicus* Thulin, 1911 was extracted from a sample collected in the Norvegian province of Finnmark (69°30'22"N, 25°28'16"E; 287 m asl; 4 km N from Karasjok, moss+lichen on a stone, forest; 29.07.2017), (2) *E. quadrispinosus* Richters, 1902 was found in a sample from St. Ulrich im Schwarzwald (47°54'28"N, 7°50'39"E; 596 m asl; lichen from tree trunk, forest; 05.2018), (3) a syntype of *E. murrayi* Iharos, 1969 was examined in the Hungarian Natural History Museum in Budapest.

The four *Echiniscus* species described as new from Africa by Murray (1907a), *E. africanus*, *E. crassispinosus*, *E. longispinosus*, and *E. perarmatus*, lack type series (Morgan 1977) and their descriptions required clarifications to meet current standards in tardigrade taxonomy. Although we found all four species in our survey, we establish neotype series only for the two latter taxa, as the low sample size did not allow us to obtain DNA barcodes for the first two species.

Distribution data, maps and ecological niche modelling

Spatial geographic distributions of species were presented in simplified maps. All available and trustworthy records extracted from the literature (after McInnes *et al*. 2017; Meyer *et al*. 2018) and those obtained in this survey were utilised. Records referring to large geographic entities (*e.g*. Cape Colony) were discarded as being too imprecise. The maps were constructed using the *R* language for statistical computing (R Core Team 2020) with the package '*maps*' (Becker *et al*. 2013).

We used the ecological niche modelling (ENM) approach to predict the current potential distribution of three widely distributed species: *E. cavagnaroi*, *E. perarmatus*, and *E. scabrospinosus*. The ENM was performed with the use of Maxent algorithm, ver. 3.4.1103, with the *kuenm* package (Cobos *et al*. 2019), in *R* (R Core Team 2020). To eliminate a potential bias of clustered occurrences, the datasets were filtered so that there was only one record per 5 arc-minute cell for each species. Thus, 15 occurrence records for *E. cavagnaroi*, 21 records for *E. perarmatus*, and 19 records for *E. scabrospinosus* were used in modelling. We used the bioclimatic variables (Fick & Hijmans 2017) available in WorldClim version 2.1106 (http://www.worldclim.com/version2), with a 5-arc-minute resolution, as environmental variables for Maxent modelling. Out of 19 available variables, we excluded those that combined temperature and precipitation (bio8, bio9, bio18 and bio19), because they displayed artificial discontinuities between adjacent grid cells in some areas, which could introduce artefacts to modelling (Escobar *et al*. 2014). From

the remaining 15 bioclimatic variables, we removed the highly correlated ones (Spearman rank correlation value <|0.85|) and selected those with the highest importance based on jack-knife procedure (regularised training gain) for each species. Finally, we used six variables in the ENM: bio2 (mean diurnal range), bio4 (temperature seasonality), bio10 (mean temperature of the warmest quarter), bio12 (annual precipitation), bio14 (precipitation of the driest month) and bio15 (precipitation seasonality). Based on these variables and randomly selected 60% of occurrence records, we created 255 candidate models for each species combining 17 values of regularisation multiplier (0.1–1.0 at intervals 0.1, 2–6, 8 and 10) and 15 combinations of four feature classes (linear = l, quadratic = q, product = p, and hinge = h). Then, all candidate models were evaluated based on the partial ROC approach (Peterson *et al*. 2008) and predictive power of model based on omission rates (Anderson *et al*. 2003), using the test data subset (40% of species records not included in training data). Statistically significant models with omission rates ≤10% were selected as the best models. Less than 10 best models for each species were selected according to these criteria. For each parameter setting selected as the best, we created 10 bootstrap replicates of models with complemental log-log (cloglog) output format (Phillips *et al*. 2017). Models were calibrated and projected using the whole world as a training area and all runs were set with 500 iterations and 10,000 background points. Final maps of potential distribution of both species were created in QGIS (QGIS Development Team 2020) by averaging all best models.

Genotyping and phylogenetics

DNA was extracted from individual animals following a Chelex® 100 resin (Bio-Rad) extraction method by Casquet *et al*. (2012) with modifications described in detail in Stec *et al*. (2015). All specimens were mounted in water on temporary slides and examined under PCM before DNA extraction to ensure correct taxonomic identifications. Hologenophores, retrieved from extraction vials, and paragenophores (Pleijel *et al*. 2008) were retrieved from extraction vials, mounted on permanent slides, and are deposited in the Institute of Zoology and Biomedical Research in Kraków. We sequenced four nuclear and one mitochondrial DNA fragments: the small and the large ribosome subunit (18S rRNA and 28S rRNA), the internal transcribed spacers 1 and 2 (ITS-1 and ITS-2), and the cytochrome oxidase subunit I (COI). All fragments were amplified and sequenced according to the protocols described in Stec *et al*. (2015); primers and original references for specific PCR programmes are listed in Table 1. Sequences were aligned using default settings of MAFFT7 (Katoh *et al*. 2002; Katoh & Toh 2008) under Q-INS-i strategy. Uncorrected pairwise distances were calculated using MEGA7 with the "complete deletion" (Kumar *et al*. 2016) and are enclosed as the Supplementary Material 2. Type DNA sequences are deposited in GenBank (Table 2).

TABLE 1. Primers and references for specific protocols for amplification of the five DNA fragments sequenced in the study.

DNA fragment	Primer name	Primer direction	Primer sequence (5'-3')	Primer source	PCR programme*
18S rRNA	18S_Tar_Ff1	forward	AGGCGAAACCGCGAATGGCTC	Stec *et al*. (2017)	Zeller (2010)
	18S_Tar_Rr2	reverse	CTGATCGCCTTCGAACCTCTAACTTTCG	Gąsiorek *et al*. (2017)	
28S rRNA	28S_Eutar_F	forward	ACCCGCTGAACTTAAGCATAT	Gąsiorek *et al*. (2018a)	Mironov *et al*. (2012)
	28SR0990	reverse	CCTTGGTCCGTGTTTCAAGAC	Mironov *et al*. (2012)	
ITS-1	ITS1_Echi_F	forward	CCGTCGCTACTACCGATTGG	Gąsiorek *et al*. (2019b)	Wełnicz *et al*. (2011)
	ITS1_Echi_R	reverse	GTTCAGAAAACCCTGCAATTCACG		
ITS-2	ITS3	forward	GCATCGATGAAGAACGCAGC	White *et al*. (1990)	
	ITS4	reverse	TCCTCCGCTTATTGATATGC		
COI	bcdF01	forward	CATTTTCHACTAAYCATAARGATATTGG	Dabert *et al*. (2008)	
	bcdR04	reverse	TATAAACYTCDGGATGNCCAAAAAA		
	LCO1490-JJ	forward	CHACWAAYCATAAAGATATYGG	Astrin & Stüben (2008)	Michalczyk *et al*. (2012)
	HCO2198-JJ	reverse	AWACTTCVGGRTGVCCAAARAATCA		

*—All PCR programmes are also provided in Stec *et al.* (2015).

TABLE 2. GenBank accession numbers for the taxa sequenced/described in this study (all barcoded populations).

Taxon	Population (s)	18S rRNA	28S rRNA	ITS–1	ITS–2	COI
Cornechiniscus madagascariensis	ZA.228	**OM516767**	**OM516973**	**OM516839–40**	–	**OM509659–60**
Echiniscus attenboroughi **sp. nov.**	ZA.015, ZA.436	**OM516768–70**	**OM516974–96**	**OM516841–3**	**OM516911–3**	**OM509661**
Echiniscus blumi	ZA.211	**OM516771**	**OM516977**	**OM516844**	**OM516914**	**OM509662**
Echiniscus capensis **sp. nov.**	ZA.378	**OM516772**	**OM516978**	**OM516845**	**OM516915**	**OM509663**
Echiniscus cavagnaroi	ZA.037, ZA.404, ZA.416	**OM516773–5**	**OM516979–81**	**OM516846–8**	**OM516916–8**	**OM509664–5**
Echiniscus dentatus **sp. nov.**	ZA.022, ZA.025	**OM516776**	**OM516982**	**OM516849**	**OM516919**	**OM509666–667**
Echiniscus draconis **sp. nov.**	ZA.056, ZA.431, ZA.436	**OM516778–80**	**OM516983–6**	**OM516850–3**	**OM516920–3**	**OM509668–71**
Echiniscus gracilis **sp. nov.**	ZA.554	**OM516781**	**OM516987**	**OM516854**	**OM516924**	**OM509672**
Echiniscus imitans **sp. nov.**	ZA.227	**OM516782**	**OM516988**	**OM516855**	**OM516925**	**OM509673**
Echiniscus intricatus **sp. nov.**	ZA.218, ZA.219	**OM516783–7**	**OM516989–93**	**OM516856–60**	**OM516926–30**	**OM509674–5**
Echiniscus irroratus **sp. nov.**	ZA.504	**OM516788**	**OM516994**	**OM516861**	**OM516931**	–
Echiniscus lapponicus	NO.379	**OM516789**	**OM516995**	**OM516862**	**OM516932**	**OM509676**
Echiniscus latruncularis **sp. nov.**	ZA.502, ZA.545	**OM516790–1**	**OM516996–7**	**OM516863–4**	**OM516933–4**	**OM509677–8**
Echiniscus lichenorum	ES.156, ES.162, ES.166	**OM516792–4**	**OM516998–517000**	**OM516865–7**	**OM516935–7**	–
	ZA.010, ZA.040	**OM516795–6**	**OM517001–2**	**OM516868–9**	**OM516938–9**	**OM509679–80**
Echiniscus longispinosus	ZA.273	**OM516797**	**OM517003**	**OM516870**	**OM516940**	–
Echiniscus oreas **sp. nov.**	ZA.183, ZA.204, ZA.206	**OM516798–801**	**OM517004–7**	**OM516871–4**	**OM516941–4**	**OM509681–3**
Echiniscus pellucidus	ZA.204	**OM516802**	**OM517008**	**OM516875**	**OM516945**	**OM509684**
Echiniscus perarmatus	ID.518	**OM516803**	**OM517009**	**OM516876**	**OM516946**	**OM509685**
	ID.850	**OM516804**	**OM517010**	**OM516877**	**OM516947**	**OM509686**
	MM.010	**OM516805**	**OM517011**	**OM516878**	**OM516948**	**OM509687**
	MU.001	**OM516806**	**OM517012**	**OM516879**	–	**OM509688**
	ZA.214	**OM516807**	**OM517013**	**OM516880**	**OM516949**	**OM509689**
Echiniscus quadrispinosus	DE.199	**OM516808**	**OM517014**	**OM516881**	**OM516950**	**OM509690**

.....continued on the next page

TABLE 2. (Continued)

Taxon	Population (s)	18S rRNA	28S rRNA	ITS–1	ITS–2	COI
Echiniscus regularis **sp. nov.**	ZA.225	**OM516809–11**	**OM517015–7**	**OM516882–4**	**OM516951–3**	–
Echiniscus scabrocirrosus **sp. nov.**	ZA.431, ZA.436	**OM516812–4**	**OM517018–20**	**OM516885–7**	**OM516954–6**	**OM509691**
Echiniscus scabrospinosus	ZA.098, ZA.196, ZA.200, ZA.202, ZA.231, ZA.288	**OM516815–23**	**OM517021–9**	**OM516888–96**	**OM516957–60**	**OM509692–3**
Echiniscus setaceus **sp. nov.**	ZA.029, ZA.490, ZA.502, ZA.513, ZA.532	**OM516824–31**	**OM517030–7**	**OM516897–904**	**OM516961–8**	–
Echiniscus similaris **sp. nov.**	ZA.449	**OM516832**	**OM517038**	**OM516905**	**OM516969**	**OM509694**
Echiniscus tetraspinosus **sp. nov.**	ZA.130	**OM516833**	**OM517039**	**OM516906**	**OM516970**	–
Echiniscus tristis	ZA.201	**OM516834–5**	**OM517040–1**	**OM516907–8**	**OM516971–2**	**OM509695**
Echiniscus virginicus	ZA.015, ZA.206	**OM516836–7**	**OM517042–3**	**OM516909–10**	–	–
Hypechiniscus africanus **sp. nov.**	ZA.246	**OM516838**	**OM517044**	–	–	–
Pseudechiniscus aquatilis **sp. nov.**	ZA.246	–	MW032094	MW032184	–	–
Pseudechiniscus cf. *ehrenbergi*	ZA.157, ZA.183, ZA.190, ZA.202, ZA.246	MW031997, MW032001, MW032002, MW032003–4, MW032005	MW032086, MW032090, MW032091, MW032092–3, MW032095	MW032176, MW032180, MW032181, MW032182–3, MW032185	–	–
Pseudechiniscus linnaei **sp. nov.**	ZA.366	MW032007–8	MW032097–8	MW032187–8	–	–
Pseudechiniscus wallacei **sp. nov.**	ZA.177, ZA.178, ZA.256	MW031998–9, MW032000, MW032006	MW032087–8, MW032089, MW032096	MW032177–8, MW032179, MW032186	–	MW031217–8

The aligned sequences of nuclear markers for all *Echiniscus* spp. sequenced to date and of sufficient quality and length were processed using GBLOCKS v.0.91b (Castresana 2000) in order to eliminate uninformative gaps, with the 'more stringent' settings. As a result, GBLOCKS trimmed all four datasets (18S rRNA, 28S rRNA, ITS-1, ITS-2) not more than to 62% of the initial alignment length. The sequences were then concatenated in SequenceMatrix (Vaidya *et al*. 2011) to produce the final, 2604 bp long, alignment. *Diploechiniscus oihonnae* (Richters, 1903) and *Testechiniscus spitsbergensis tropicalis* Gąsiorek *et al*., 2018 were used as an outgroup. The COI was not implemented in the phylogenetic analysis due to many gaps in the dataset (see Table 2), and because this marker is unsuitable in the phylogenetic inference, with the exception of close relationships (e.g. in complexes of species, or in monospecific multipopulation studies), which was not the case. Each marker was treated as a separate partition, and the models of evolution were chosen using ModelFinder in the Maximum Likelihood (ML) analysis (Chernomor *et al*. 2016; Kalyaanamoorthy *et al*. 2017), and Partition Finder 2.1.1 in the Bayesian inference (BI) analysis (Lanfear *et al*. 2017), according to the Bayesian Information Criterion. ML topologies were constructed using IQ-TREE (Nguyen *et al*. 2015; Trifinopoulos *et al*. 2016). Strength of support for internal nodes of ML construction was measured using 1000 ultrafast bootstrap replicates (Hoang *et al*. 2018). BI marginal posterior probabilities were calculated using MrBayes v.3.2 (Ronquist & Huelsenbeck 2003). Random starting trees were used, and the analysis was run for ten million generations, sampling the Markov chain every 1000 generations. An average standard deviation of split frequencies of <0.01 was used as a guide to ensure that the two independent analyses had converged. The program Tracer v.1.3 (Rambaut *et al*. 2014) was then used to ensure that Markov chains had reached stationarity and to determine the correct 'burn-in' for the analysis, which was the first 10% of generations. The ESS values were >200, and a consensus tree was obtained after summarising the resulting topologies and discarding the 'burn-in'. All final consensus trees were viewed and visualised using FigTree v.1.4.3 (available at: https://tree.bio.ed.ac.uk/software/figtree). Analogous phylogenetic inference was applied to the recently published phylogenies of *Hypechiniscus* and *Pseudechiniscus* (Gąsiorek *et al*. 2021a, d), with the exception of the GBLOCKS trimming.

Data deposition
All DNA sequences are deposited in GenBank, and morphometric data are available as Supplementary Material 3 and at Tardigrada Register.

Results

Systematic account

Phylum: Tardigrada Doyère, 1840

Class: Heterotardigrada Marcus, 1927

Order: Echiniscoidea Richters, 1926

Family: Echiniscidae Thulin, 1928

Genus: *Bryodelphax* Thulin, 1928

1. Bryodelphax sp. nov.
Figures 2–5, Tables 3–4

Data Source:
A total of 23 specimens (12 ♀♀, 5 juveniles and 6 specimens of unknown life stage):
- Sample ZA.261: 17 specimens (12 ♀♀ and 5 juveniles on slides) + 6 specimens used for an unsuccesful DNA sequencing; found together with *Pseudechiniscus (Pseudechiniscus)* cf. *ehrenbergi* and *P. (Meridioniscus) wallacei* **sp. nov.**

Description. Mature females (*i.e*. from the third instar onwards; measurements and statistics in Table 3). Body stubby (Fig. 2–3), slightly yellowish with minuscule red eyes present in live specimens; colours disappeared soon after mounting in Hoyer's medium. Elongated cephalic papillae (secondary clavae, Fig. 2), attached to the head cuticle along most of their length (Fig. 4A) and small, elongated (primary) clavae; cirri growing out from bulbous cirrophores (Fig. 2, 4A). Cirri *A* of a moderate size (*ca*. 25–30% of the body length). Ten weakly outlined peribuccal papulae present around the mouth opening (visible only under SEM; Fig. 4A).

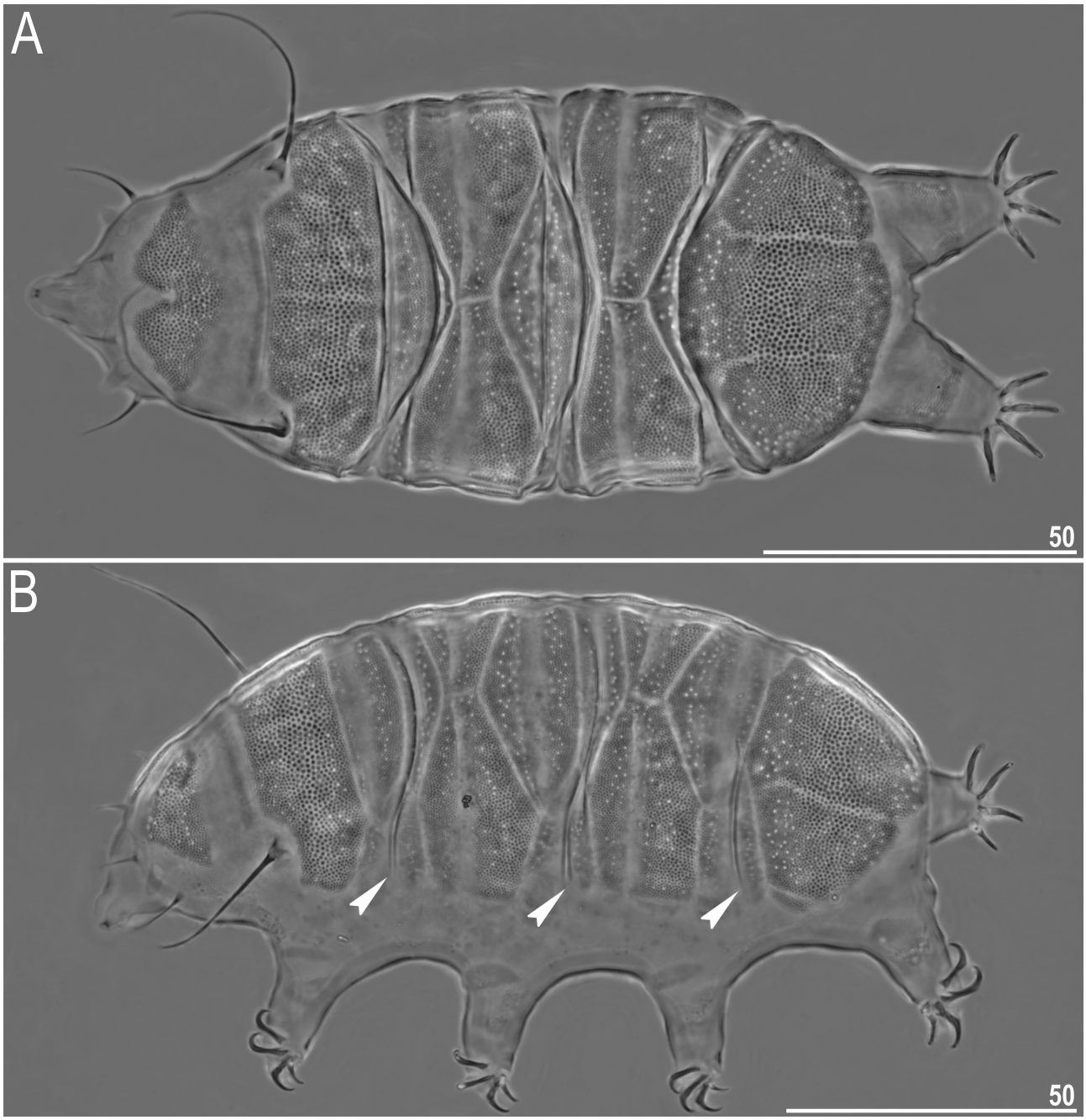

FIGURE 2. Habitus of *Bryodelphax* **sp. nov.** (PCM, females): A—dorsal view, B—dorsolateral view. Arrowheads indicate supplementary dorsolateral platelets. Scale bars = 50 μm.

Dorsal plates with a simple type of sculpturing, comprising an evident layer of endocuticular pillars visible as black dots under PCM, and numerous pores visible as bright dots under PCM (Fig. 2–3, 4B–D). The largest pillars distributed in the central and centrolateral portions of the scapular and caudal (terminal) plates (Fig. 2). Mean pore density ±SD (N=10 measured specimens): (1) central portion of the scapular plate: 12 ±2 pores/100 μm^2, (2) anterior portion of the median plate 2: 16 ±3 pores/100 μm^2, (3) posterior portion of the paired segmental plate II: 11 ±3 pores/100 μm^2, (4) anterior portion of the caudal plate: 16 ±3 pores/100 μm^2. Epicuticular ornamentation or sutures

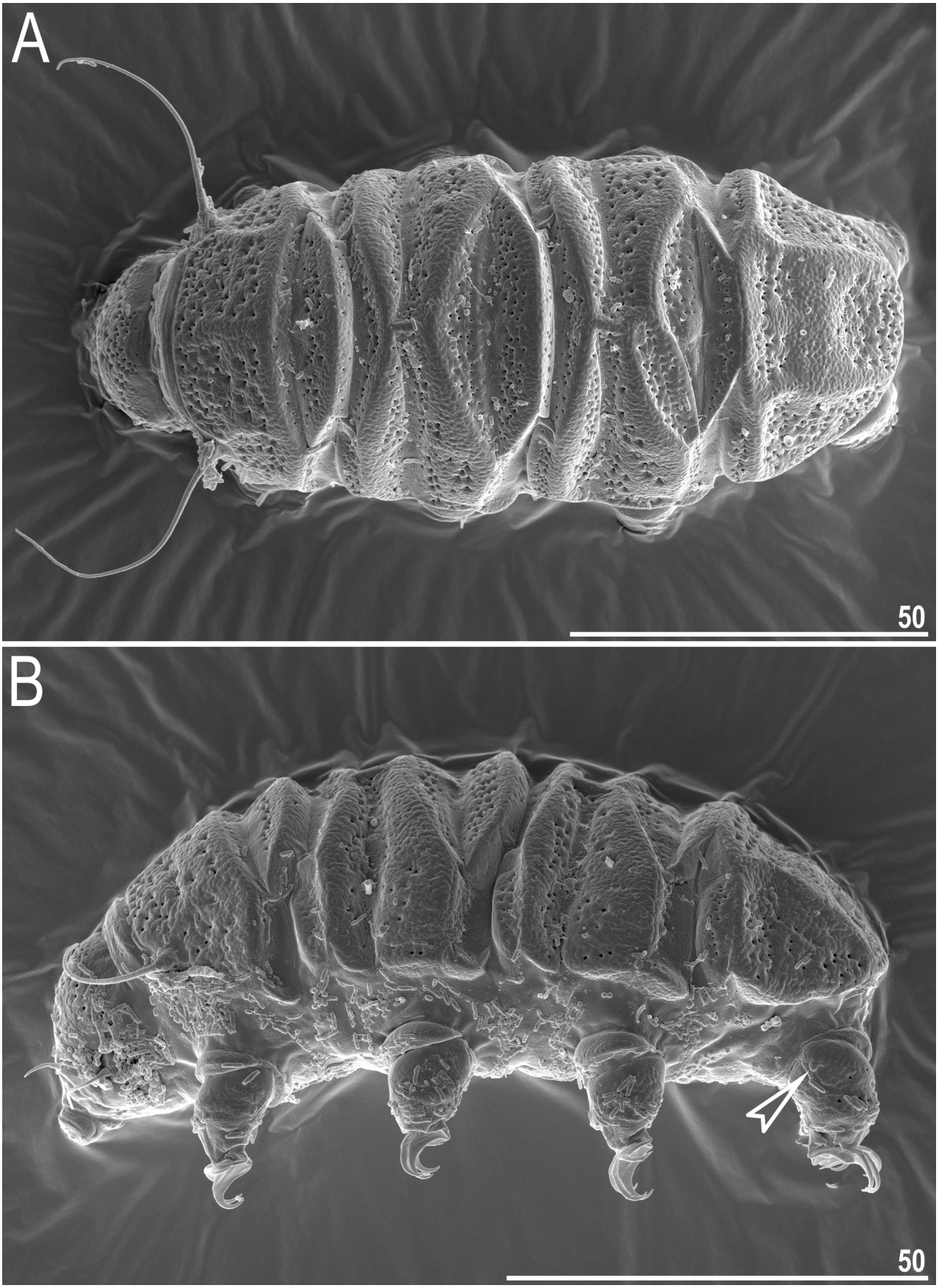

FIGURE 3. Habitus of *Bryodelphax* **sp. nov.** (SEM, females): A—dorsal view, B—lateral view (empty arrowhead indicates papilla IV). Scale bars = 50 μm.

absent. The cephalic plate with a wide funnel-shaped anterior incision, the cervical (neck) plate is barely demarcated from the scapular plate, formed only as thin grey belt without pillars (Fig. 2, 4B). The scapular plate rectangular (Fig. 2, 4B). Paired segmental plates divided into much narrower anterior and a dominant posterior part by a smooth, thin transverse stripe (Fig. 2–3, 4C). The caudal (terminal) plate with longitudinal crests reaching its anterior margin (Fig. 2), clearly visible as ridges under SEM (Fig. 3, 4D). Median plate 1 unipartite, whereas median plate 2 divided into well-defined parts, with a wide smooth space between them (Fig. 2, 3A, 4C). Median plate 3 bipartite and also porous (Fig. 2B, 3A, 4D). Three pairs of supplementary lateral platelets between the scapular and paired segmental plates I, between the paired segmental plates I–II, and between paired segmental plate I and the caudal plate (Fig. 2B, 3B). Within each pair of platelets, the posterior portion may be more porous (Fig. 3B). Ventral cuticle with minute endocuticular pillars distributed throughout the whole venter, but ventral plates absent. Sexpartite gonopore placed anteriorly to legs IV, and a trilobed anus between legs IV.

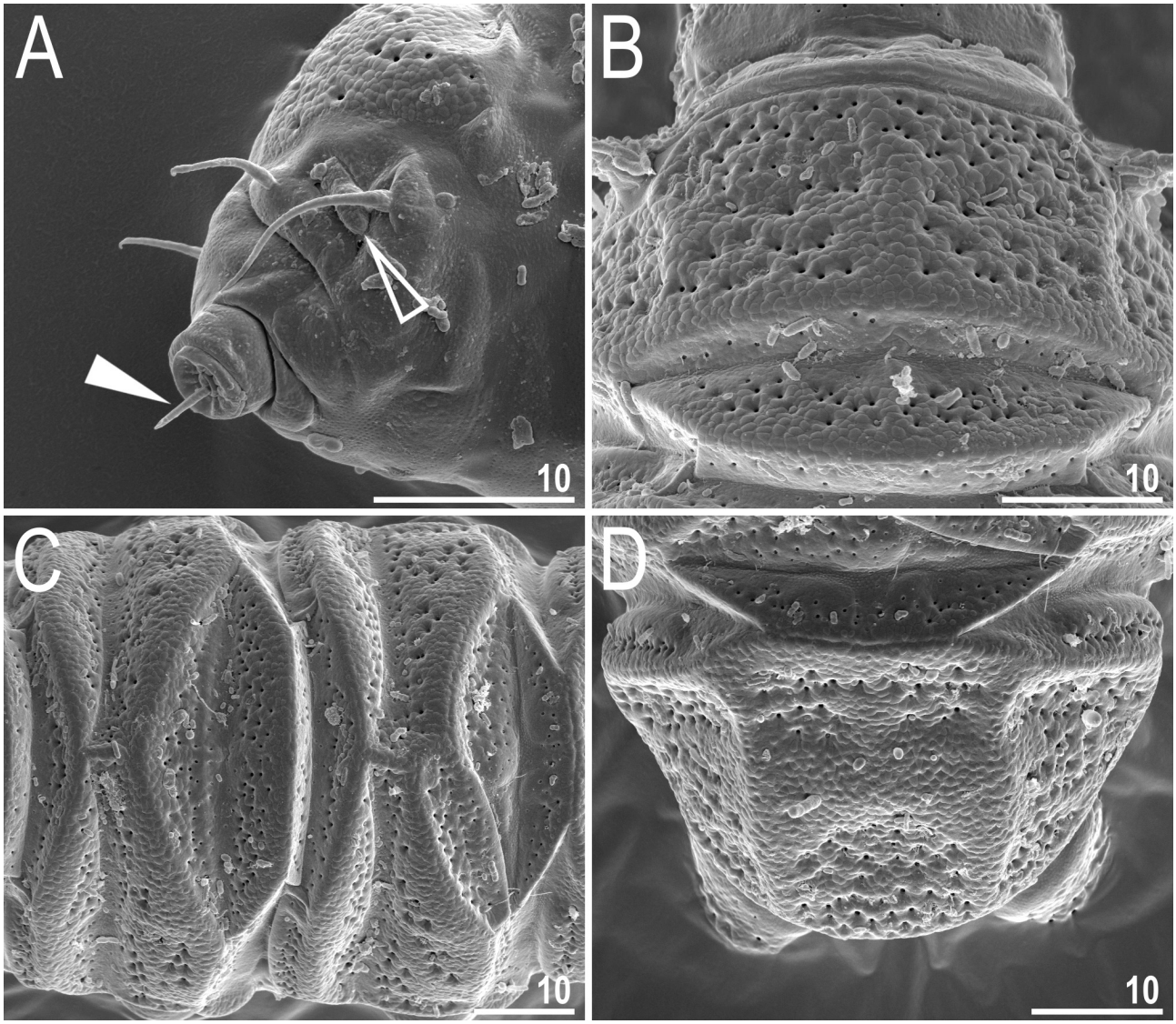

FIGURE 4. Head and dorsal sculpturing of *Bryodelphax* **sp. nov.** (SEM, females): A—cephalic appendages (arrowhead indicates the stylet protruding through the mouth opening, whereas empty arrowhead points cephalic papilla), B—scapular plate, C—paired segmental and median plates, D—caudal (terminal) plate. Scale bars = 10 μm.

Pedal plates I–III absent, pedal plate IV developed as an irregular thickening in the central portion of the leg (Fig. 2A). Distinct pulvini on all legs (Fig. 2B). Papilla or spine on leg I absent and a papilla on leg IV present, hardly visible under PCM (see Table 3), but obvious under SEM (Fig. 3B). Claws slender and *Pseudechiniscus*-like. Claws IV slightly longer than claws I–III (Table 3). All external claws smooth (Fig. 5). All internal claws with acute spurs positioned at *ca.* 1/4 of the claw height and closely adjacent to the claw.

TABLE 3. Measurements [in µm] of selected morphological structures of the adult females of *Bryodelphax* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD	
		µm			*sp*			µm	*sp*	µm	*sp*
Body length	12	126	–	157	*692*	–	*836*	143	*766*	8	*42*
Scapular plate length	12	17.8	–	19.3		–		18.6	–	0.5	–
Head appendages lengths											
Cirrus *internus*	12	5.8	–	7.2	*30.2*	–	*40.4*	6.4	*34.2*	0.4	*2.9*
Cephalic papilla	11	3.9	–	6.3	*20.2*	–	*35.4*	5.1	*27.6*	0.6	*3.8*
Cirrus *externus*	12	9.9	–	13.7	*54.4*	–	*73.8*	12.1	*64.8*	1.1	*5.2*
Clava	7	3.9	–	4.9	*20.7*	–	*26.5*	4.4	*23.4*	0.4	*2.1*
Cirrus *A*	9	34.5	–	42.4	*188.5*	–	*225.5*	38.4	*204.9*	2.7	*11.8*
Cirrus *A*/Body length ratio	9	24%	–	31%		–		27%	–	2%	–
Body appendages lengths											
Papilla on leg IV length	2	1.2	–	1.4	*6.5*	–	*7.3*	1.3	*6.9*	0.1	*0.6*
Claw I heights											
Branch	12	7.1	–	8.4	*38.7*	–	*45.5*	7.9	*42.4*	0.4	*2.2*
Spur	10	1.1	–	1.7	*6.0*	–	*9.2*	1.4	*7.3*	0.2	*1.0*
Spur/branch height ratio	10	14%	–	21%		–		17%	–	2%	–
Claw II heights											
Branch	12	7.1	–	8.2	*38.8*	–	*44.8*	7.6	*40.9*	0.4	*2.0*
Spur	10	1.1	–	1.7	*6.0*	–	*9.2*	1.3	*7.2*	0.2	*1.0*
Spur/branch height ratio	10	15%	–	24%		–		18%	–	3%	–
Claw III heights											
Branch	12	6.7	–	8.3	*36.6*	–	*46.6*	7.7	*41.1*	0.5	*2.5*
Spur	11	1.0	–	1.8	*5.3*	–	*9.7*	1.3	*7.1*	0.3	*1.6*
Spur/branch height ratio	11	12%	–	23%		–		17%	–	4%	–
Claw IV heights											
Branch	12	7.6	–	10.0	*41.5*	–	*56.2*	9.0	*48.5*	0.8	*4.2*
Spur	5	1.4	–	1.9	*7.7*	–	*10.4*	1.7	*9.1*	0.2	*1.1*
Spur/branch height ratio	5	17%	–	21%		–		19%	–	2%	–

Juveniles (*i.e*. the second instar, measurements and statistics in Table 4). On average smaller, but with no qualitative differences with regard to adults.

Larvae. Unknown.

Eggs. Up to one round, yellowish egg per exuvia was found.

DNA markers and phylogenetic position. The position remains unknown, because all four DNA markers failed to amplify despite the use of numerous primer combinations (this suggests that the genetic material deteriorated prior to our analyses).

Geographic distribution. Only reported from a single locality in South Africa (Fig. 120B).

Remarks. This new species belongs to the *B. parvulus* group, which is taxonomically challenging, especially for the lack of an integrative redescription of *B. parvulus* Thulin, 1928. This African population was compared to congeners without the dentate collar on legs IV, but given the lack of DNA sequences and vague original description of *B. parvulus*, we refrained from naming the African specimens as a new species.

Raw measurements. Supplementary Materials (SM.03).

TABLE 4. Measurements [in µm] of selected morphological structures of the juvenile females of *Bryodelphax* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD	
		µm			*sp*			µm	*sp*	µm	*sp*
Body length	5	116	–	138	*686*	–	*794*	130	*755*	9	*44*
Scapular plate length	5	15.5	–	18.8		–		17.3	–	1.2	–
Head appendages lengths											
Cirrus *internus*	5	4.3	–	6.5	*27.7*	–	*37.4*	5.7	*33.0*	0.9	*4.1*
Cephalic papilla	4	3.2	–	5.0	*20.6*	–	*28.2*	4.4	*26.0*	0.8	*3.6*
Cirrus *externus*	5	9.8	–	11.3	*52.1*	–	*67.1*	10.5	*61.2*	0.5	*5.6*
Clava	3	2.8	–	4.2	*18.1*	–	*24.1*	3.6	*20.8*	0.7	*3.1*
Cirrus *A*	5	28.0	–	38.4	*180.6*	–	*219.0*	35.7	*205.7*	4.4	*15.0*
Cirrus *A*/Body length ratio	5	24%	–	30%		–		27%	–	2%	–
Claw I heights											
Branch	5	6.2	–	7.6	*36.8*	–	*41.2*	6.9	*39.8*	0.6	*1.7*
Spur	3	1.0	–	1.0	*5.6*	–	*6.5*	1.0	*6.0*	0.0	*0.4*
Spur/branch height ratio	3	14%	–	16%		–		15%	–	1%	–
Claw II heights											
Branch	5	5.9	–	7.8	*38.1*	–	*45.9*	7.0	*40.4*	0.8	*3.2*
Spur	5	0.9	–	1.4	*5.1*	–	*8.0*	1.1	*6.1*	0.2	*1.1*
Spur/branch height ratio	5	13%	–	21%		–		15%	–	3%	–
Claw III heights											
Branch	5	5.7	–	7.5	*36.8*	–	*41.8*	6.8	*39.5*	0.7	*1.9*
Spur	5	0.9	–	1.3	*5.8*	–	*7.6*	1.2	*6.9*	0.2	*0.7*
Spur/branch height ratio	5	16%	–	19%		–		18%	–	1%	–
Claw IV heights											
Branch	5	6.8	–	9.3	*43.7*	–	*49.5*	8.0	*45.9*	0.9	*2.4*
Spur	3	1.1	–	1.3	*7.1*	–	*7.6*	1.2	*7.3*	0.1	*0.3*
Spur/branch height ratio	3	16%	–	16%		–		16%	–	0%	–

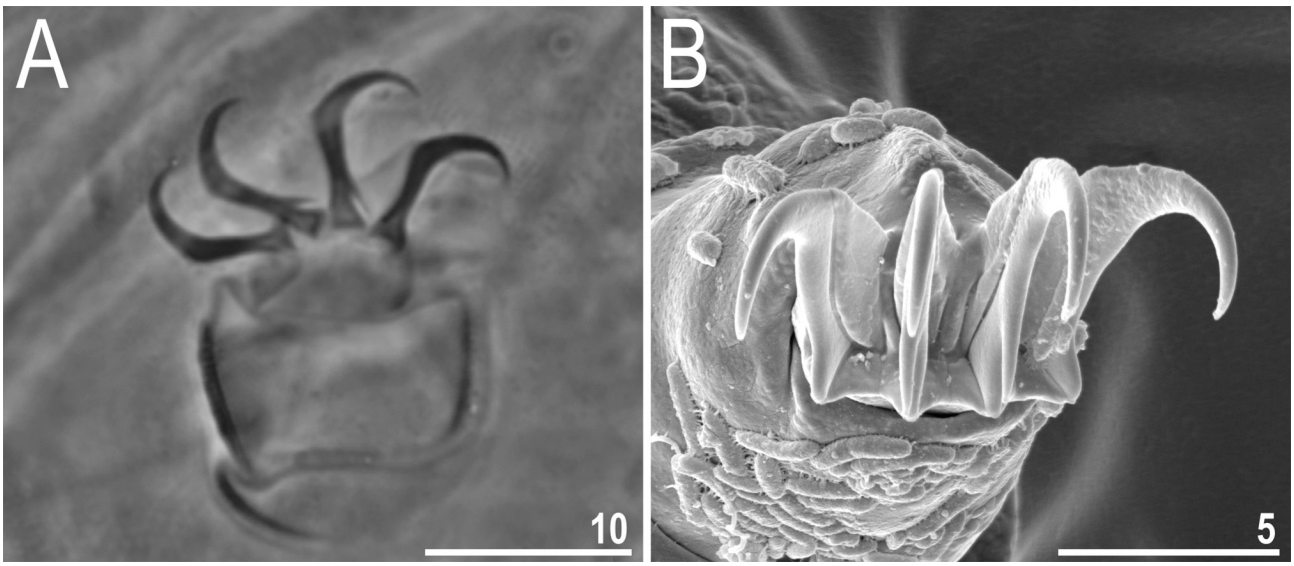

FIGURE 5. Claws of *Bryodelphax* **sp. nov.** (females): A—claws II (PCM), B—claws I (SEM). Scale bars in µm.

Genus: *Cornechiniscus* Maucci & Ramazzotti, 1981

***1. Cornechiniscus madagascariensis* Maucci, 1993**

Figures 6–8

Data source:

A total of 68 specimens (59 ♀♀ and 9 specimens of unknown instar/sex):

- Sample ZA.228: 65 specimens (47 ♀♀ on slides, 10 ♀♀ on SEM stub 18.17, 8 specimens used for DNA extraction); found with *Echiniscus pellucidus* Gąsiorek *et al*., 2021.
- Sample ZA.242: 1 specimen (1 ♀ on slide); found with *E. blumi* and *E. virginicus*.
- Sample ZA.502: 2 specimens (1 ♀ and 1 specimen of unknown sex on a slide); found with *E. dentatus* **sp. nov.**, *E. irroratus* **sp. nov.**, *E. latruncularis* **sp. nov.** and *E. setaceus* **sp. nov.**

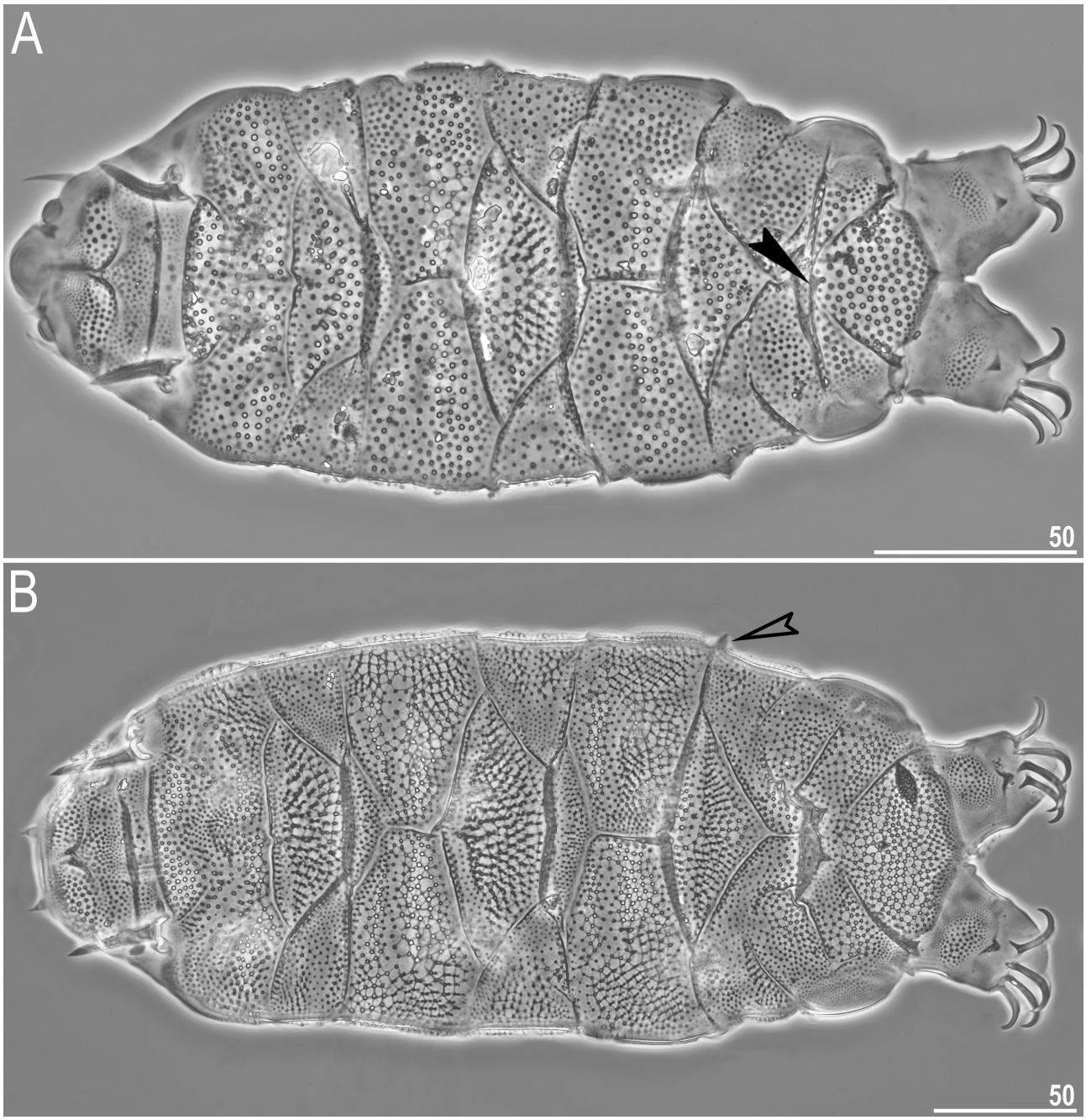

FIGURE 6. Habitus of *Cornechiniscus madagascariensis* Maucci, 1993 (PCM, females): A, B—dorsal view. Black arrowhead indicates rudimentary triangular projection on the posterior margin of the pseudosegmental plate IV', whereas empty arrowhead—lateral spicule *D*. Scale bars = 50 µm.

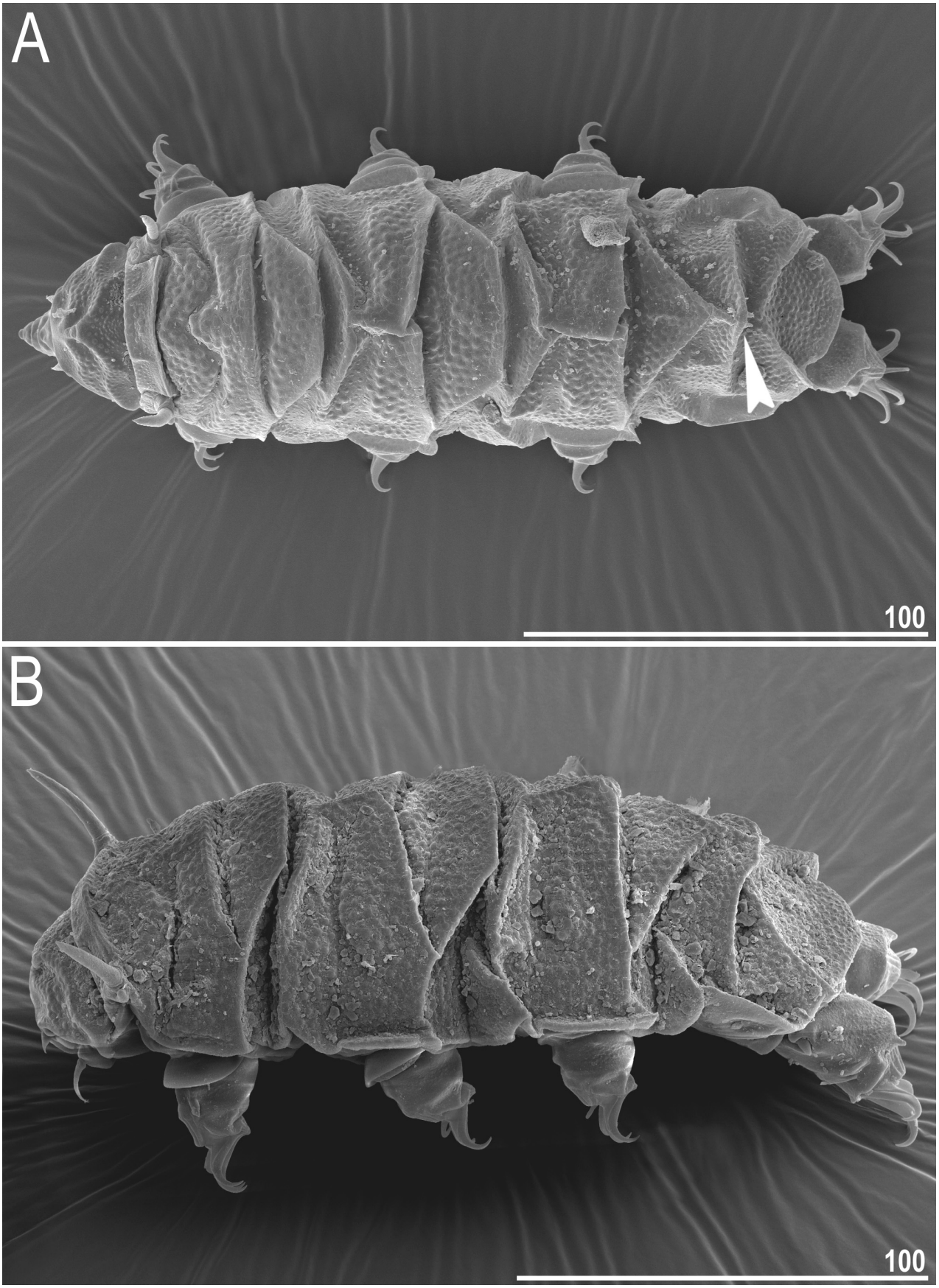

FIGURE 7. Habitus of *Cornechiniscus madagascariensis* (SEM, females): A—dorsal view (arrowhead indicates rudimentary triangular projections on the posterior margin of the pseudosegmental plate IV'), B—lateral view. Scale bars = 100 μm.

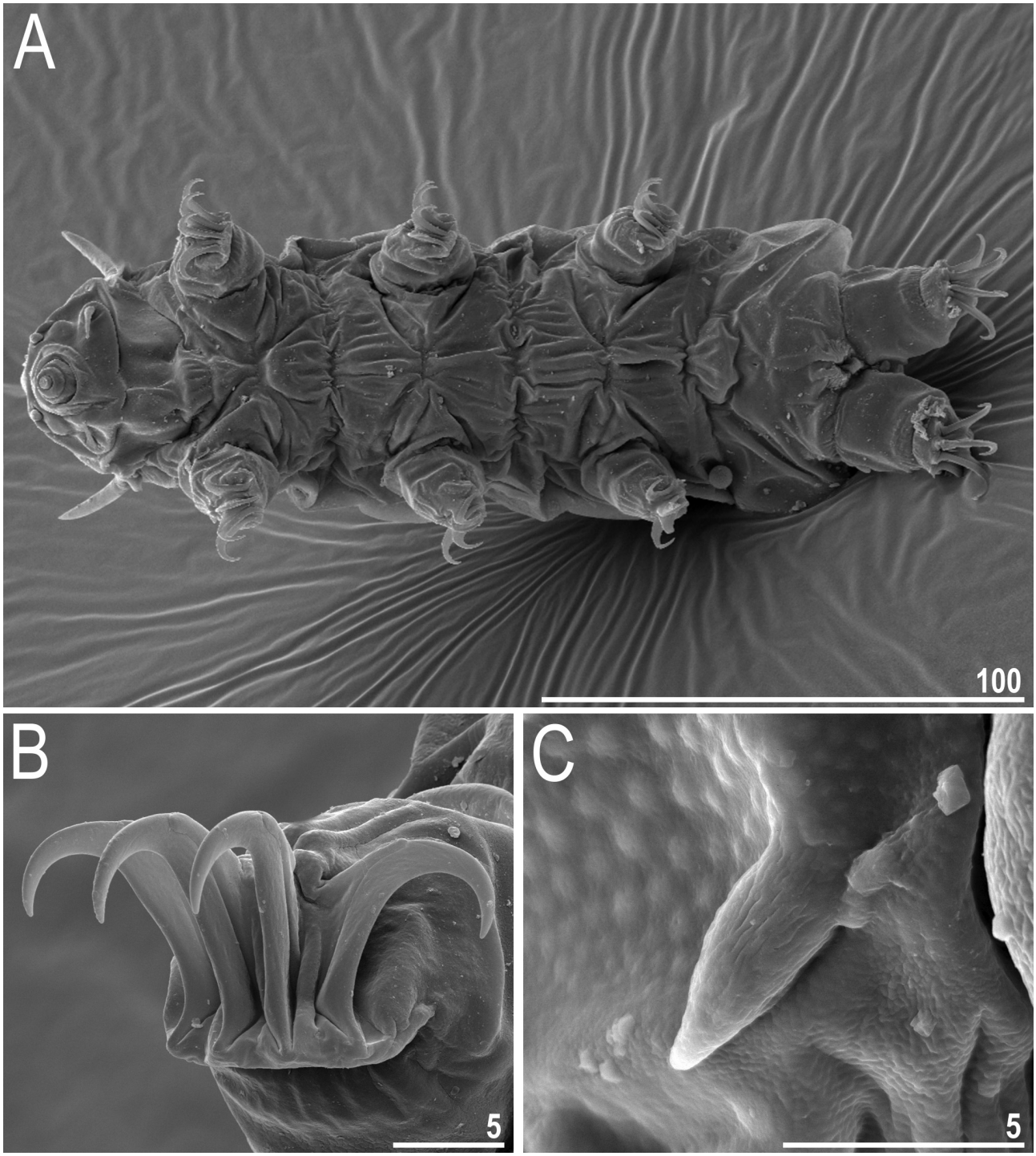

FIGURE 8. Morphology of *Cornechiniscus madagascariensis* (SEM, females): A—ventral view (evident cuticular grooves present), B—claws I, C—spine I. Scale bars in μm.

Literature:

- Original description: Maucci (1993).
- Later records: Abe & Takeda (2000); Séméria (2003); Gąsiorek & Michalczyk (2020a).

Shortened description. Massive body with strongly sclerotised dorsal plates (Fig. 6–7). *Striae* between endocuticular pillars may be poorly (Fig. 6A) or well-developed (Fig. 6B), but, irrespectively, only the protruding *capituli* of pillars are visible as epicuticular granules under SEM (Fig. 7). Paired segmental plates undivided by transverse stripes; three large supplementary lateral plates on each side of the body (Fig. 6–7). Median plates 1–2

bipartite, with very large anterior portions and reduced posterior portions. Median plate 3 large and triangular. Only pseudosegmental plate IV' present, divided by a longitudinal suture. Typical projections on the posterior margin of the pseudosegmental plate IV' (Fig. 6B) can be reduced to minute spicules (Fig. 6A, 7A). Additional lateral spicules in positions *C* and *D* may be asymmetrically present (Fig. 6B). Venter with characteristic cuticular wrinkling (Fig. 8A). Claws spurless (Fig. 8B). Spine I small (Fig. 8C).

DNA markers and phylogenetic position. The sister species of *C. lobatus* (Ramazzotti, 1943) (Gąsiorek & Michalczyk 2020a). Identical 18S rRNA haplotype as for Ethiopian individuals (Gąsiorek & Michalczyk 2020a), negligible genetic disparities in other markers (*p*-distance in 28S rRNA = 0.1%, in ITS-1 = 0.5–08%, and in COI = 0.2%).

Geographic distribution. The available data suggest that *C. madagascariensis* is widely distributed along the coasts of the Indian Ocean (including Madagascar (*terra typica*), Ethiopia, and South Africa, Fig. 120B), reaching the Himalayas in the northernmost part of the range (Maucci 1993; Abe & Takeda 2000; Gąsiorek & Michalczyk 2020a; present study). In other words, the species inhabits both the Afrotropic and the Oriental realm. Populations found in the present study are the southernmost records of this parthenogenetic species, as well as of the genus *Cornechiniscus*.

Remarks. In South Africa, *C. madagascariensis* was found in samples with seven *Echiniscus* spp.

Genus: *Echiniscus* C.A.S. Schultze, 1840

1. Echiniscus africanus Murray, 1907

Figure 9A

Data source:

A total of 1 specimen (1 ♀):

- Sample ZA.214: 1 specimen (1 ♀ on a slide); found with *Echiniscus baius*, *E. oreas* **sp. nov.**, *E. perarmatus*, *E. virginicus*, *Pseudechiniscus (P.)* cf. *ehrenbergi*, *Doryphoribius bindae* Lisi, 2011, and *Ramazzottius szeptycki* Dastych, 1980.

Literature:

- Original description: Murray (1907a).
- Later trustworthy records: Murray (1913); da Cunha & do Nascimento Ribeiro (1964); Binda & Pilato (1995a); Gąsiorek & Vončina (2019).

Shortened description of the specimen found in this study. Body small (160 µm in length) and stubby (Fig. 9A), dark orange with red eyes in a live specimen (colours disappeared after mounting). Cephalic appendages lengths: *cirrus internus* 14.0 µm, cephalic papilla 6.2 µm, *cirrus externus* 14.4 µm, primary clava 5.2 µm, and cirrus *A* 29.9 µm. Body appendage formula *A*-*B*-*C*-C^{d}-C^{cd}-*D*-D^{d}-D^{cd}-*E*, all trunk appendages in the form of spines (11.3–23.6 µm). Four short spicules distributed irregularly along the posterior margin of the scapular plate (3.3–8.6 µm).

Dorsal plate sculpturing of a mixed type under PCM: the scapular and the caudal (terminal) plate with the clear *blumi-canadensis* type, whereas in the remaining plates endocuticular pillars dominate and make the epicuticular ornamentation less obvious. Venter with fine uniform endocuticular punctuation, genital plates present.

Lengths of leg appendages and claw heights: spine I 3.3 µm, papilla IV 3.9 µm, claw branches 8.3–9.8 µm and internal spurs 1.6–1.8 µm. Dentate collar IV with eight teeth. Pulvini dim; pedal plates absent.

DNA markers and phylogenetic position. Given that the only individual found in this study was mounted on a permanent slide, no DNA analysis was conducted. Consequently, the phylogenetic position of the species remains unknown.

Geographic distribution. This extremely rare species, originally described from South Africa, was also reported from other sub-Saharan countries: Angola (da Cunha & do Nascimento Ribeiro 1964), Lesotho (Middleton 2003), Tanzania (Binda & Pilato 1995a), as well as from Madagascar (Gąsiorek & Vončina 2019). In South Africa, *E. africanus* was found only in five localities in the interior regions of the country (Fig. 120C).

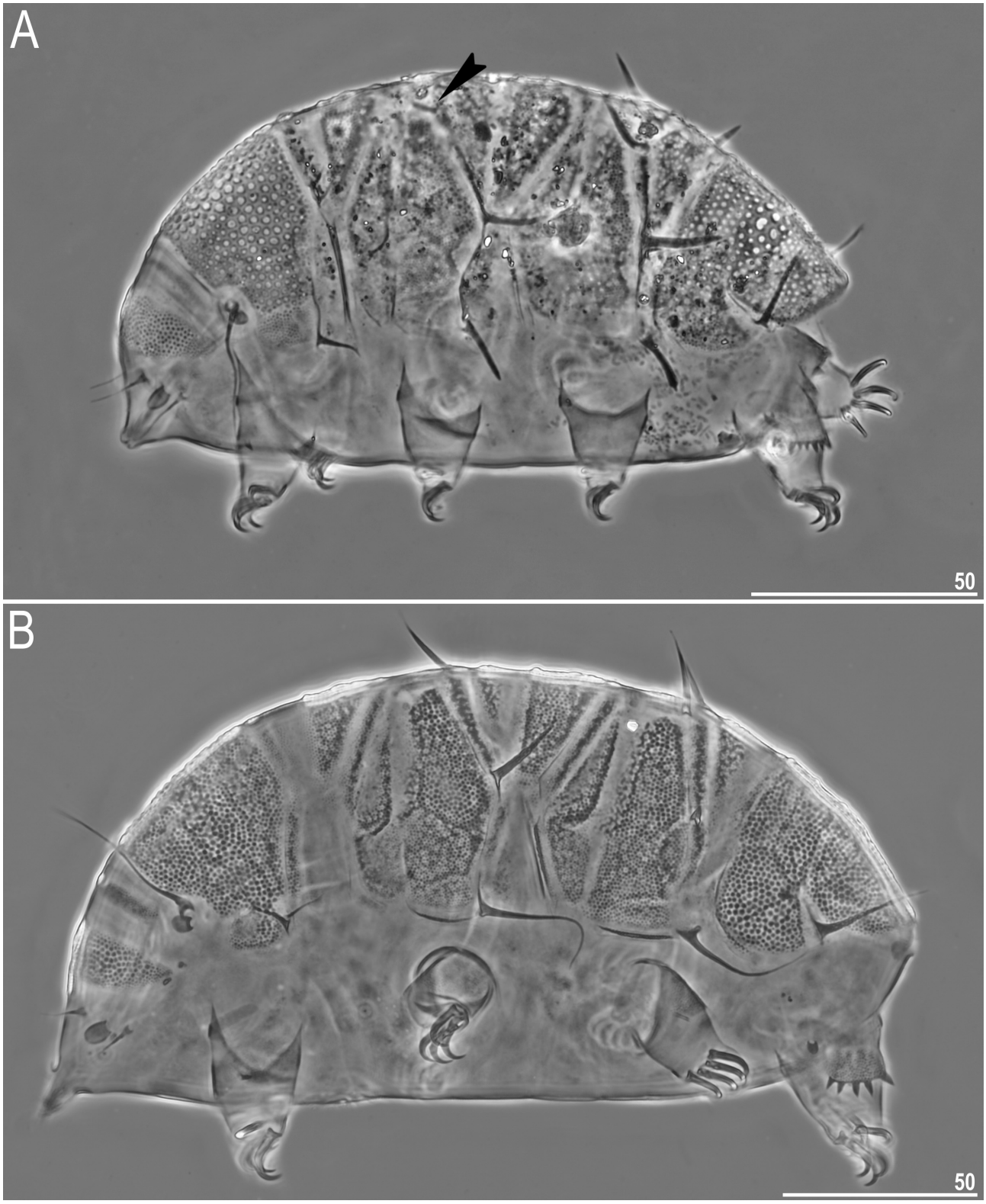

FIGURE 9. Emblematic *Echiniscus* spp. with centrodorsal spines: A—*Echiniscus africanus* Murray, 1907 (female, black arrowhead indicates one of the centrodorsal spines), B—*Echiniscus lapponicus* Thulin, 1911 (female). Scale bars = 50 µm.

Remarks. Thulin (1911) hypothesised that *Echiniscus lapponicus*, described from the Scandinavian Peninsula, is related to *E. africanus*, especially due to the development of unique centrodorsal spines. Nevertheless, both taxa are easily morphologically distinguishable by:

- the type of sculpturing of the scapular and the caudal plate (polygonal pores in *E. africanus vs* large pillars in *E. lapponicus*, Fig. 9B);
- the morphology of lateral trunk appendages (spines in *E. africanus vs* short, but flexible cirri in *E. lapponicus*);
- the presence of pedal plates I–III (absent in *E. africanus vs* present, with minute endocuticular pillars in *E. lapponicus*).

If Thulin's supposition on the close relationship between *E. africanus* and *E. lappponicus* is confirmed, the two species will constitute a sister clade to three clades of *Echiniscus*: the *granulatus*, *virginicus-perarmatus,* and *blumi-canadensis* complexes (Fig. 117).

2. Echiniscus attenboroughi sp. nov. Gąsiorek, Vončina, Morek & Michalczyk

urn:lsid:zoobank.org:act:CF9EA7D2-815C-4B08-B58A-43D89C547F7F
Figures 10–12, Tables 5–7

Data source:
A total of 119 specimens (54 ♀♀, 16 ♂♂, 9 juveniles, 1 larva, and 39 specimens of unknown instar/sex):
- Sample ZA.015: 23 specimens (14 ♀♀and 1 juvenile on slides, 3 specimens used for DNA extraction, 5 specimens on a SEM stub 19.07); found with *Echiniscus draconis* **sp. nov.**, *E. lichenorum*, *E. setaceus* **sp. nov.**, and *E. virginicus*.
- Sample ZA.022: 1 specimen (1 ♀ on a slide); found with *Echiniscus dentatus* **sp. nov.**, *E. gracilis* **sp. nov.**, *E. irroratus* **sp. nov.**, *E. lichenorum*, *E. longispinosus*, and *E. setaceus* **sp. nov.**
- Sample ZA.436: 62 specimens (27 ♀♀, 16 ♂♂, 7 juveniles, 1 larva and 2 specimens of unknown instar/sex on slides, 9 specimens used for DNA extraction, including 5 hologenophores); found with *Echiniscus draconis* **sp. nov.**, *E. scabrocirrosus* **sp. nov.**, and *E. setaceus* **sp. nov.**
- Sample ZA.437: 29 specimens (8 ♀♀ and 1 juvenile on slides, 20 frozen specimens); found with *Echiniscus draconis* **sp. nov.**
- Sample ZA.442: 3 specimens (3 ♀♀ on slides).
- Sample ZA.479: 1 specimen (1 ♀ on a slide); found with *Echiniscus longispinosus*.

Description. Mature females (*i.e.* from the third instar onwards; measurements and statistics in Table 5). *Echiniscus* of medium-size, with orange body and red eyes (colour and eyes disappeared soon after mounting in Hoyer's medium). *Echiniscus*-type cephalic papillae (secondary clavae) and (primary) clavae; cirri growing out from bulbous cirrophores (Fig. 10, 11B). The body appendage configuration is *A-B-C-C^{d}-D-D^{d}-E*, with all trunk appendages formed as smooth spines. Asymmetries in the development of spines infrequent.

Dorsal plates with a simple pattern of polygonal epicuticular granules (Fig. 10–11), flattened and partially merged on the cephalic, cervical and scapular plates, and along the posterior margin of the median plate 2, and more prominent and separated on the remaining plates (Fig. 11A–C). Minute pores distributed sparsely and irregularly between the granules, with the scapular plate being most porous (Fig. 10A, 11C). Granules in anterior portions of median plate 2 and paired segmental plates, and the entire median plate 3 are more elevated and joined by fine *striae* (Fig. 10, 11D). In a single female, the sculpturing was undeveloped and granules merged to form a uniform matrix. The cephalic plate large and with a T-shaped anterior incision (Fig. 10). The cervical (neck) plate thin, but clearly visible (Fig. 10). The scapular plate large, with additional lateral sutures separating narrow rectangular lateral portions (Fig. 10, 11A–C). Paired segmental plates divided into a smaller, much narrower anterior and a dominant posterior part by a smooth, thin transverse stripe (Fig. 10, 11A–B, D). The caudal (terminal) plate with short incisions and connected by a transverse suture (Fig. 10). Median plate 1 unipartite, and median plate 2 bipartite, with a poorly sculptured, small anterior portion, and a posterior portion of similar size with regard to m1. Median plate 3 reduced (Fig. 10B, 11A). Ventral cuticle with minute endocuticular pillars distributed throughout the whole venter (Fig. 12A), but ventral plates absent. Sexpartite gonopore placed anteriorly to legs IV, and a trilobed anus between legs IV.

Pedal plates I–IV present and large, composed of small dark granules and pores (Fig. 10B, 11B). Distinct pulvini on all legs (Fig. 10B, 11B). A minuscule spine on leg I placed at the margin of pedal plate (Fig. 10B, 11B) and a papilla on leg IV present (Fig. 10, 11B). Claws IV slightly longer than claws I–III (Table 5). Claws large and robust,

with thick branches (Fig. 12). All external claws smooth. All internal claws with large spurs positioned at *ca.* 25% of the claw height and bent downwards (Fig. 12).

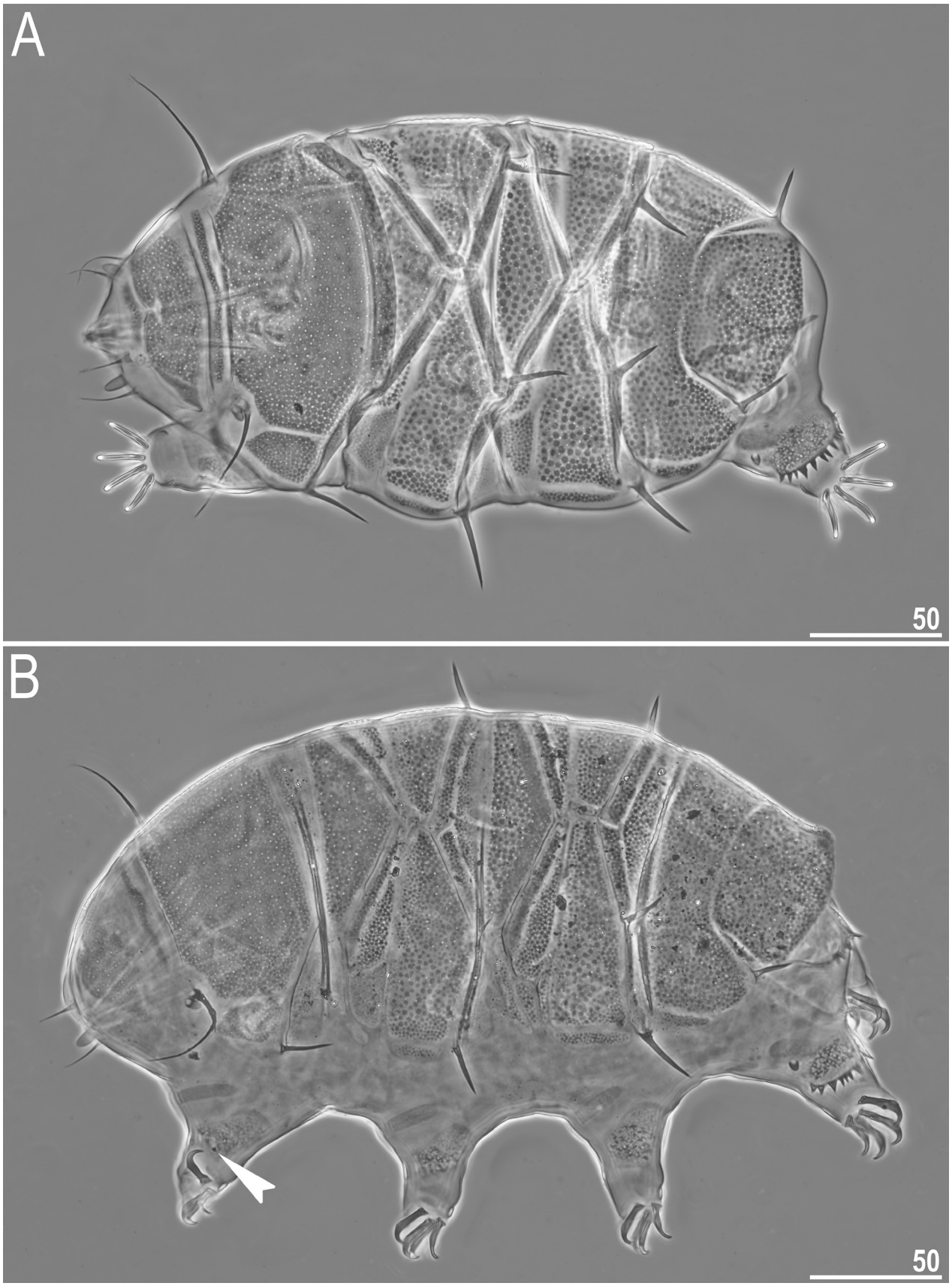

FIGURE 10. Habitus of *Echiniscus attenboroughi* **sp. nov.** (PCM, females): A—holotype in dorsal view, B—paratype in dorsolateral view (arrowhead indicates minute spine I). Scale bars = 50 μm.

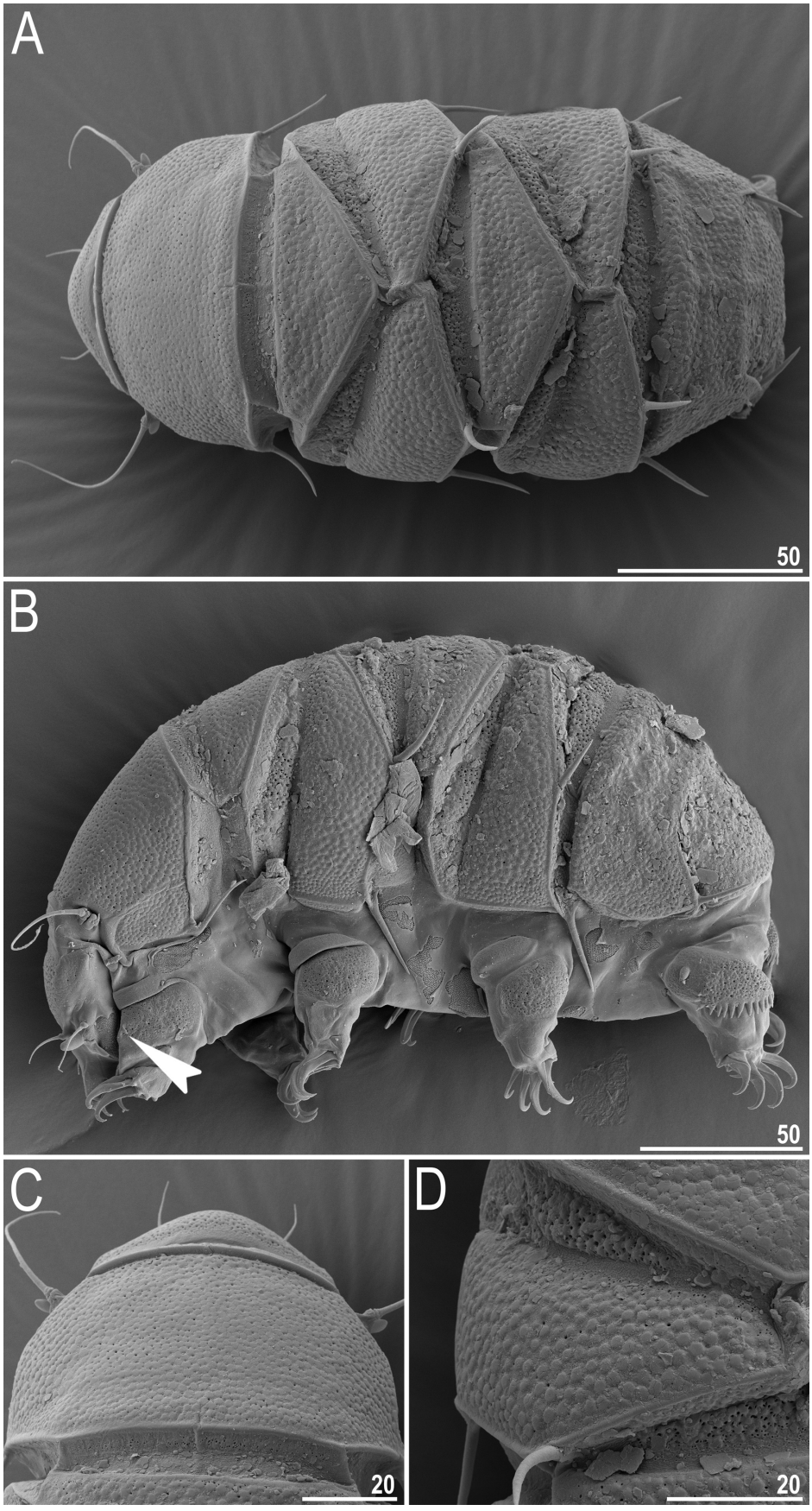

FIGURE 11. Habitus and dorsal sculpturing of *Echiniscus attenboroughi* **sp. nov.** (SEM, sex unidentified): A—dorsal view, B—lateral view (arrowhead indicates minute spine I), C—scapular plate, D—segmental plate. Scale bars in μm.

Mature males and sexually dimorphic traits (*i.e*. from the second or third instar onwards, see below; measurements and statistics in Table 6). Beside lower mean body size (♂♂: 180–243 µm, ♀♀: 230–315 µm), only primary sexual dimorphism exists (different gonoporal shapes). Qualitatively both sexes are identical.

Juveniles (*i.e*. the second instar, measurements and statistics in Table 7). Qualitatively identical to sexually mature individuals, beside the lack of gonopore and the lower mean body size compared to females. No morphometric gap between adults and juveniles.

Larvae. Unknown.

Eggs. Up to four round, yellow eggs per exuvia were found.

DNA markers and phylogenetic position. The sister species of the clade (*E. latruncularis* **sp. nov.** + *E. scabrocirrosus* **sp. nov.**) (Fig. 117). The species closest in COI is *E. latruncularis* **sp. nov.** (p-distance = 11.7–11.9%), in ITS-1—*E. scabrocirrosus* **sp. nov.** (2.3–2.6%), and in ITS-2—*E. latruncularis* **sp. nov.** (0.9–1.2%).

Type material. 20 specimens: holotype: mature ♀ on slide ZA.015.05 (mounted together with 3 ♀♀ and 6 juveniles of *Echiniscus draconis* **sp. nov.**, 30 ♀♀ and 4 juveniles of *E. lichenorum*, 27 ♀♀, 2 ♂♂, 4 juveniles, and a larva of *E. setaceus* **sp. nov.**); 19 paratypes: 13 ♀♀ and 1 juvenile on slides ZA.015.01–7, 5 ♀♀ on SEM stub 19.07.

Type locality. 33°34’23.6’’S, 19°08’9.5’’E, 345 m asl: Republic of South Africa, Western Cape, Bain’s Kloof Pass; fynbos, lichen from a rock. Found together with *Echiniscus draconis* **sp. nov.**, *E. lichenorum*, *E. setaceus* **sp. nov.**, and *E. virginicus* (sample ZA.015).

Etymology. The name honours Sir David Attenborough, a famous English natural historian, who devoted his life to popularising biology of a wide range of organisms inhabiting various ecosystems to people throughout the World. We would like to express our highest appreciation for the unparalleled quality of his renowned documentaries. A noun in the genitive singular.

Geographic distribution. Only reported from several locations in the Western Cape Province in the Republic of South Africa (Fig. 120D).

Remarks. Dioecious. Juveniles reach the same size as males, thus probably the species is heterochronous (males develop directly from larvae). The species was found with nine other *Echiniscus* spp. in all examined samples.

Differential diagnosis. This species resembles members of the *E. virginicus* complex by the presence of trunk spines and reduced pores in the dorsal plates, but it never exhibits epicuticular ornamentation typical for this group (Gąsiorek *et al*. 2019b). Large polygonal epicuticular granules make Japanese *E. laterosetosus* and *E. polygonalis* (Ito 1993) similar to *E. attenboroughi* **sp. nov.**, but these two species have long lateral cirri, absent in the latter. The same sculpturing exists also in *E. zetotrymus* (Horning *et al*. 1978; Pilato *et al*. 2005), but the two species differ by the body appendage configuration (*A-B-C-C^d-D-D^d-E* in *E. attenboroughi* **sp. nov.** *vs A-(B)-C-C^d-(D)-E* in *E. zetotrymus*), and appendages *E* are filamentous cirri in *E. zetotrymus*. The new species is phenotypically closest to *E. egnatiae* Durante Pasa & Maucci, 1979 and *E. weisseri* Maucci 1978, but differs from:

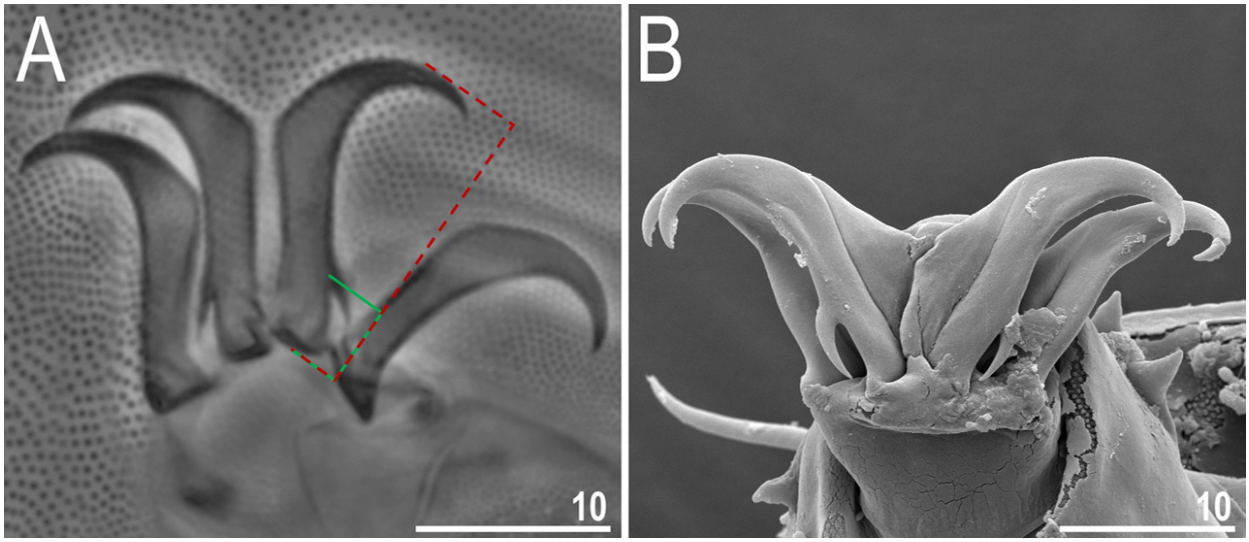

FIGURE 12. Claws of *Echiniscus attenboroughi* **sp. nov.** (females): A—claws I (PCM), B—claws IV (SEM). Scale bars = 10 µm. The red and green lines show how the claw branch heights and height at which a spur was embedded on a branch were measured, respectively.

TABLE 5. Measurements [in µm] of selected morphological structures of the adult females of *Echiniscus attenboroughi* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Holotype	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	20	230	–	315	*414*	–	*537*	279	*464*	23	*31*	279	*421*
Scapular plate length	20	47.3	–	70.2		–		60.3	–	6.2	–	66.2	–
Head appendages lengths													
Cirrus *internus*	19	11.2	–	19.9	*19.9*	–	*29.5*	15.4	*25.6*	2.3	*2.8*	18.0	*27.2*
Cephalic papilla	20	8.4	–	11.1	*13.4*	–	*18.2*	9.4	*15.6*	0.8	*1.4*	8.9	*13.4*
Cirrus *externus*	20	16.2	–	30.0	*26.7*	–	*43.0*	22.1	*36.7*	3.6	*4.3*	22.9	*34.6*
Clava	20	5.8	–	8.0	*9.9*	–	*13.1*	7.0	*11.6*	0.6	*1.0*	6.7	*10.1*
Cirrus *A*	18	41.0	–	61.8	*73.5*	–	*95.0*	49.5	*83.2*	5.8	*6.7*	50.6	*76.4*
Cirrus *A*/Body length ratio	18	14%	–	21%		–		18%	–	2%	–	18%	–
Body appendages lengths													
Spine *B*	20	11.8	–	32.3	*22.5*	–	*49.1*	24.5	*40.4*	5.2	*6.5*	31.4	*47.4*
Spine *C*	20	20.1	–	33.0	*32.5*	–	*52.0*	26.7	*44.3*	3.3	*4.4*	33.0	*49.8*
Spine C^d	20	9.5	–	30.7	*15.3*	–	*48.7*	24.3	*40.3*	4.8	*7.1*	24.9	*37.6*
Spine *D*	20	20.9	–	33.9	*35.7*	–	*53.5*	26.5	*44.1*	3.3	*4.8*	30.9	*46.7*
Spine D^d	20	13.5	–	25.5	*22.6*	–	*37.7*	19.4	*32.2*	3.0	*3.8*	19.7	*29.8*
Spine *E*	20	11.5	–	25.0	*18.5*	–	*41.5*	17.9	*29.7*	3.8	*5.7*	23.1	*34.9*
Spine on leg I length	18	2.1	–	3.3	*3.6*	–	*5.9*	2.7	*4.5*	0.4	*0.6*	3.2	*4.8*
Papilla on leg IV length	19	3.7	–	5.3	*6.4*	–	*8.9*	4.4	*7.4*	0.4	*0.7*	4.7	*7.1*
Number of teeth on the collar	19	8	–	16		–		12.7	–	2.5	–	11	–
Claw I heights													
Branch	20	14.7	–	21.1	*25.0*	–	*32.6*	17.4	*28.9*	1.6	*1.8*	17.8	*26.9*
Spur	16	2.5	–	4.5	*4.1*	–	*6.4*	3.1	*5.1*	0.6	*0.6*	3.8	*5.7*
Spur/branch height ratio	16	15%	–	21%		–		18%	–	2%	–	21%	–
Claw II heights													
Branch	20	13.8	–	20.1	*25.0*	–	*31.1*	16.8	*27.9*	1.5	*1.4*	17.5	*26.4*
Spur	18	2.5	–	3.2	*3.9*	–	*5.4*	2.9	*4.8*	0.3	*0.5*	2.6	*3.9*
Spur/branch height ratio	18	15%	–	19%		–		17%	–	1%	–	15%	–
Claw III heights													
Branch	20	14.5	–	20.6	*25.4*	–	*31.1*	17.0	*28.2*	1.5	*1.5*	17.3	*26.1*
Spur	18	2.4	–	3.5	*3.7*	–	*5.9*	2.8	*4.7*	0.3	*0.5*	2.8	*4.2*
Spur/branch height ratio	18	14%	–	19%		–		17%	–	1%	–	16%	–
Claw IV heights													
Branch	20	16.0	–	24.2	*29.0*	–	*37.0*	19.7	*32.7*	1.8	*2.0*	19.2	*29.0*
Spur	13	2.9	–	4.6	*5.5*	–	*6.9*	3.7	*6.2*	0.5	*0.4*	4.0	*6.0*
Spur/branch height ratio	13	16%	–	23%		–		19%	–	2%	–	21%	–

TABLE 6. Measurements [in µm] of selected morphological structures of the adult males of *Echiniscus attenboroughi* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD	
		µm			*sp*			µm	*sp*	µm	*sp*
Body length	5	180	–	243	*429*	–	*513*	221	*480*	24	*41*
Scapular plate length	5	40.8	–	56.7		–		46.3	–	6.1	–
Head appendages lengths											
Cirrus *internus*	5	9.8	–	13.2	*23.3*	–	*27.7*	11.8	*25.6*	1.3	*2.0*
Cephalic papilla	5	6.7	–	8.9	*15.0*	–	*20.2*	8.2	*17.8*	0.9	*2.1*
Cirrus *externus*	5	15.0	–	20.1	*30.2*	–	*44.1*	17.0	*37.1*	1.9	*5.4*
Clava	5	4.7	–	6.8	*11.5*	–	*14.7*	6.1	*13.1*	0.8	*1.4*
Cirrus *A*	5	32.5	–	41.9	*73.9*	–	*84.6*	36.6	*79.4*	3.5	*3.8*
Cirrus *A*/Body length ratio	5	16%	–	18%		–		17%	–	1%	–
Body appendages lengths											
Spine *B*	5	14.4	–	26.0	*35.3*	–	*49.3*	20.5	*44.0*	4.2	*5.3*
Spine *C*	5	16.5	–	26.3	*40.4*	–	*54.8*	22.9	*49.3*	3.8	*5.9*
Spine C^d	5	16.4	–	23.5	*40.0*	–	*53.3*	20.9	*45.3*	3.0	*6.0*
Spine *D*	5	17.1	–	25.8	*41.9*	–	*55.0*	22.8	*49.4*	3.4	*5.7*
Spine D^d	5	12.5	–	17.6	*28.2*	–	*36.2*	15.0	*32.5*	2.1	*3.1*
Spine *E*	5	13.4	–	19.5	*32.8*	–	*38.5*	16.8	*36.3*	2.2	*2.5*
Spine on leg I length	5	1.5	–	3.5	*3.4*	–	*6.2*	2.1	*4.5*	0.8	*1.0*
Papilla on leg IV length	5	3.1	–	4.1	*7.2*	–	*9.1*	3.6	*7.8*	0.4	*0.7*
Number of teeth on the collar	5	9	–	13		–		10.6	–	1.8	–
Claw I heights											
Branch	5	13.0	–	15.2	*26.8*	–	*31.9*	14.0	*30.4*	0.8	*2.1*
Spur	5	2.1	–	2.7	*4.8*	–	*6.1*	2.5	*5.3*	0.3	*0.5*
Spur/branch height ratio	5	16%	–	19%		–		18%	–	1%	–
Claw II heights											
Branch	5	12.6	–	15.7	*27.7*	–	*31.3*	13.7	*29.8*	1.2	*1.5*
Spur	5	2.0	–	2.3	*3.7*	–	*5.2*	2.1	*4.6*	0.1	*0.6*
Spur/branch height ratio	5	13%	–	17%		–		16%	–	1%	–
Claw III heights											
Branch	5	12.4	–	15.1	*26.6*	–	*30.4*	13.4	*29.1*	1.0	*1.5*
Spur	5	1.9	–	3.2	*4.5*	–	*5.6*	2.3	*4.9*	0.5	*0.4*
Spur/branch height ratio	5	15%	–	21%		–		17%	–	2%	–
Claw IV heights											
Branch	5	14.4	–	17.2	*30.3*	–	*35.8*	15.8	*34.4*	1.0	*2.3*
Spur	2	3.1	–	3.3	*6.8*	–	*7.4*	3.2	*7.1*	0.1	*0.4*
Spur/branch height ratio	2	19%	–	21%		–		20%	–	1%	–

TABLE 7. Measurements [in µm] of selected morphological structures of the juveniles of *Echiniscus attenboroughi* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	**RANGE**						**MEAN**		**SD**	
		µm			***sp***			**µm**	***sp***	**µm**	***sp***
Body length	5	162	–	249	*429*	–	*488*	199	*458*	35	*27*
Scapular plate length	5	37.7	–	52.3		–		43.2	–	5.8	–
Head appendages lengths											
Cirrus *internus*	4	11.9	–	15.6	*28.2*	–	*31.6*	13.0	*29.5*	1.7	*1.6*
Cephalic papilla	5	6.2	–	8.3	*15.7*	–	*19.5*	7.5	*17.4*	0.9	*1.9*
Cirrus *externus*	5	11.1	–	18.7	*28.5*	–	*38.4*	15.0	*34.7*	2.8	*3.9*
Clava	5	4.9	–	5.5	*10.3*	–	*14.1*	5.3	*12.4*	0.3	*1.4*
Cirrus *A*	5	26.1	–	45.6	*69.2*	–	*89.2*	34.8	*80.2*	7.2	*9.9*
Cirrus *A*/Body length ratio	5	14%	–	20%		–		18%	–	2%	–
Body appendages lengths											
Spine *B*	5	13.1	–	20.4	*33.7*	–	*47.7*	17.4	*40.3*	2.7	*5.0*
Spine *C*	5	18.0	–	23.0	*40.5*	–	*51.5*	19.9	*46.3*	2.2	*4.6*
Spine C^d	5	9.1	–	22.8	*23.4*	–	*46.2*	16.2	*37.1*	4.9	*8.9*
Spine *D*	5	17.6	–	24.6	*44.1*	–	*50.2*	20.4	*47.2*	2.7	*2.2*
Spine D^d	5	10.0	–	18.3	*25.7*	–	*45.1*	15.0	*34.8*	3.3	*7.1*
Spine *E*	5	12.2	–	18.1	*27.3*	–	*42.7*	14.5	*33.9*	2.5	*5.6*
Spine on leg I length	4	1.9	–	2.4	*4.6*	–	*5.4*	2.2	*5.1*	0.2	*0.4*
Papilla on leg IV length	5	3.1	–	4.7	*7.3*	–	*9.0*	3.6	*8.4*	0.6	*0.6*
Number of teeth on the collar	5	7	–	12		–		9.6	–	2.1	–
Claw I heights											
Branch	5	10.8	–	16.3	*28.6*	–	*33.2*	13.3	*30.9*	2.0	*1.6*
Spur	5	2.0	–	2.6	*5.0*	–	*6.4*	2.4	*5.6*	0.2	*0.6*
Spur/branch height ratio	5	16%	–	22%		–		18%	–	3%	–
Claw II heights											
Branch	5	10.3	–	14.6	*27.3*	–	*32.1*	12.5	*28.9*	1.5	*1.9*
Spur	5	1.8	–	2.5	*4.6*	–	*5.9*	2.2	*5.2*	0.3	*0.6*
Spur/branch height ratio	5	14%	–	21%		–		18%	–	3%	–
Claw III heights											
Branch	5	10.1	–	15.1	*26.8*	–	*32.1*	12.7	*29.3*	1.9	*2.1*
Spur	3	1.9	–	2.2	*4.5*	–	*5.7*	2.1	*4.9*	0.2	*0.6*
Spur/branch height ratio	3	15%	–	18%		–		16%	–	1%	–
Claw IV heights											
Branch	5	13.2	–	17.0	*32.5*	–	*35.7*	14.9	*34.7*	1.5	*1.3*
Spur	2	2.4	–	3.1	*5.9*	–	*6.2*	2.8	*6.0*	0.5	*0.2*
Spur/branch height ratio	2	17%	–	18%		–		18%	–	1%	–

- *E. egnatiae*, only reported from Greece, by: a different body appendage formula (*A-B-C-C^d-D-D^d-E* in *E. attenboroughi* **sp. nov.** *vs A-C-C^d-D-D^d* in *E. egnatiae*), heteromorphic trunk spines (spines of equal lengths in *E. attenboroughi* **sp. nov.** *vs* spines *C^d* clearly longer than other spines in *E. egnatiae*), and claw shape (robust claws, external claws IV smooth in *E. attenboroughi* **sp. nov.** *vs* long, slender claws, external claws IV with minute spurs directed upwards in *E. egnatiae*);
- *E. weisseri*, only reported from the foot of the Hindukush in Afghanistan, by a different appendage formula (*A-B-C-C^d-D-D^d-E* in *E. attenboroughi* **sp. nov.** *vs A-B-B^d-C-C^d-D-D^d-E* in *E. weisseri*), morphology of the appendage *E* (spine in *E. attenboroughi* **sp. nov.** *vs* cirrus clearly longer than spines in *E. weisseri*), and claw shape (robust claws, internal claws with spurs in *E. attenboroughi* **sp. nov.** *vs* long, slender and spurless claws in *E. weisseri*). Sculpture in *E. weisseri* was confusingly described by Maucci (1978) as composed of pores, but, in fact, polygonal elements correspond with epicuticular granules.

Raw measurements. Supplementary Materials (SM.03) and Tardigrada Register (www.tardigrada.net/register/0081.htm).

3. Echiniscus baius Marcus, 1928

Figure 13

Data source:

A total of 6 specimens (4 ♀♀ and 2 juveniles):

- Sample ZA.214: 3 specimens (3 ♀♀ on slides); found with *Doryphoribius bindae*, *Echiniscus africanus*, *E. oreas* **sp. nov.**, *E. perarmatus*, *E. virginicus*, *Pseudechiniscus (P.)* cf. *ehrenbergi*, and *Ramazzottius szeptycki*.
- Sample ZA.260: 3 specimens (1 ♀ and 2 juveniles on slides); found with *Echiniscus cavagnaroi*, *E. longispinosus*, *E. oreas* **sp. nov.**, *E. pellucidus*, *E. virginicus*, and *Doryphoribius bindae*.

Literature:

- Original description: Marcus (1928).
- Later trustworthy records: Iharos (1967); Gąsiorek & Kristensen (2018).

FIGURE 13. Habitus of *Echiniscus baius* Marcus, 1928 (PCM, female in dorsolateral view). Scale bar = 50 µm.

Shortened description. A small representative of the *E. spinulosus* complex. Body appendage formula: *A-E*. Pores without dark endocuticular rings. Scapular plate with a median longitudinal suture (Fig. 13). Median plates 1, 3 unipartite, but m2 bipartite. Pedal plates developed as unsculptured thicker cuticle in the central portions of legs. Pulvini present. Spine I minute.

DNA markers and phylogenetic position. This species cohabited samples with numerous other echiniscids, and we were not able to separate them under a stereomicroscope, thus no DNA barcodes were obtained. However, its morphology undoubtedly indicates affinity within the *E. spinulosus* complex.

Geographic distribution. Originally described from the Malay Archipelago (Java and Lombok), the species has potentially a wide tropical and subtropical distribution (McInnes 1994, Gąsiorek & Kristensen 2018), therefore records from the temperate zone (Bozhko 1936, Iharos 1968) are not trustworthy, as they may signify different species within the complex. This is the first record of the species in southern Africa, but given no DNA sequences are known for the type population (and for the current record), the geographic range of the species cannot be confidently determined.

Remarks. In South Africa, the species was found only in the highest elevations of Drakensberg (Fig. 120E).

4. Echiniscus blumi Richters, 1903

Figure 14

Data source:

A total of 238 specimens (197 ♀♀, 1 ♂, 31 juveniles, 2 larvae, and 7 specimens of unknown instar/sex):

- Sample ZA.211: 55 specimens (48 ♀♀ on slides and 7 specimens used for DNA extraction, including 5 holo-genophores).
- Sample ZA.217: 2 specimens (2 ♀♀ on a slide); found with *Echiniscus intricatus* **sp. nov.**
- Sample ZA.222: 3 specimens (3 ♀♀ on a slide); found with *Echiniscus draconis* **sp. nov.**, *E. imitans* **sp. nov.**, and *E. longispinosus*.
- Sample ZA.225: 18 specimens (13 ♀♀, 4 juveniles and 1 larva on slides); found with *Echiniscus intricatus* **sp. nov.** and *E. regularis* **sp. nov.**
- Sample ZA.227: 2 specimens (2 ♀♀ on a slide); found with *Echiniscus imitans* **sp. nov.** and *E. regularis* **sp. nov.**
- Sample ZA.230: 5 specimens (4 juveniles and 1 larva on a slide); found with *Echiniscus oreas* **sp. nov.**, *E. regularis* **sp. nov.**, and *E. scabrospinosus*.
- Sample ZA.242: 1 specimen (1 ♀ on a slide); found with *Cornechiniscus madagascariensis* and *Echiniscus virginicus*.
- Sample ZA.248: 117 specimens (101 ♀♀ and 16 juveniles on slides); found with *Echiniscus imitans* **sp. nov.**
- Sample ZA.255: 2 specimens (2 juveniles on a slide); found with *Echiniscus imitans* **sp. nov.** and *E. regularis* **sp. nov.**
- Sample ZA.257: 1 specimen (1 juvenile on a slide); found with *Echiniscus longispinosus* and *E. oreas* **sp. nov.**
- Sample ZA.258: 32 specimens (27 ♀♀, 1 ♂ and 4 juveniles on slides); found with *Echiniscus longispinosus*, *E. oreas* **sp. nov.**, and *Pseudechiniscus (P.)* cf. *ehrenbergi*.

Literature:

- Original description: Richters (1903).
- Later records: summarised in McInnes (1994) and McInnes *et al*. (2017), all should be treated as *sensu lato* reports.

Shortened description. Large representative of the *E. blumi-canadensis* complex. Body appendage formula *A-(B)-C-C^{d}-D-D^{d}* in adults (Fig. 14A) and *A-C-C^{d}-D-D^{d}* in larvae (Fig. 14B). Median plates 1, 3 unipartite, but m2 bipartite. Subcephalic and genital plates present. Pedal plates large and sculptured as dorsal plates. Pulvini present. External claws IV with secondary and tertiary spurs (Fig. 14A), but other external claws spurless (Fig. 14B, insert).

DNA markers and phylogenetic position. *E. blumi* belongs to the *E. blumi-canadensis* clade, being one of the first lineages branching off at the base of the generic tree (Fig. 117). The closest species are *E. canadensis* Murray, 1910 and *E. trisetosus* Cuénot, 1932: COI (p-distance = 1.0–1.2%), ITS-1 (0.6–0.9%), and ITS-2 (0.0–1.2%).

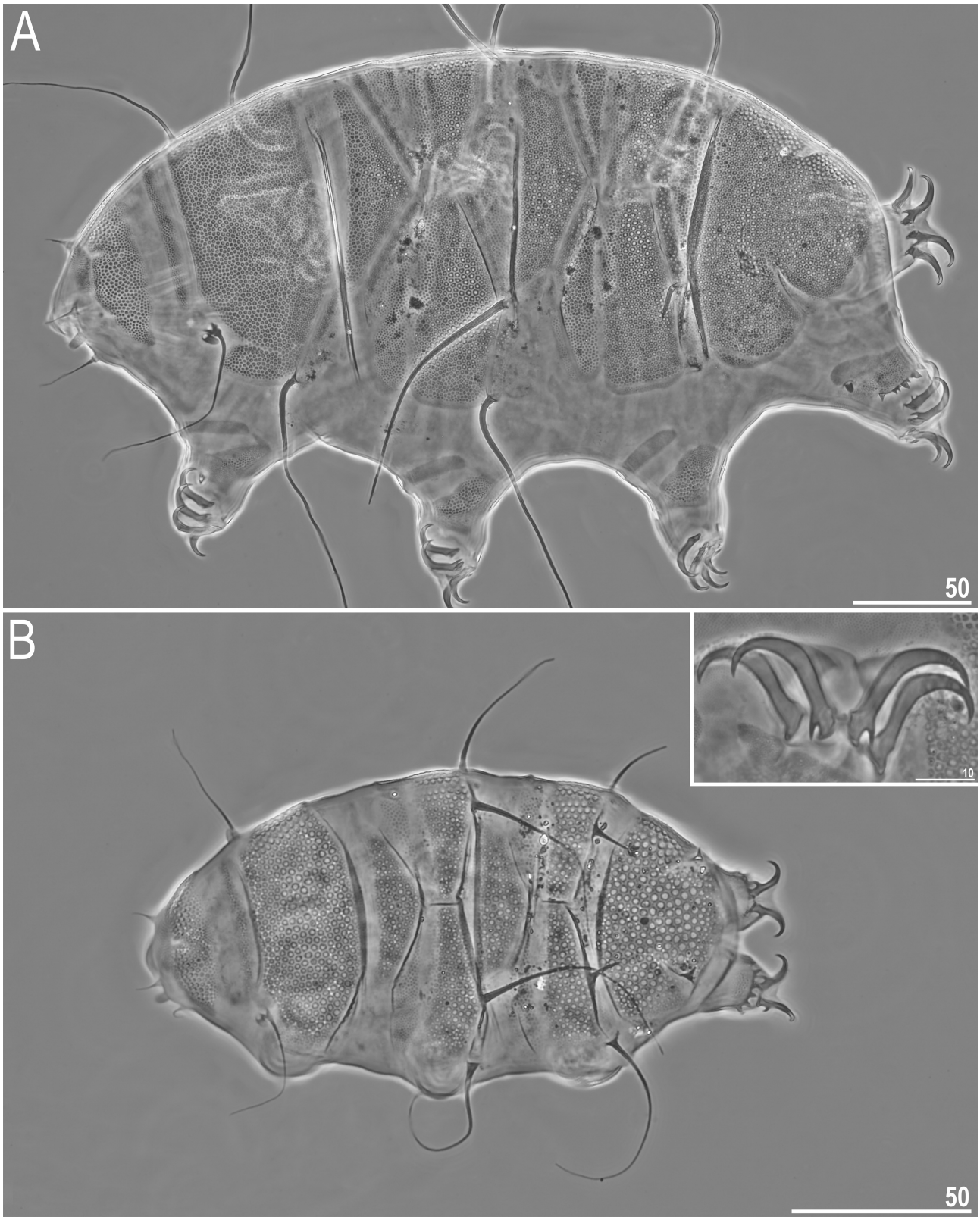

FIGURE 14. Habitus of *Echiniscus blumi* Richters, 1903 (PCM): A—adult female, dorsolateral view, B—larva, dorsal view (insert shows claws I). Scale bars in μm.

Geographic distribution. Originally described from the Svalbard Archipelago, later found in numerous localities throughout the Holarctic and other regions (McInnes 1994). Given the unsolved taxonomic position of *E. blumi*, which may conceal many species (Guil & Giribet 2009), the precise geographic range is uncertain. The origin of South African populations is unknown, as natural *vs* anthropogenic tardigrade dispersal is notoriously difficult to tell apart (Gąsiorek *et al*. 2019b), however high rates of endemism among South African invertebrates (see Morek *et al*. 2021 for *Milnesium*) suggest the species could be anthropogenically introduced to the region.

Remarks. Dioecious, although males are rare (cyclical parthenogenesis could be in place). This likely cosmopolitan species (McInnes 1994) has clear stenothermic preferences towards cold habitats, thus it occurs only at the high elevations in Drakensberg in South Africa (Fig. 120F).

5. Echiniscus capensis sp. nov. Gąsiorek, Vončina, Morek & Michalczyk

urn:lsid:zoobank.org:act:C4039F90-2681-425E-A23C-AF8C150EE6A0

Figure 15, Table 8

Data source:

A total of 3 specimens (2 ♀♀ and 1 specimen of unknown instar/sex):

- Sample ZA.378: 3 specimens (2 ♀♀ on slides and 1 specimen used for DNA extraction); found with *Echiniscus dentatus* **sp. nov.**

Description. Mature females (*i.e*. from the third instar onwards; measurements and statistics in Table 8). Small yellow *Echiniscus* with red eyes; body colour and eyes disappeared soon after mounting in Hoyer's medium. *Echiniscus*-type cephalic papillae (secondary clavae) and (primary) clavae; cirri growing out from bulbous cirrophores (Fig. 15A). The body appendage configuration is *A*-*C*-*D*, with all trunk appendages formed as short cirri.

Dorsal plates with a thick, solid layer of endocuticular matrix; pores may be both sparsely (Fig. 15A) and densely arranged (Fig. 15B). The sculpturing bears resemblance to that of the *E. quadrispinosus* type. The cephalic plate is narrow and with a T-shaped anterior incision (Fig. 15B). The cervical (neck) plate is also narrow and may be well-visible (Fig. 15A) or indiscernible (Fig. 15B). The scapular plate large, with deep median longitudinal suture dividing it into two equal portions (Fig. 15B), and weakly marked additional lateral sutures separating narrow rectangular lateral portions (Fig. 15). Paired segmental plates divided into a smaller, much narrower anterior and a dominant posterior part by a smooth, very wide transverse stripe. The sculpturing of the anterior portions much darker than on their posterior counterparts, which have no pores at their thick posteriormost margins (Fig. 15B). The caudal (terminal) plate with short incisions, completely unsclerotised; epicuticular ridges of considerable thickness demarcate clear facets in the plate (Fig. 15B). Median plates 1, 3 unipartite. Median plate 2 bipartite, with mostly smooth anterior portion (the darker sculpture similar to that of the anterior portions of paired segmental plates occurs in its anteriormost portion, Fig. 15A), and a posterior portion of similar size and morphology as in m1. Posterior margins of m1–2 strongly thickened and non-porous (Fig. 15B). Ventral cuticle with minute, faint endocuticular pillars distributed throughout the whole venter; genital plates present. Sexpartite gonopore placed anteriorly to legs IV, and a trilobed anus between legs IV.

Pedal plates I–III absent (Fig. 15A), pedal plates IV present and with minute pores (Fig. 15A, insert). Poorly marked pulvini on all legs (Fig. 15B). A minuscule spine on leg I and a papilla on leg IV. Claws IV slightly longer than claws I–III (Table 8). Claws short and robust. All external claws spurless. All internal claws with robust spurs, positioned at *ca.* 30–40% of the claw length (Fig. 15A, insert).

Juveniles. Unknown.

Larvae. Unknown.

Eggs. Unknown.

DNA markers and phylogenetic position. *E. capensis* **sp. nov.** is the sister species of the clade (*E. gracilis* **sp. nov.** + *E. irroratus* **sp. nov.**) (Fig. 117). The closest species is *E. gracilis* **sp. nov.**: COI (p-distance = 15.2%), ITS-1 (3.4%), ITS-2 (1.2%).

Type material. 2 specimens: holotype (mature ♀ on slide ZA.378.01) and paratype (mature ♀ on slide ZA.378.02). A single specimen was used for DNA extraction.

Type locality. 34°17'21.24"S, 18°26'53.46"E, 145 m asl: Republic of South Africa, Western Cape, Cape of Good Hope; fynbos, lichen from a rock. Found together with *Echiniscus dentatus* **sp. nov.** (sample ZA.378).

Etymology. The name refers to *locus typicus*. An adjective in the nominative singular.

Geographic distribution. This rare species is probably endemic to South Africa (Fig. 120G).

Remarks. None.

Differential diagnosis. *E. capensis* **sp. nov.** is similar only to its closest congeners, *E. gracilis* **sp. nov.** and *E. irroratus* **sp. nov.**, but can be distinguished from:

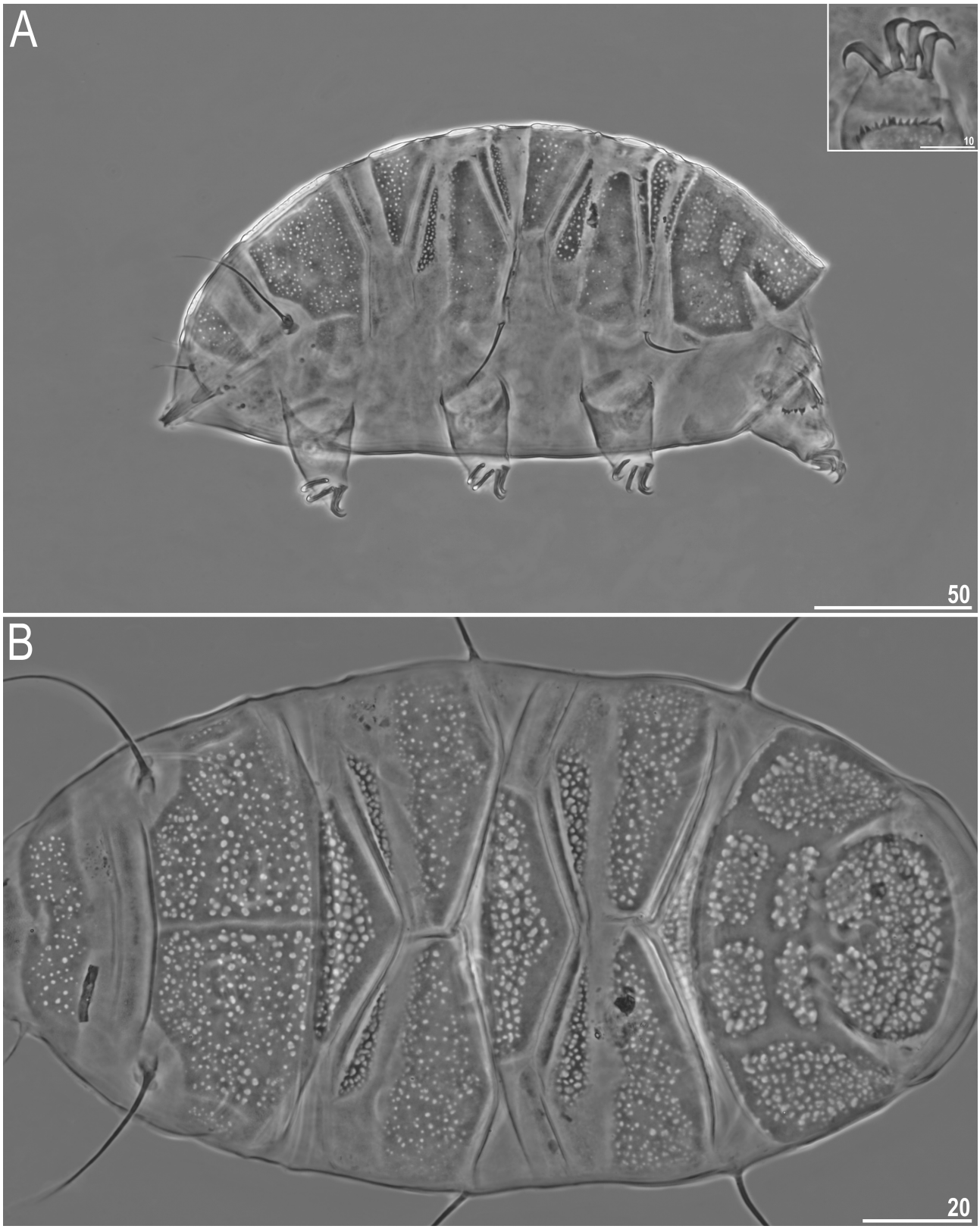

FIGURE 15. Habitus of *Echiniscus capensis* **sp. nov.** (PCM, females): A—paratype in lateral view (insert shows claws IV in holotype), B—close-up on the dorsal sculpturing of holotype. Scale bars in μm.

- *E. gracilis* **sp. nov.**, by claw morphology (claws short and robust, with robust spurs positioned at *ca.* 30–40% of the internal claw length in *E. capensis* **sp. nov.** *vs* claws slender, with delicate, acute spurs positioned at *ca.* 25% of the internal claw length in *E. gracilis* **sp. nov.**);
- *E. irroratus* **sp. nov.**, by body appendage configuration (*A-C-D* in *E. capensis* **sp. nov.** *vs A-(B)-(C)-(D)-(D^d)-(E)* in *E. irroratus* **sp. nov.**), and sculpturing (dark epicuticular granules absent in *E. capensis* **sp. nov.** *vs* dark epicuticular granules present in *E. irroratus* **sp. nov.**).

Raw measurements. Supplementary Materials (SM.03) and Tardigrada Register (www.tardigrada.net/register/0082.htm).

TABLE 8. Measurements [in µm] of selected morphological structures of the adult females of *Echiniscus capensis* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Holotype	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	2	186	–	206	*571*	–	*574*	196	*572*	14	*2*	186	*571*
Scapular plate length	2	32.6	–	35.9		–		34.3	–	2.3	–	32.6	–
Head appendages lengths													
Cirrus *internus*	2	10.9	–	13.2	*33.4*	–	*36.8*	12.1	*35.1*	1.6	*2.4*	10.9	*33.4*
Cephalic papilla	2	7.7	–	8.3	*23.1*	–	*23.6*	8.0	*23.4*	0.4	*0.4*	7.7	*23.6*
Cirrus *externus*	2	15.6	–	15.8	*44.0*	–	*47.9*	15.7	*45.9*	0.1	*2.7*	15.6	*47.9*
Clava	2	5.2	–	6.3	*16.0*	–	*17.5*	5.8	*16.7*	0.8	*1.1*	5.2	*16.0*
Cirrus *A*	2	43.7	–	44.3	*123.4*	–	*134.0*	44.0	*128.7*	0.4	*7.5*	43.7	*134.0*
Cirrus *A*/Body length ratio	2	22%	–	23%		–		22%	–	1%	–	23%	–
Body appendages lengths													
Cirrus *C*	2	23.7	–	24.8	*66.0*	–	*76.1*	24.3	*71.0*	0.8	*7.1*	24.8	*76.1*
Cirrus *D*	2	21.5	–	21.9	*61.0*	–	*66.0*	21.7	*63.5*	0.3	*3.5*	21.5	*66.0*
Spine on leg I length	2	1.9	–	2.2	*5.8*	–	*6.1*	2.1	*6.0*	0.2	*0.2*	1.9	*5.8*
Papilla on leg IV length	2	3.0	–	3.8	*9.2*	–	*10.6*	3.4	*9.9*	0.6	*1.0*	3.0	*9.2*
Number of teeth on the collar	1	13	–	13		–		13.0	–	?	–	13	–
Claw I heights													
Branch	2	9.8	–	10.6	*29.5*	–	*30.1*	10.2	*29.8*	0.6	*0.4*	9.8	*30.1*
Spur	2	3.0	–	3.7	*9.2*	–	*10.3*	3.4	*9.8*	0.5	*0.8*	3.0	*9.2*
Spur/branch height ratio	2	31%	–	35%		–		33%	–	3%	–	31%	–
Claw II heights													
Branch	2	9.3	–	9.5	*26.5*	–	*28.5*	9.4	*27.5*	0.1	*1.5*	9.3	*28.5*
Spur	2	2.4	–	3.3	*7.4*	–	*9.2*	2.9	*8.3*	0.6	*1.3*	2.4	*7.4*
Spur/branch height ratio	2	26%	–	35%		–		30%	–	6%	–	26%	–
Claw III heights													
Branch	2	9.7	–	10.3	*28.7*	–	*29.8*	10.0	*29.2*	0.4	*0.8*	9.7	*29.8*
Spur	2	2.4	–	2.6	*7.2*	–	*7.4*	2.5	*7.3*	0.1	*0.1*	2.4	*7.4*
Spur/branch height ratio	2	25%	–	25%		–		25%	–	0%	–	25%	–
Claw IV heights													
Branch	2	10.8	–	11.6	*32.3*	–	*33.1*	11.2	*32.7*	0.6	*0.6*	10.8	*33.1*
Spur	2	2.7	–	3.7	*8.3*	–	*10.3*	3.2	*9.3*	0.7	*1.4*	2.7	*8.3*
Spur/branch height ratio	2	25%	–	32%		–		28%	–	5%	–	25%	–

6. Echiniscus cavagnaroi Schuster & Grigarick, 1966

Figures 16–18

Data source:

A total of 54 specimens (29 ♀♀, 5 juveniles, 3 larvae, and 7 specimens of unknown instar/sex):

- Sample ZA.031: 1 specimen (1 ♀ on a slide).
- Sample ZA.037: 4 specimens (2 ♀♀ on a slide and 2 specimens used for DNA extraction, including 1 hologenophore).
- Sample ZA.080: 1 specimen (1 juvenile on a slide).
- Sample ZA.256: 1 specimen (1 ♀ on a slide); found with *Doryphoribius bindae*, *Pseudechiniscus (Meridionis-cus) wallacei* **sp. nov.**, and *Ramazzottius szeptycki*.
- Sample ZA.404: 2 specimens (1 ♀ on a slide, 1 specimen used for DNA extraction); found with *Echiniscus scabrospinosus*.
- Sample ZA.416: 45 specimens (18 ♀♀, 14 juveniles and 3 larvae on slides, 6 ♀♀ on SEM stub 18.17, and 4 specimens used for DNA extraction, including 1 hologenophore).

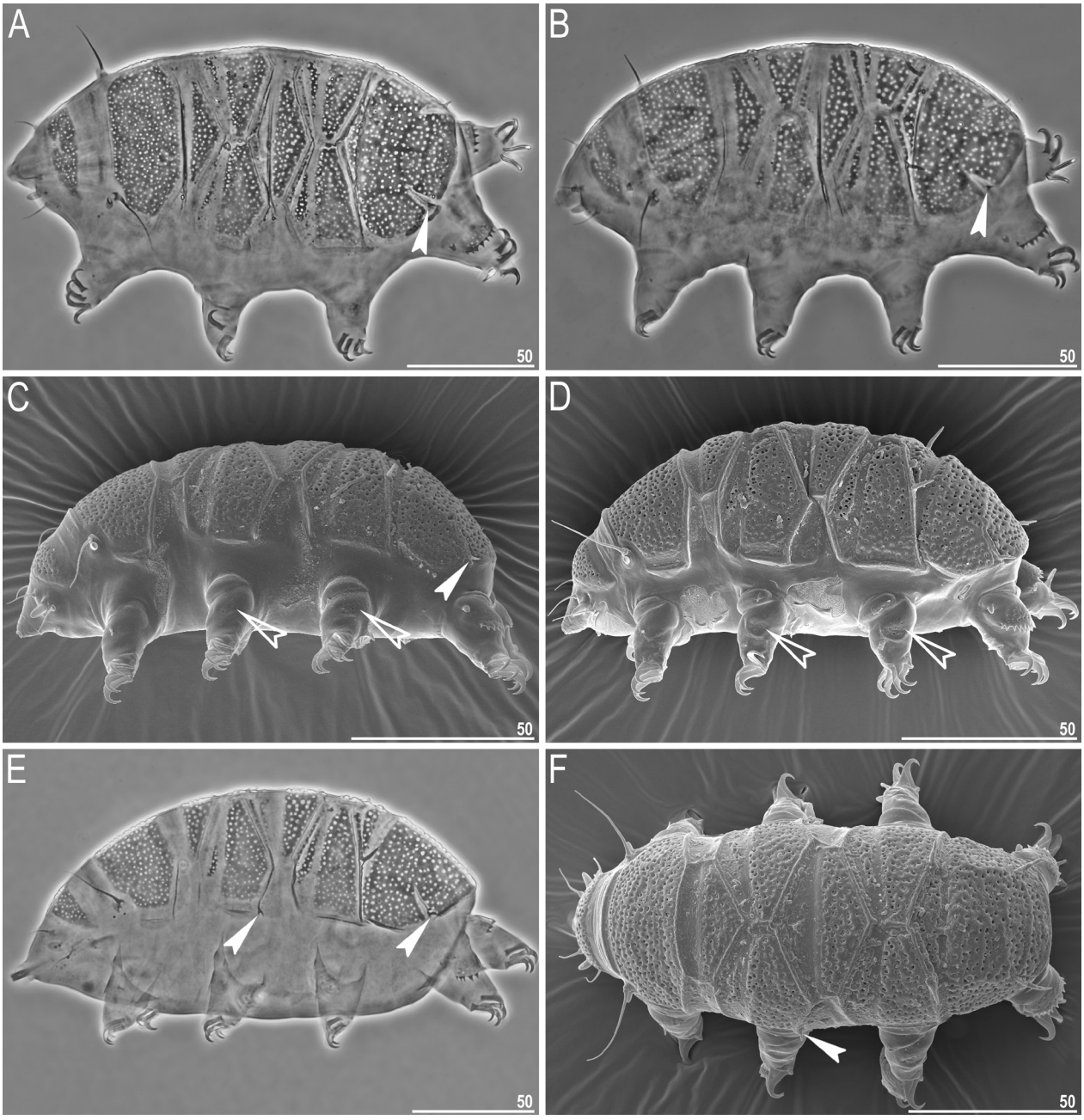

FIGURE 16. Intraspecific variability of *Echiniscus cavagnaroi* Schuster & Grigarick, 1966 (females). Arrowheads indicate lateral spicules, and empty arrowheads point out weakly developed pedal plates with pores. Scale bars = 50 µm.

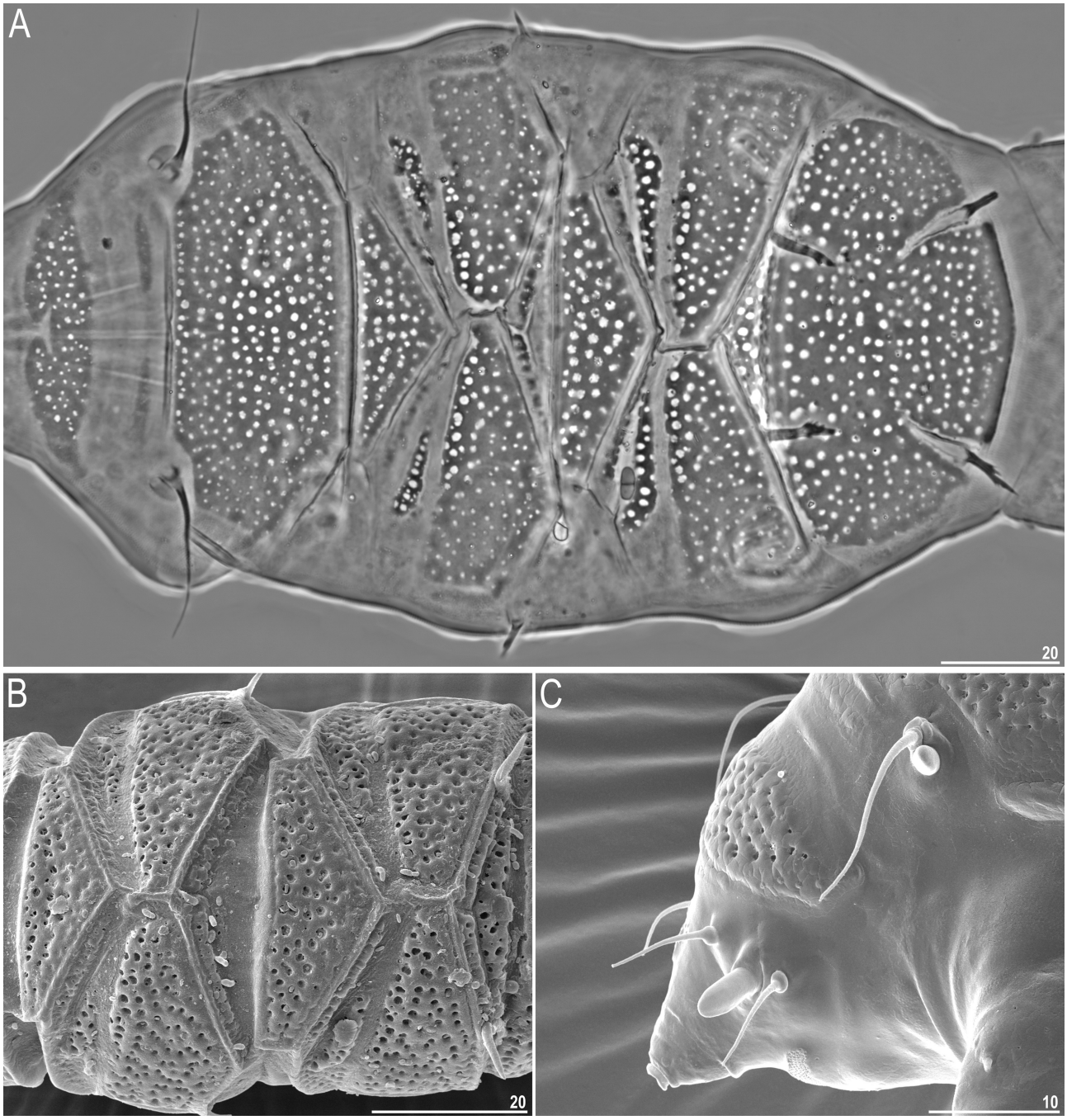

FIGURE 17. Head and dorsal sculpturing of *Echiniscus cavagnaroi* (females): A—close-up on the dorsal sculpturing (PCM), B—close-up on the dorsal sculpturing (SEM), C—cephalic appendages. Scale bars in μm.

Shortened description. Small representative of the *E. spinulosus* complex. Body appendage formula *A-(C)-(D^d)-(E)*, highly unstable. All trunk appendages formed as spines, usually spicules (Fig. 16), and only sometimes longer spines, especially in the position *D^d* (Fig. 16B, 17A). Spines may be gently serrated (Fig. 16D, 17A). Cirri *A* short (<25% of the body length). Regularly distributed pores in all plates (Fig. 16–17), only some of them have dark endocuticular rings. Subcephalic and genital plates absent. Pedal plates reduced to accumulations of few pores in the central thickening on each leg (Fig. 16C–D). Pulvini present (Fig. 16A–D). Minute spine I (Fig. 17C). External claws spurless, internal ones with delicate, thin spurs positioned at *ca.* 25% of the claw height and closely adjacent to the claw branches (Fig. 18).

DNA markers and phylogenetic position. *E. cavagnaroi* is a sister species to the clade (*E. manuelae* + *E. tris-*

tis) (Fig. 117) within the *E. spinulosus* group. The species closest in COI are *E. draconis* **sp. nov.** and *E. similaris* **sp. nov.** (p-distance = 12.9–14.1%), and in ITS—*E. manuelae* (ITS-1: 2.3%, ITS-2: 3.2%).

Geographic distribution. This parthenogenetic species has a wide distribution embracing islands in the Pacific Ocean, southeast Nearctic, and the West Indies (Meyer 2016), thus first records from South Africa make it potentially pantropical-subtropical. Rare, but widely distributed in South-Eastern Africa (Fig. 120D).

Remarks. Most often occurs without the admixture of other tardigrade species.

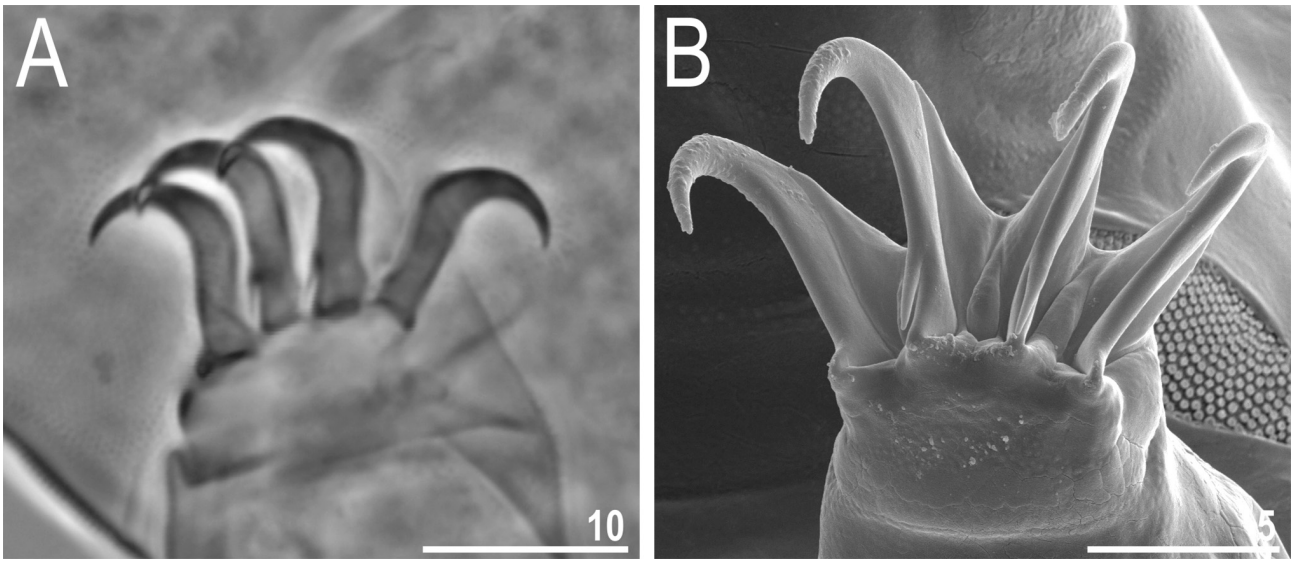

FIGURE 18. Claws of *Echiniscus cavagnaroi* (females): A—claws IV (PCM), B—claws I (SEM). Scale bars in μm.

7. Echiniscus crassispinosus Murray, 1907

Figure 19

Data source:

A total of 1 specimen (1 ♀):

- Sample ZA.274: 1 specimen (1 ♀ on a slide); found with *Echiniscus longispinosus* and *E. regularis* **sp. nov.**

Literature:

- Original description: Murray (1907a).
- Later trustworthy records: Murray (1913); Teunissen (1938).

Shortened description. A large representative (body length 254 μm, scapular plate length 43.9 μm) of the *E. spinulosus* complex with roundish body and short, stout legs. Peribuccal appendages lengths: *cirrus internus* 14.6 μm, cephalic papilla 8.5 μm, *cirrus externus* 18.8 μm, (primary) clava 8 μm. Body appendage formula *A-C-D-D*^{d}*-E* (all trunk spines asymmetrically lacking in the single specimen found in the present study, Fig. 19). Spines smooth, and those in the position *D*^{d} much thicker than the lateral appendages. Spine lengths: *C* 13.2 μm, *D* 11.2 μm, *D*^{d} 24.1 μm, *E* 9.5 μm. Cirri *A* short (39.4 μm, <25% of the body length). Anterior and posterior margins of paired segmental plates thickened, irregular. Pores with dark endocuticular rings. Subcephalic and genital plates absent. Pedal plates absent, but pulvini present. Minuscule spine I and papilla IV (4.9 μm). Dentate collar IV with 13 teeth. Claws robust and relatively short (12.1–13.5 μm), external claws spurless, internal ones with minute, thin spurs (2.0–2.6 μm) positioned at *ca.* 25% of the claw height and closely adjacent to the claw branches.

DNA markers and phylogenetic position. Only a single specimen found, thus no DNA was secured and elucidating its position within the *E. spinulosus* complex was not possible.

Etymology. From Latin *crassus* = thick + *spinosus* = spiny. The name underlines the dissimilarity in the thickness of spines *D*^{d} and lateral spines.

Geographic distribution. Originally described from the Republic of South Africa (Murray 1907a), the species was later recorded in Africa from central part of the continent: the Republic of Kenya (Murray 1913) and the Democratic Republic of Congo (Teunissen 1938). In the present study, *E. crassispinosus* was found only in a single

sample (ZA.274; Fig. 120H). Thus, it is extremely rare and the records outside Africa, i.e. from Asia, Central and South America (McInnes 1994) need to be re-examined, as they most likely represent other members of the species-rich *E. spinulosus* complex.

Remarks. Both Murray's descriptions of his species (1907a, 1913) are inconsistent, as specimens from Kenya had two transverse belts on paired segmental plates, but those from South Africa—putatively uniform plates without the belts. The individual found in the Tradouw Pass (Western Cape) in the present study exhibits an ordinary transverse belt dividing segmental plates into the anterior and the posterior portion, and, additionally, smooth surface (= the second belt in Murray 1913) just before the anterior plate margin, with a narrow strip of thicker cuticle between the belts. Murray's description (1907a) is unreliable for two reasons: (1) all other known *Echiniscus* spp. possess transverse belts on paired segmental plates, thus undivided plates in *E. crassispinosus* would be the only exception in the entire genus; (2) the characterisation of sculpturing according to Murray was confusing, as he claimed that it resembles the *E. perarmatus* type (*i.e*. densely packed endocuticular pillars and sparsely, regularly distributed pores; see the redescription below), however, he also noted that the large distant dots may be homologous to depressions (= large pores), and smaller dots resemble pellucid granules (= small pores), which conforms with the definition of the *E. spinulosus* group. Since pores are diversified in terms of size in the individual found in the present study (Fig. 19), dorsal plate sculpturing could be said to correspond to the ambiguous diagnosis of Murray (1907a). The type series of *E. crassispinosus* does not exist (Morgan 1977), and we ascertain that this species is a member of the *E. spinulosus* complex, characterised as above.

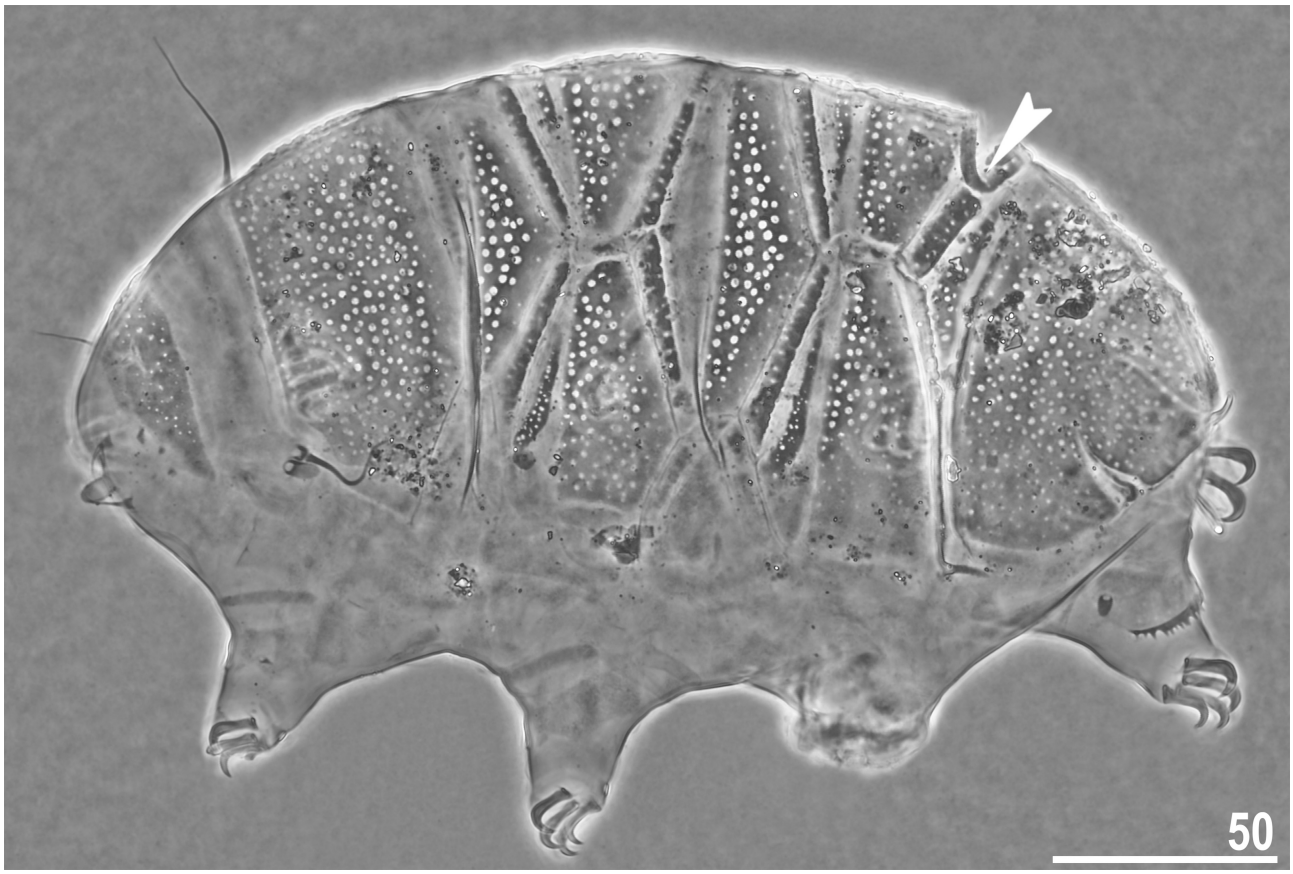

FIGURE 19. Habitus of *Echiniscus crassispinosus* Murray, 1907 (PCM, female in dorsolateral view). Arrowhead indicates thick dorsal spine D^d. Scale bar = 50 µm.

8. Echiniscus dentatus sp. nov. Vončina, Gąsiorek, Morek & Michalczyk

urn:lsid:zoobank.org:act:A2C2DE27-8041-49F7-BC40-D7C076D51113

Figures 20–25, Tables 9–11

Data source:

A total of 558 specimens (216 ♀♀, 42 juveniles, 8 larvae, and 292 specimens of unknown instar/sex):

- Sample ZA.020: 90 specimens (33 ♀♀, 7 juveniles on slides, 50 specimens used for SEM analysis on SEM stub 19.03); found with *Echiniscus draconis* **sp. nov.**, *E. lichenorum*, *E. longispinous*, *E. setaceus* **sp. nov.**
- Sample ZA.021: 42 specimens (42 ♀♀ on slides).
- Sample ZA.022: 35 specimens (32 ♀♀ and 1 larva on slides, and 2 specimens used for DNA extraction, including 2 hologenophores); found with *Echiniscus attenboroughi* **sp. nov.**, *E. gracilis* **sp. nov.**, *E. lichenorum*, *E. longispinous*, *E. setaceus* **sp. nov.**
- Sample ZA.023: 7 specimens (5 ♀♀ and 2 specimens used for DNA extraction, including 1 hologenophore); found with *Echiniscus gracilis* **sp. nov.** and *E. irroratus* **sp. nov.**
- Sample ZA.024: 18 specimens (15 ♀♀ on slides and 3 specimens used for DNA extraction, including 2 hologenophores).
- Sample ZA.025: 16 specimens (12 ♀♀, 3 juveniles on slides, and 1 specimen used for DNA extraction, including 1 hologenophore); found with *Echiniscus gracilis* **sp. nov.**
- Sample ZA.164: 2 specimens (2 ♀♀ on slides).
- Sample ZA.165: 1 specimen (1 ♀ on slide).
- Sample ZA.376: 103 specimens (3 ♀♀ and and 100 frozen specimens).
- Sample ZA.377: 3 specimens (2 ♀♀ and 1 juvenile on slides).
- Sample ZA.378: 4 specimens (2 ♀♀ and 2 juveniles on slides); found with *Echiniscus capensis* **sp. nov.**
- Sample ZA.471: 1 specimen (1 ♀ on a slide).
- Sample ZA.495: 1 specimen (1 ♀ on a slide); found with *Echiniscus setaceus* **sp. nov.**
- Sample ZA.499: 1 specimen (1 ♀ on a slide).
- Sample ZA.502:1 specimen (1 ♀ on slide); found with *Cornechiniscus madagascariensis*, *Echininscus irroratus* **sp. nov.**, *E. latruncularis* **sp. nov.**, and *E. setaceus* **sp. nov.**
- Sample ZA.504: 16 specimens (7 ♀♀, 4 juveniles on and 5 specimens of unidentified sex on slides); found with *E. irroratus* **sp. nov.**
- Sample ZA.505: 47 specimens (23 ♀♀, 11 juveniles, 7 larvae and 6 specimens of unidentified sex on slides); found with *E. setaceus* **sp. nov.**
- Sample ZA.507: 1 specimen (1 ♀ on a slide); found with *Echiniscus longispinosus* and *E. setaceus* **sp. nov.**
- Sample ZA.518: 7 specimens (2 ♀♀ and 5 juveniles on slides); found with *Echiniscus irroratus* **sp. nov.**, *E. scabrospinous*, *Pseudechiniscus (Pseudechiniscus)* cf. *ehrenbergi*, and *P. (Meridioniscus) wallacei* **sp. nov.**
- Sample ZA.524: 1 specimen (1 ♀ on a slide); found with *E. scabrospinous* and *Pseudechiniscus (Pseudechiniscus)* cf. *ehrenbergi*.
- Sample ZA.531: 1 specimen (1 ♀ on a slide); found with *Pseudechiniscus (Meridioniscus) wallacei* **sp. nov.**
- Sample ZA.537: 4 specimens (4 ♀♀ on slides); found with *Echiniscus setaceus* **sp. nov.**
- Sample ZA.551: 10 specimens (10 ♀♀ on slides); found with *Echiniscus irroratus* **sp. nov.**
- Sample ZA.554: 135 specimens (10 ♀♀, 4 juveniles and 2 specimens of unknown sex on slides, 19 specimens used for SEM analysis on stub 19.06, 100 frozen specimens); found with *Echinicus gracilis* **sp. nov.**
- Sample ZA.555: 10 specimens (3 ♀♀, 5 juveniles and 2 specimens of unknown sex on slides); found with *Echinicus gracilis* **sp.nov.**, *E. irroratus* **sp. nov.**, and *E. latruncularis* **sp. nov.**
- Sample ZA.558: 1 specimen (1 ♀ on a slide); found with *Echiniscus irroratus* **sp. nov.** and *E. longispinosus*.

Description. Mature females (*i.e*. from the third instar onwards; measurements and statistics in Table 9). Body plump (Fig. 20–21), dark orange to red with minute scarlet eyes; body colour and eyes disappeared soon after mounting in Hoyer's medium. Conoidal cephalic papillae (secondary clavae) and (primary) clavae, clearly tapering at the distal end (Fig. 21, 23A–B, F); cirri growing out from bulbous cirrophores (Fig. 23A–B); peribuccal cirri of similar lengths (Table 9). Cirri *A* of a moderate length (usually between 25–30% of the body length). The body appendage configuration is *A-(B)-(C)-C^{d}-(D)-D^{d}-(E)*, with all trunk appendages formed as spines of variable lengths. Typically, spines *C^{d}* and *D^{d}* are much longer than lateral appendages (Fig. 20A, D, 21, 22), but sometimes appendage *D* is developed as a spine similar in length to spines *C^{d}* and *D^{d}* (Fig. 20B–C). Asymmetries in the development of dorsal spines infrequent (*e.g*. Fig. 20C). Supernumerary spines and spicules along the margins of all dorsal plates and caudal incisions are characteristic for the new species (Fig. 20A, D, 21, 22A, C, 23B–G). Rarely, these shortest appendages may be restricted only to some plates (*e.g*. the posterior margin of the scapular plate, Fig. 22B), or absent (Fig. 20B–C). Spicules usually irregularly microgranulated at their ends (Fig. 23D, G).

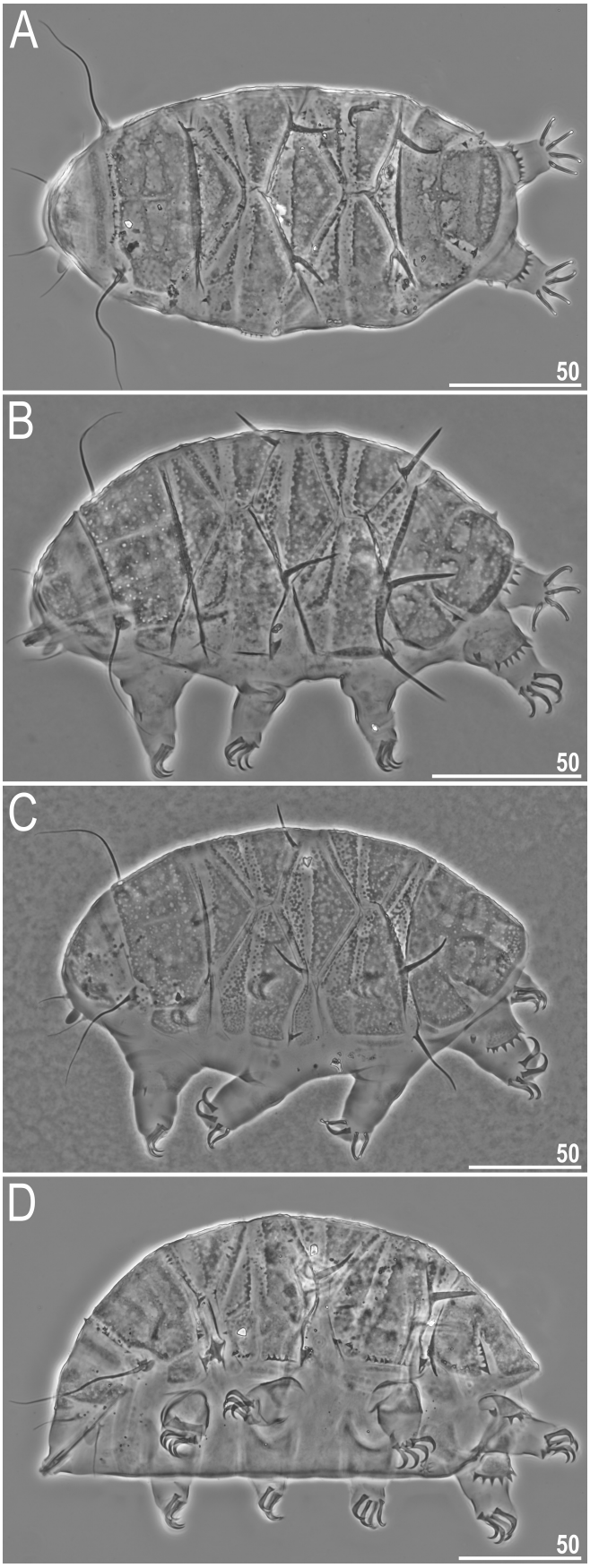

FIGURE 20. Habitus and intraspecific variability of *Echiniscus dentatus* **sp. nov.** (PCM, females): A—holotype in dorsal view, B, C—paratypes in dorsolateral view, D—paratype in lateral view. Scale bars = 50 μm.

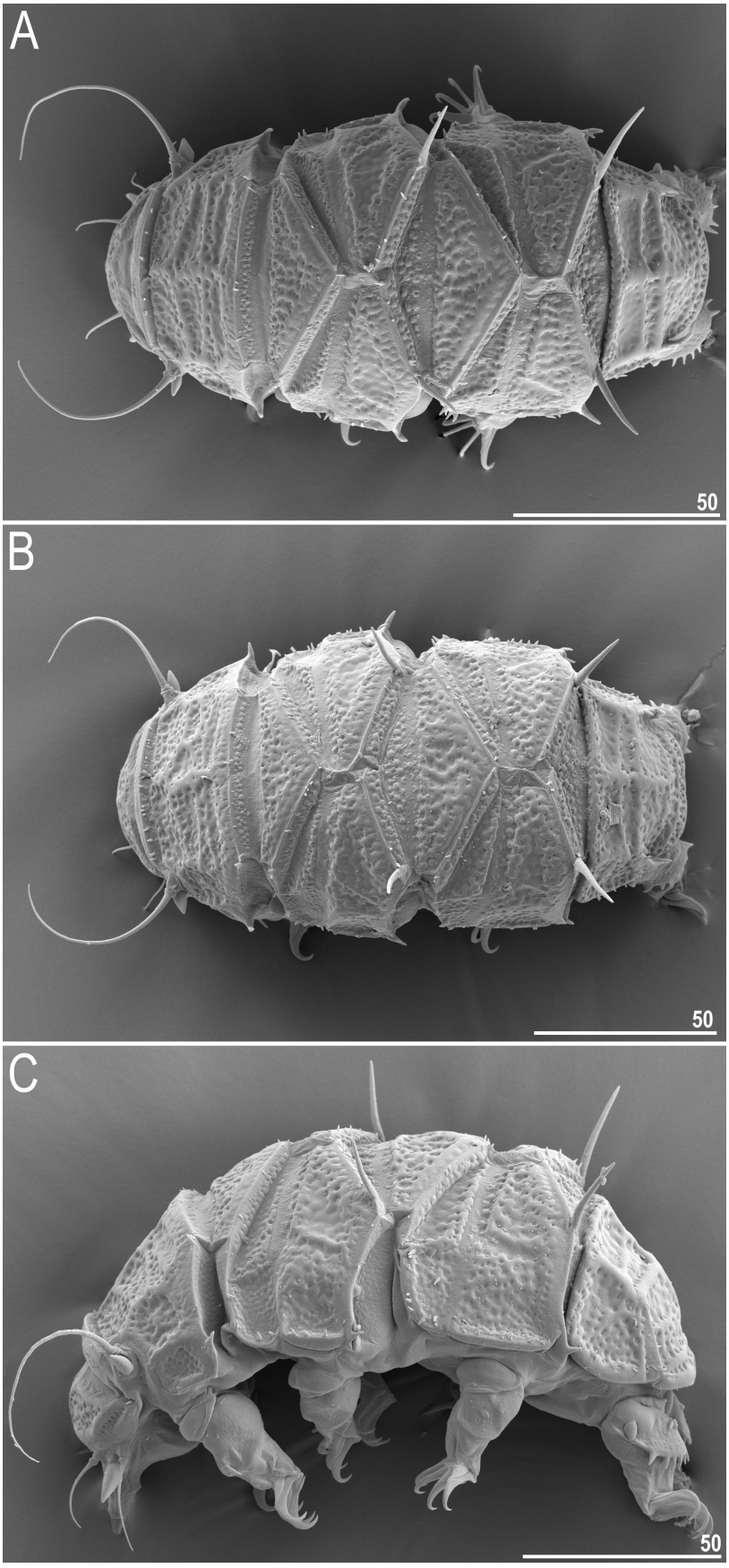

FIGURE 21. Habitus and intraspecific variability of *Echiniscus dentatus* **sp. nov.** (SEM, females): A, B—dorsal view, C—lateral view. Scale bars = 50 μm.

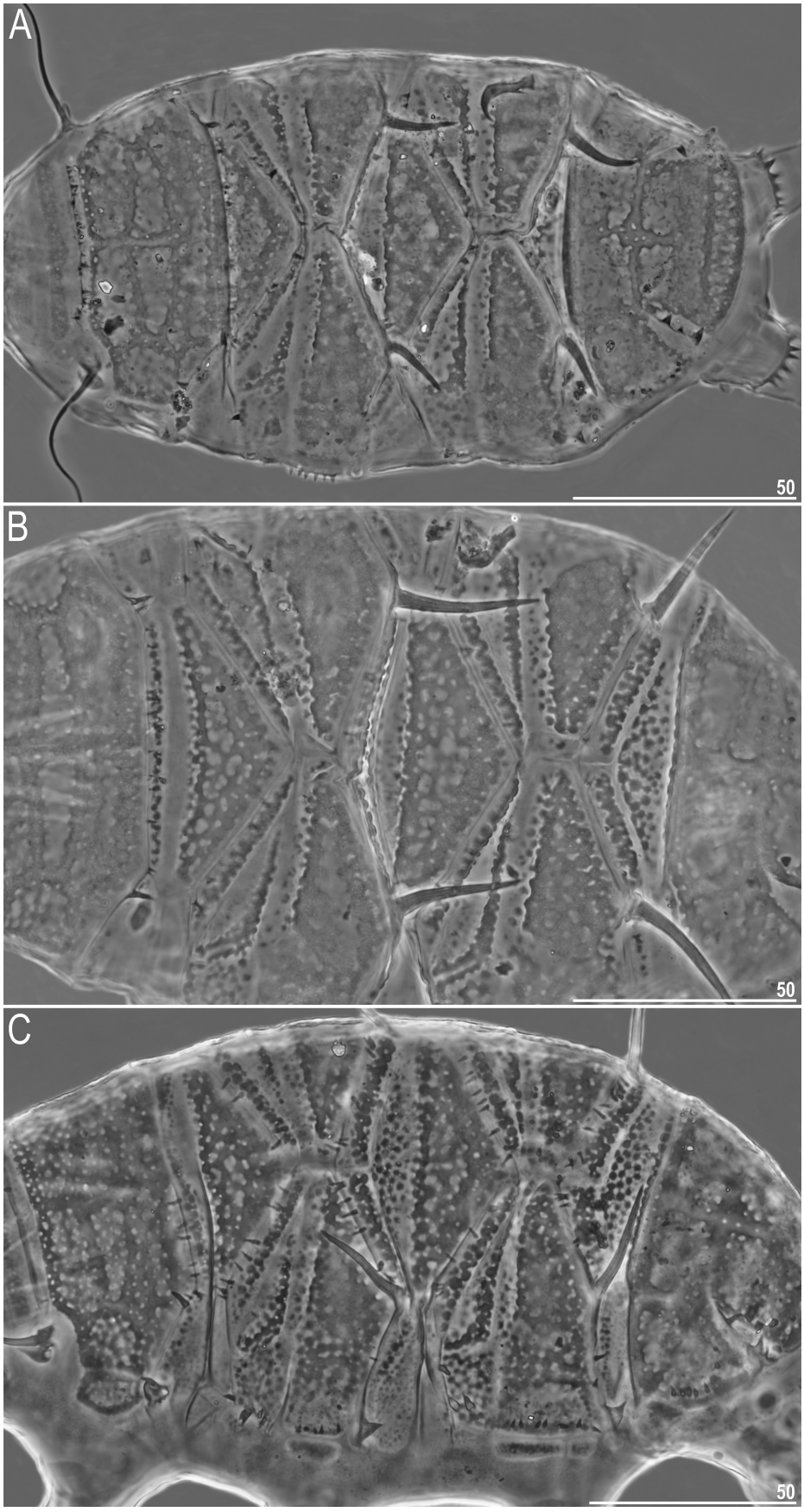

FIGURE 22. Dorsal sculpturing of *Echiniscus dentatus* **sp. nov.** (PCM, females), showing the variability in the development of epicuticular layer and spicules distributed along the margins of dorsal plates. Scale bars = 50 μm.

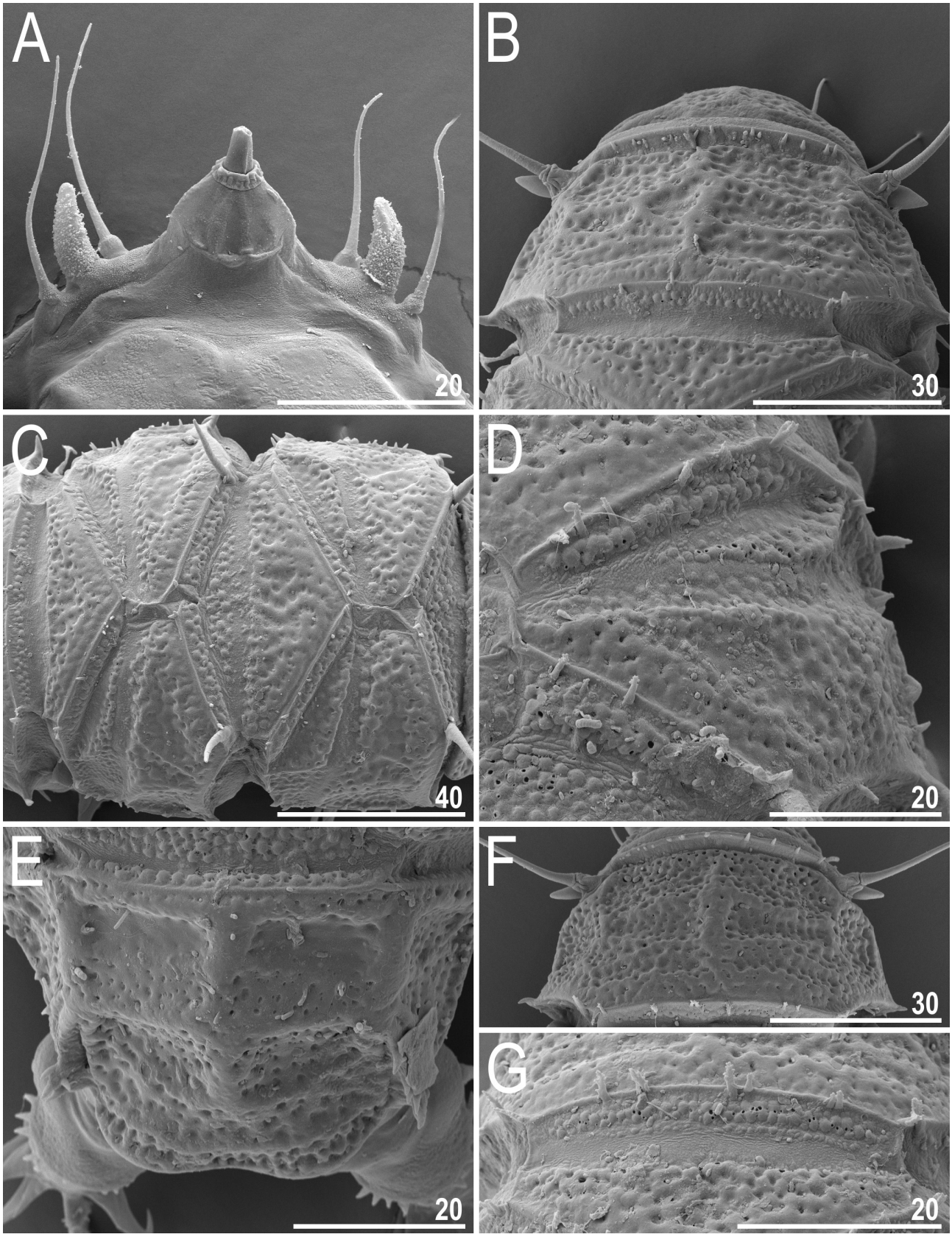

FIGURE 23. Head and dorsal sculpturing of *Echiniscus dentatus* **sp. nov.** (SEM, females): A—cephalic appendages and subcephalic plates, B—scapular plate (pores absent), C—paired segmental and median plates, D—segmental plate in close-up, E—caudal (terminal) plate, F—scapular plate (pores present in the anterior portion), G—close-up on marginal spicules. Scale bars in μm.

Dorsal plates with complex epicuticular ornamentation (Fig. 21, 23B–G) visible as dark grey matrix under PCM (Fig. 22); pores minute, rare and irregularly distributed (Fig. 23B, D, F–G), difficult to identify under PCM. The cephalic plate semicircular, not halved (Fig. 20A–C); the cervical (neck) plate moderately wide, developed as a prolonged rectangle anterior to the scapular plate (Fig. 20A–B, 22A, 23B). The scapular plate with lateral sutures separating pentagonal lateral portions (Fig. 20B–D, 21C, 22C). If present, pores in the scapular plate are usually distributed along its posterior margin (Fig. 23B), or in the anterocentral portion (Fig. 23F). Paired segmental plates with the usual transverse stripes, but anterior and posterior portions are similar in sculpturing (Fig. 20–22, 23C–D). The caudal (terminal) plate with variously developed epicuticular ridges forming a faceted pattern (Fig. 20A–C, 21–22, 23E). Median plate 1 unipartite, median plate 2 bipartite, with the posterior portion much larger and similar to m1, whereas the anterior portion similar to reduced, unipartite m3 (Fig. 20A–C, 21–22, 23C). Ventral cuticle with minute endocuticular pillars distributed throughout the whole venter, and a pair of multangular subcephalic (Fig. 23A) and genital plates (Fig. 20D). Sexpartite gonopore placed between genital plates, and a trilobed anus between legs IV.

Pedal plates I–III absent, pedal plate IV weakly sculptured above the dentate collar IV (Fig. 20B-C). Pulvini weakly visible under PCM (Fig. 20C), evident under SEM (Fig. 21C). Needle-like spine on leg I (Fig. 20B–C, 21C) and a papilla on leg IV (Fig. 20, 21C). Claws I–IV of similar lengths (Table 9). All external claws smooth (Fig. 24). All internal claws with large spurs positioned at *ca.* 30–50% of the claw height, highly divergent from the claw branch and bent downwards (Fig. 24).

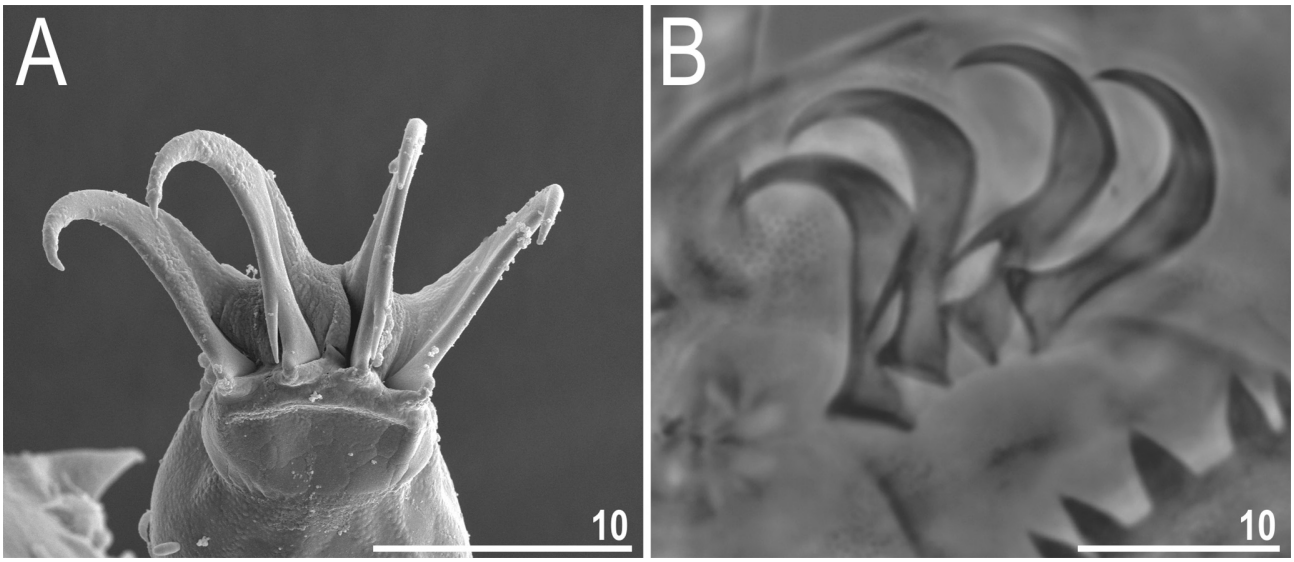

FIGURE 24. Claws of *Echiniscus dentatus* **sp. nov.** (females): A—claws I (SEM), B—claws IV (PCM). Scale bars in µm.

Juveniles (*i.e.* the second instar, measurements and statistics in Table 10). Phenotypically identical to adult females, beside of the lacking gonopore. However, clearly smaller in the majority of morphometrically informative traits (body and scapular plate length, lengths of cephalic appendages and claws; compare Tables 9–10).

Larvae (*i.e.* the first instar, measurements and statistics in Table 11). Body appendage formula *A-(B)-(C)-C^{d}-(D)-D^{d}-(E)*, with lateral spines *B*, *C*, *D* being often absent (Fig. 25). Supernumerary spicules on dorsal plates greatly reduced. Lacking gonopore and anus. Evidently smaller than juveniles (compare Tables 10–11).

Eggs. Up to two round, yellow eggs per exuvia were found.

DNA markers and phylogenetic position. *Echiniscus dentatus* **sp. nov.** is the sister species of the clade (*E. longispinosus* (*E. capensis* **sp. nov.** (*E. gracilis* **sp. nov.** + *E. irroratus* **sp. nov.**))) within the mostly South-African endemic clade (Fig. 117). The species closest in COI are *E. draconis* **sp. nov.** and *E. imitans* **sp. nov.** (p-distance = 14.5–14.9%), in ITS-1—*E. draconis* **sp. nov.** (6.3–8.6%), and in ITS-2—*E. irroratus* **sp. nov.** and *E. setaceus* **sp. nov.** (5.0–5.3%).

Type material. 33 ♀♀, 7 juveniles and 2 specimens of unknown sex on slides ZA.020.01–2, 5, 7–9; holotype: mature ♀ on slide ZA.020.02. Mounted together with 3 ♀♀ and 3 juveniles of *Echiniscus lichenorum*, 1 ♀ of *E. longispinosus*, 2 ♀♀, 7 juveniles, and 2 larvae of *E. setaceus* **sp. nov.** 50 specimens on SEM stub 19.03.

FIGURE 25. Habitus of larval *Echiniscus dentatus* **sp. nov.** (PCM). Scale bar = 20 µm.

Type locality. 33°34’30.7’’S, 19°08’3.3’’E, 430 m asl: Republic of South Africa, Western Cape, Bainskloof Pass; fynbos, mosses and lichens from rocks, trees, soil, and termite mounds. Found together with *Echiniscus attenboroughi* **sp. nov.**, *E. gracilis* **sp. nov.**, *E. irroratus* **sp. nov.**, *E. lichenorum*, *E. longispinosus*, and *E. setaceus* **sp. nov.** (sample ZA.020).

Etymology. From Latin *dentatus* = toothed. The name underlines the presence of supernumerary teeth and spicules in positions atypical for *Echiniscus* and along margins of all dorsal plates. An adjective in the nominative singular.

Geographic distribution. Probably endemic to South Africa, widely distributed and common in the region (Fig. 120C).

Remarks. The large number of individuals with no males among them suggest that the species is parthenogenetic.

Differential diagnosis. *E. dentatus* **sp. nov.** has so exceptional phenotype that it is hard to confuse it with other known species of *Echiniscus*; in fact, numerous appendages make this species superficially similar to *Acanthechiniscus* (Vecchi *et al*. 2016). Nevertheless, centrodorsal spines distinguish *E. africanus*, which also exhibits additional spines along the posterior margin of the scapular plate, from the new species. The new species is most similar to the recently described *E. insularis* Gąsiorek *et al*., 2021 (Kiosya *et al*. 2021), which also exhibits numerous spicules on margins of the dorsal plates, but, in contrast to *E. dentatus* **sp. nov.**, it has porous cuticle and it belongs in the *E. spinulosus* group. Similarly, *E. baloghi* sometimes has spines on the posterior margin of the paired segmental plate II (Iharos 1973), but it also has cuticular pores, and it represents the *E. spinulosus* group.

Raw measurements. Supplementary Materials (SM.03) and Tardigrada Register (www.tardigrada.net/register/0083.htm).

TABLE 9. Measurements [in µm] of selected morphological structures of the adult females of *Echiniscus dentatus* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Holotype	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	20	163	–	246	*463*	–	*562*	197	*510*	21	*30*	201	*498*
Scapular plate length	20	31.6	–	51.6		–		38.8	–	4.8	–	40.3	–
Head appendages lengths													
Cirrus *internus*	18	14.1	–	19.2	*36.6*	–	*51.3*	17.3	*44.8*	1.3	*4.0*	16.8	*41.7*
Cephalic papilla	20	5.9	–	10.4	*16.3*	–	*23.2*	7.8	*20.2*	1.1	*2.1*	6.9	*17.1*
Cirrus *externus*	17	16.1	–	24.6	*39.9*	–	*67.6*	19.6	*51.6*	2.2	*6.1*	17.5	*43.4*
Clava	19	4.8	–	8.4	*11.5*	–	*21.2*	6.1	*15.8*	0.9	*2.9*	7.0	*17.4*
Cirrus *A*	19	41.3	–	62.7	*105.4*	–	*150.0*	51.6	*134.2*	6.3	*11.7*	54.6	*135.5*
Cirrus *A*/Body length ratio	19	22%	–	30%		–		26%	–	3%	–	27%	–
Body appendages lengths													
Spine *B*	14	3.7	–	6.5	*8.1*	–	*18.3*	5.0	*12.5*	0.9	*2.9*	?	?
Spine *C*	14	4.1	–	9.3	*10.0*	–	*23.9*	5.8	*14.8*	1.6	*4.4*	?	*?*
Spine C^d	20	16.6	–	22.6	*34.3*	–	*59.3*	19.4	*50.5*	1.7	*6.4*	19.9	*49.4*
Spine *D*	11	3.6	–	7.4	*10.0*	–	*17.4*	5.2	*12.7*	1.0	*2.8*	?	*?*
Spine D^d	19	17.0	–	24.0	*39.9*	–	*69.2*	21.5	*55.9*	2.0	*7.7*	23.6	*58.6*
Spine *E*	15	3.8	–	16.1	*9.0*	–	*44.6*	5.8	*15.3*	2.9	*8.4*	4.6	*11.4*
Spine on leg I length	20	2.4	–	5.7	*6.0*	–	*14.3*	3.4	*8.8*	0.9	*1.9*	2.4	*6.0*
Papilla on leg IV length	18	3.4	–	5.6	*8.4*	–	*14.1*	4.6	*11.8*	0.6	*1.6*	3.4	*8.4*
Number of teeth on the collar	20	5	–	12		–		8.1	–	1.5	–	9	–
Claw I heights													
Branch	18	10.3	–	15.1	*27.2*	–	*37.2*	12.1	*31.3*	1.2	*2.8*	11.9	*29.5*
Spur	16	2.1	–	3.2	*5.0*	–	*9.0*	2.7	*7.0*	0.3	*1.2*	2.6	*6.5*
Spur/branch height ratio	16	15%	–	27%		–		22%	–	3%	–	22%	–
Claw II heights													
Branch	19	9.3	–	14.3	*26.3*	–	*34.9*	11.6	*29.9*	1.3	*2.1*	?	*?*
Spur	17	1.5	–	3.7	*3.5*	–	*8.6*	2.5	*6.5*	0.5	*1.1*	?	?
Spur/branch height ratio	17	11%	–	26%		–		21%	–	4%	–	?	–
Claw III heights													
Branch	16	9.9	–	15.1	*26.6*	–	*36.0*	11.9	*30.4*	1.4	*2.8*	10.7	*26.6*
Spur	13	1.7	–	3.5	*4.9*	–	*8.0*	2.6	*6.6*	0.5	*0.9*	?	*?*
Spur/branch height ratio	13	17%	–	28%		–		22%	–	3%	–	?	–
Claw IV heights													
Branch	16	10.7	–	16.3	*27.5*	–	*40.1*	13.2	*33.4*	1.5	*2.8*	?	*?*
Spur	13	1.8	–	3.9	*4.2*	–	*10.1*	2.9	*7.1*	0.6	*1.5*	?	*?*
Spur/branch height ratio	13	15%	–	25%		–		21%	–	4%	–	?	–

TABLE 10. Measurements [in µm] of selected morphological structures of the juvenile females of *Echiniscus dentatus* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD	
		µm			*sp*			µm	*sp*	µm	*sp*
Body length	5	133	–	163	*496*	–	*575*	151	*537*	12	*36*
Scapular plate length	5	23.1	–	31.8		–		28.3	–	3.9	–
Head appendages lengths											
Cirrus *internus*	5	9.4	–	13.7	*36.2*	–	*51.8*	11.7	*41.8*	1.7	*6.2*
Cephalic papilla	5	5.3	–	6.1	*18.6*	–	*25.5*	5.8	*20.9*	0.3	*2.7*
Cirrus *externus*	5	13.6	–	15.2	*43.8*	–	*65.8*	14.2	*51.4*	0.6	*9.6*
Clava	5	4.0	–	5.1	*14.7*	–	*20.2*	4.6	*16.4*	0.4	*2.4*
Cirrus *A*	5	33.0	–	38.7	*105.4*	–	*167.5*	36.9	*133.1*	2.3	*24.5*
Cirrus *A*/Body length ratio	5	21%	–	29%		–		25%	–	3%	–
Body appendages lengths											
Spine *B*	4	3.2	–	4.5	*12.6*	–	*19.5*	4.0	*14.7*	0.6	*3.2*
Spine *C*	3	4.1	–	6.9	*17.7*	–	*23.2*	5.4	*20.4*	1.4	*2.7*
Spine C^d	5	6.6	–	19.1	*21.1*	–	*64.1*	12.9	*46.4*	4.4	*16.3*
Spine *D*	3	3.6	–	5.3	*14.2*	–	*17.8*	4.3	*16.3*	0.9	*1.8*
Spine D^d	4	15.9	–	28.4	*63.8*	–	*90.7*	20.1	*72.7*	5.7	*12.2*
Spine *E*	4	3.0	–	5.5	*9.4*	–	*18.5*	4.0	*14.7*	1.1	*3.8*
Spine on leg I length	5	2.3	–	3.4	*7.3*	–	*13.4*	2.6	*9.5*	0.5	*2.5*
Papilla on leg IV length	5	2.5	–	3.9	*9.3*	–	*15.4*	3.2	*11.3*	0.5	*2.4*
Number of teeth on the collar	5	5	–	10		–		6.2	–	2.2	–
Claw I heights											
Branch	5	8.1	–	9.5	*27.4*	–	*37.2*	8.9	*32.0*	0.6	*4.0*
Spur	4	1.9	–	2.2	*6.6*	–	*8.7*	2.1	*7.7*	0.1	*0.9*
Spur/branch height ratio	4	23%	–	24%		–		24%	–	1%	–
Claw II heights											
Branch	5	8.3	–	9.9	*26.1*	–	*39.1*	8.8	*31.9*	0.6	*5.8*
Spur	5	1.9	–	2.6	*6.3*	–	*8.7*	2.1	*7.6*	0.3	*1.2*
Spur/branch height ratio	5	21%	–	30%		–		24%	–	3%	–
Claw III heights											
Branch	5	8.2	–	9.2	*27.4*	–	*36.4*	8.8	*31.6*	0.4	*4.0*
Spur	5	1.6	–	2.5	*6.0*	–	*8.0*	1.9	*6.9*	0.4	*0.7*
Spur/branch height ratio	5	18%	–	27%		–		22%	–	3%	–
Claw IV heights											
Branch	4	9.1	–	10.5	*28.6*	–	*45.5*	9.8	*36.3*	0.7	*7.8*
Spur	4	2.1	–	2.7	*7.2*	–	*9.1*	2.3	*8.5*	0.3	*0.9*
Spur/branch height ratio	4	20%	–	29%		–		24%	–	4%	–

TABLE 11. Measurements [in µm] of selected morphological structures of the larvae of *Echiniscus dentatus* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD	
		µm			*sp*			µm	*sp*	µm	*sp*
Body length	5	110	–	128	*502*	–	*599*	122	*571*	8	*40*
Scapular plate length	5	20.2	–	22.3		–		21.4	–	0.8	–
Head appendages lengths											
Cirrus *internus*	4	8.3	–	9.7	*37.2*	–	*45.1*	9.0	*42.2*	0.6	*3.5*
Cephalic papilla	5	4.4	–	6.0	*20.2*	–	*26.9*	5.2	*24.2*	0.6	*2.5*
Cirrus *externus*	5	10.2	–	12.4	*47.2*	–	*59.0*	11.1	*52.3*	0.9	*5.8*
Clava	5	3.5	–	5.7	*16.3*	–	*27.1*	4.3	*20.2*	0.9	*4.4*
Cirrus *A*	5	25.1	–	30.0	*114.7*	–	*143.4*	27.7	*129.8*	1.9	*10.5*
Cirrus *A*/Body length ratio	5	21%	–	24%		–		23%	–	1%	–
Body appendages lengths											
Spine *B*	2	5.0	–	5.1	*24.3*	–	*24.9*	5.1	*24.6*	0.1	*0.4*
Spine *C*	4	2.3	–	4.3	*10.9*	–	*19.3*	3.4	*15.6*	0.9	*3.9*
Spine C^d	5	2.3	–	13.5	*11.5*	–	*62.8*	8.9	*41.2*	4.2	*19.6*
Spine *D*	3	2.5	–	3.2	*11.9*	–	*14.6*	2.9	*13.5*	0.4	*1.4*
Spine D^d	5	9.7	–	14.4	*47.5*	–	*67.1*	11.9	*55.7*	2.2	*9.4*
Spine *E*	3	3.7	–	4.6	*16.9*	–	*21.4*	4.2	*19.2*	0.5	*2.3*
Spine on leg I length	5	1.7	–	2.4	*8.4*	–	*11.1*	2.0	*9.6*	0.3	*1.3*
Papilla on leg IV length	5	2.5	–	3.3	*11.2*	–	*15.1*	3.0	*13.9*	0.3	*1.6*
Number of teeth on the collar	5	4	–	6		–		4.8	–	0.8	–
Claw I heights											
Branch	5	6.7	–	8.4	*30.0*	–	*41.5*	7.8	*36.6*	0.7	*4.5*
Spur	5	1.5	–	2.2	*7.0*	–	*10.4*	1.9	*8.9*	0.3	*1.5*
Spur/branch height ratio	5	18%	–	31%		–		25%	–	6%	–
Claw II heights											
Branch	5	6.8	–	8.3	*31.1*	–	*38.6*	7.4	*34.8*	0.6	*2.6*
Spur	4	1.4	–	2.2	*6.5*	–	*10.5*	1.7	*8.2*	0.4	*1.9*
Spur/branch height ratio	4	17%	–	30%		–		23%	–	6%	–
Claw III heights											
Branch	5	7.3	–	8.0	*35.3*	–	*37.2*	7.7	*36.1*	0.3	*0.7*
Spur	5	1.5	–	2.4	*7.0*	–	*11.4*	1.8	*8.4*	0.4	*1.8*
Spur/branch height ratio	5	19%	–	32%		–		23%	–	5%	–
Claw IV heights											
Branch	4	8.4	–	9.4	*39.5*	–	*44.5*	8.8	*41.4*	0.4	*2.3*
Spur	4	1.7	–	2.4	*8.4*	–	*11.2*	2.1	*9.9*	0.3	*1.2*
Spur/branch height ratio	4	20%	–	26%		–		24%	–	3%	–

9. Echiniscus draconis sp. nov. Vončina, Gąsiorek, Morek & Michalczyk

urn:lsid:zoobank.org:act:BEC9402F-FE67-4B2B-8CEC-293FB2D8EBA1

Figures 26–29, Tables 12–14

Data source:

A total of 1352 specimens (145 ♀♀, 7 ♂♂, 24 juveniles, 32 larvae, and 1144 specimens of unknown instar/sex):

- Sample ZA.015: 9 specimens (4 ♀♀, 1 juvenile and 4 specimens of unknown sex on slides); found with *Echiniscus attenboroughi* **sp. nov.**, *E. lichenorum*, *E. setaceus* **sp. nov.**, and *E. virginicus*.
- Sample ZA.020: 5 specimens (2 ♀♀ and 3 juveniles on slides); found with *Echiniscus dentatus* **sp. nov.**, *E. lichenorum*, *E. longispinosus*, *E. setaceus* **sp. nov.**
- Sample ZA.056: 8 specimens (4 ♀♀, 2 ♂♂ and 2 specimens used for DNA extraction).
- Sample ZA.057: 12 specimens (8 ♀♀ and 4 juveniles on slides).
- Sample ZA.059: 2 specimens (2 ♀♀ on slides).
- Sample ZA.60: 84 specimens (44 ♀♀, 4 juveniles, 2 larvae on slides, 30 specimens for SEM analysis, and 4 specimens used for DNA extraction).
- Sample ZA.098: 1 specimen (1 ♀ on a slide); found with *Echiniscus lichenorum*, *E. marginatus* Binda & Pilato, 1994, and *E. scabrospinosus*.
- Sample ZA.218: 2 specimens (1 ♀ and 1 juvenile on slides); found with *Echiniscus intricatus* **sp. nov.**, *E. lichenorum*, and *E. tetraspinosus* **sp. nov.**
- Sample ZA.222: 3 specimens (2 ♀♀ and 1 juvenile on slides); found with *Echiniscus blumi*, *E. draconis* **sp. nov**., *E. imitans* **sp. nov.**, and *E. longispinosus*.
- Sample ZA.360: 1 specimen (1 ♀ on a slide); found with *Echiniscus lichenorum*, *E. longispinosus*, and *E. scabrospinosus*.
- Sample ZA.431: 137 specimens (16 ♀♀, 6 juveniles and 18 larvae on slides, 4 specimens used for DNA extraction, and 93 frozen specimens); found with *Echiniscus imitans* **sp. nov.**, *E. lichenorum*, and *E. scabrocirrosus* **sp. nov.**
- Sample ZA.432: 10 specimens (10 ♀♀ on slides); found with *Echiniscus scabrocirrosus* **sp. nov.**
- Sample ZA.434: 443 specimens (40 ♀♀, 1 juvenile and 2 specimens of unknown sex on slides, and 400 frozen specimens); found with *Echiniscus scabrocirrosus* **sp. nov.**
- Sample ZA.435: 403 specimens (2 ♀♀, 1 ♂ on slides, and 400 frozen specimens).
- Sample ZA.436: 25 specimens (4 ♀♀, 4 ♂♂, 11 larvae and 2 specimens of unknown sex on slides, and 4 specimens used for DNA extraction); found with *Echiniscus attenboroughi* **sp. nov.**, *E. scabrocirrosus* **sp. nov.**, and *E. setaceus* **sp. nov.**
- Sample ZA.437: 193 specimens (3 ♀♀, and 190 frozen specimens); found with *Echiniscus attenboroughi* **sp. nov.**
- Sample ZA.450: 13 specimens (2 juveniles and 1 larva on slides, and 10 frozen specimens); found with *Echiniscus lichenorum.*
- Sample ZA.480: 1 specimen (1 juvenile on a slide); found with *Echiniscus imitans* **sp. nov.** and *E. scabrocirrosus* **sp. nov.**

Description. Mature females (*i.e*. from the third instar onwards; measurements and statistics in Table 12). Large *Echiniscus* with a plump body (Fig. 26A, 27), yellow to dark orange with minute red eyes; body colour and eyes disappeared soon after mounting in Hoyer's medium. Dactyloid cephalic papillae (secondary clavae) and minute (primary) clavae (Fig. 26A); cirri growing out from bulbous cirrophores. Cirri *A* short. The body appendage configuration is *A*-*C*-C^d-*D*-D^d, with all trunk appendages formed as smooth spines of variable lengths. Typically, spines *C* and *D* longer than the dorsal appendages (Fig. 26A, 27). Asymmetries in the development of dorsal spines very rare (Fig. 26A).

Dorsal plates with a dense endocuticular layer (Fig. 28) forming uniform dark matrix under PCM (Fig. 26A). Pores of similar size, irregularly and densely distributed in plates (Fig. 26A, 27–28). The cephalic plate with a straight anterior incision (Fig. 26A). The cervical (neck) plate may be either indiscernible (Fig. 26A) or present in the form of an unsculptured, thin belt closely adjacent to the anterior margin of the scapular plate (Fig. 27A, 28A). The scapular plate large, without epicuticular ridges (Fig. 26A, 27A, 28A), with lateral sutures separating trapezoid lateral portions (Fig. 26A). Paired segmental plates with poorly developed transverse stripes (Fig. 26A, 27, 28B–C),

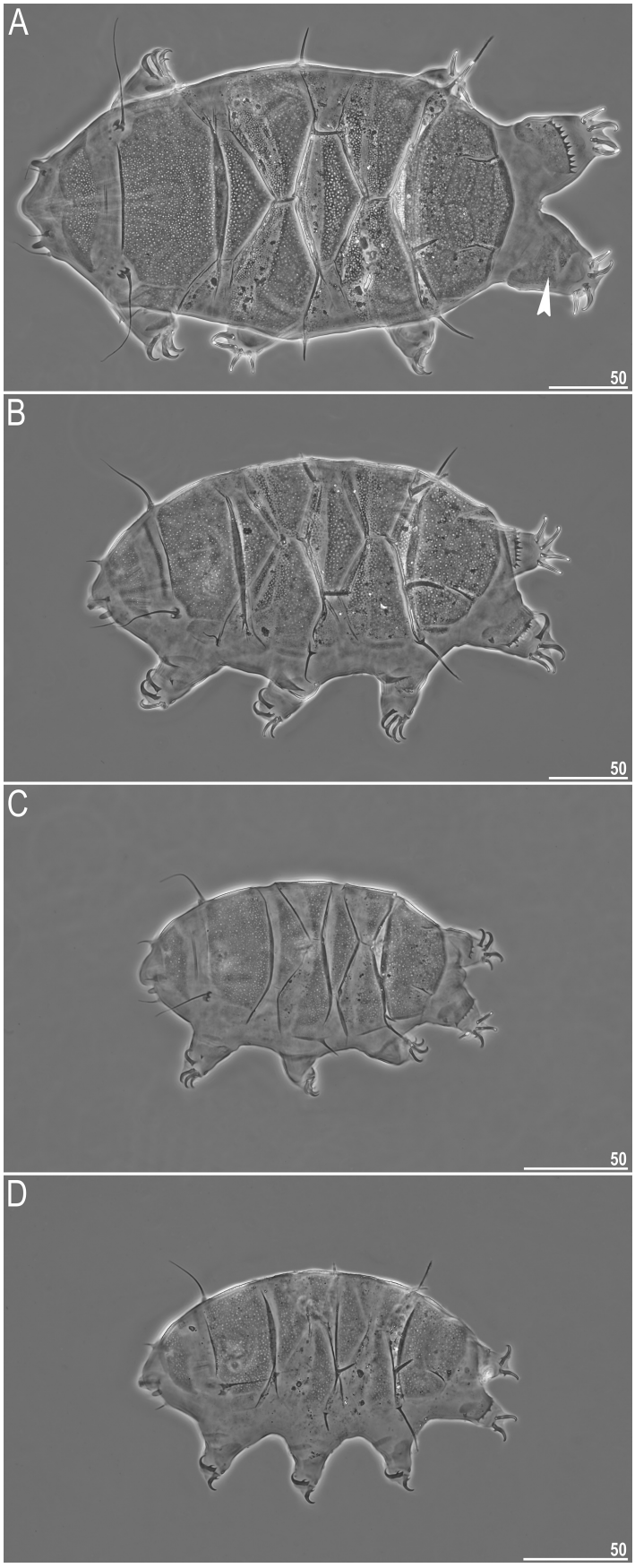

FIGURE 26. Habitus and intraspecific variability of *Echiniscus draconis* **sp. nov.** (PCM): A—holotype, female in dorsal view (arrowhead indicates the lack of dentate collar IV on one leg), B—paratype, male in dorsolateral view, C—juvenile in dorsolateral view, D—larva in dorsolateral view. Scale bars = 50 µm.

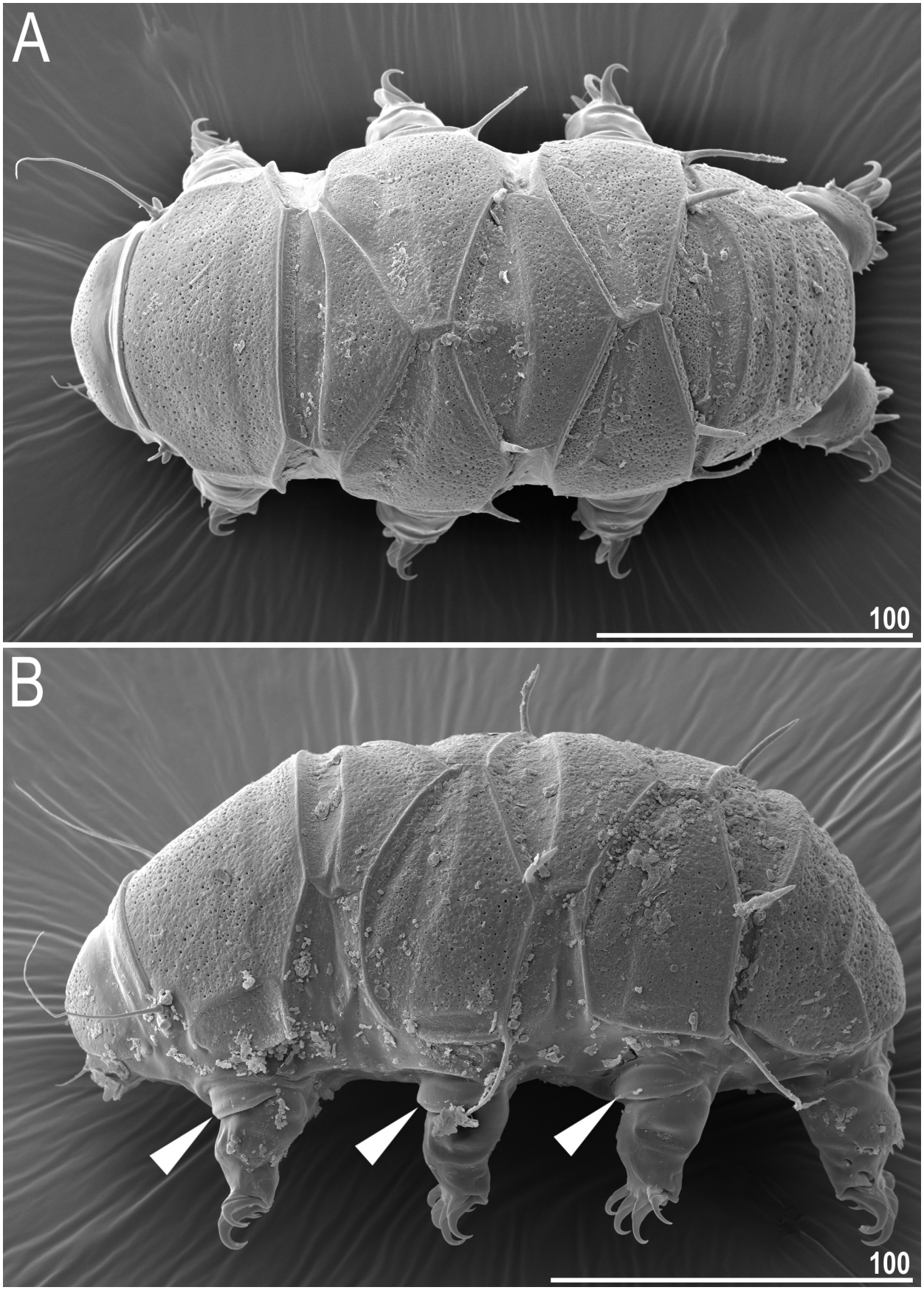

FIGURE 27. Habitus of *Echiniscus draconis* **sp. nov.** (SEM, sex unidentified): A—dorsal view, B—lateral view (arrowheads indicate pulvini). Scale bars = 100 μm.

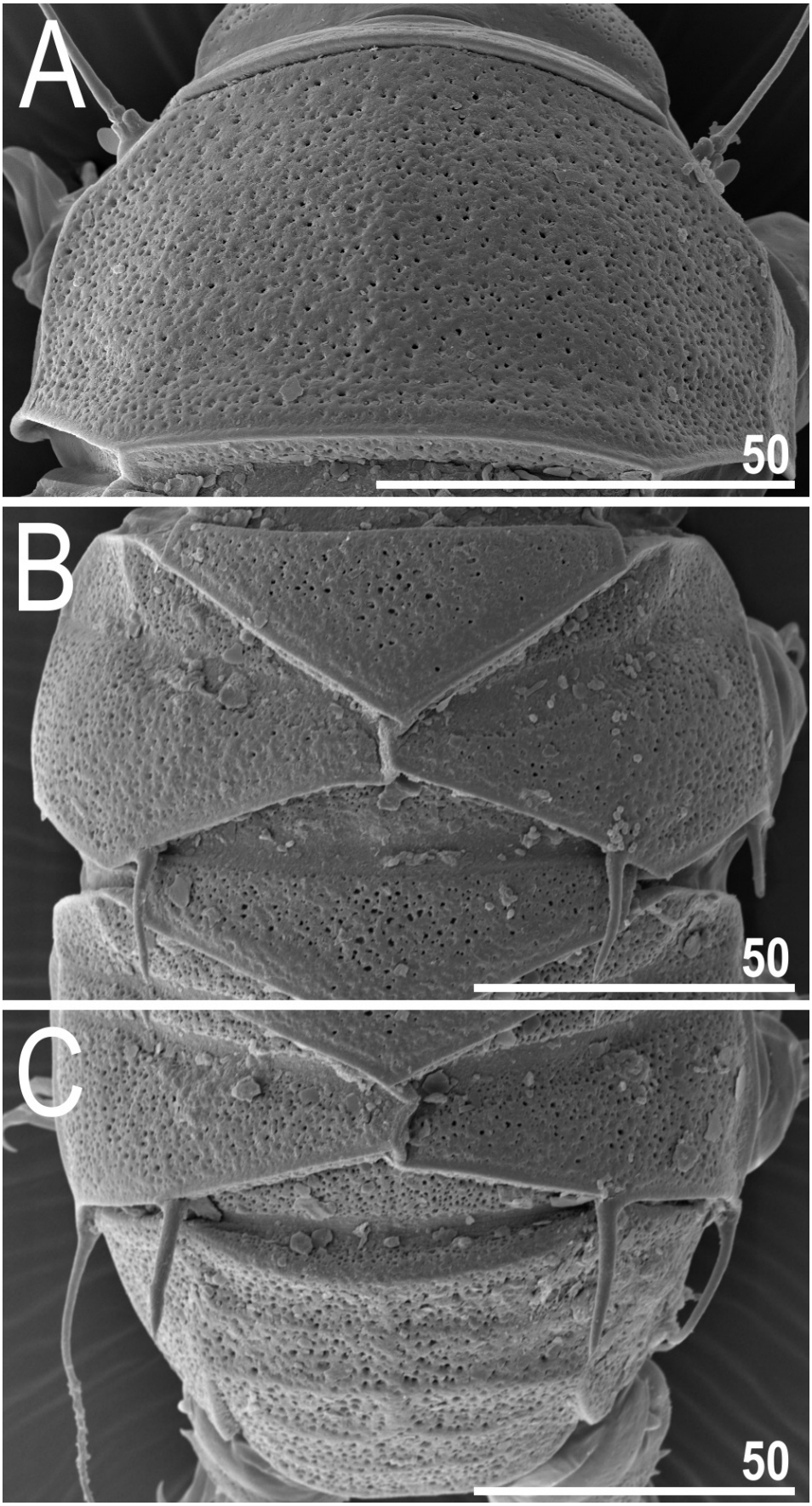

FIGURE 28. Dorsal sculpturing of *Echiniscus draconis* **sp. nov.** (SEM, female): A—scapular plate, B—paired segmental and median plates, C—median plate 3 and caudal (terminal) plate. Scale bars = 50 μm.

but their anterior portions have a darker matrix and finer pores, and in the result thinner accumulations of matrix seem to be connected by *striae*, also in the anteriormost portion of the median plate 2 (Fig. 26A, 28B). The caudal (terminal) plate with variously developed epicuticular ridges forming a faceted/carinate pattern (Fig. 26A, 27A, 28C). Caudal incisions sclerotised. Median plate 1 unipartite and similar to the posterior part of the bipartite m2, its anterior part is narrow and mostly unsculptured (Fig. 26A, 27A, 28B). Ventral cuticle with minute endocuticular pillars distributed throughout the whole venter; ventral plates lacking. Sexpartite gonopore placed anteriorly to legs IV, and a trilobed anus between legs IV.

Legs short and massive. Pedal plates I–III absent (Fig. 27B), pedal plate IV weakly sculptured, and sometimes with dentate collar IV asymmetrically lacking (Fig. 26A). Pulvini invisible under PCM, evident under SEM (Fig. 27B). A minute spine on leg I and a tiny papilla on leg IV. Claws I–IV large, robust, of similar lengths (Table 12). External claws on all legs smooth (Fig. 29). Internal claws with large spurs positioned at *ca.* 25–30% of the claw height, highly divergent from the claw branch and bent downwards.

Mature males and sexually dimorphic traits (*i.e.* from the third instar onwards; measurements and statistics in Table 13). Sexual dimorphism rudimentary, expressed only in the smaller body size of the only measurable male and the round gonopore. An asymmetrically developed spine in the aberrant position *B* (Fig. 26B). Apart from this, very similar to females.

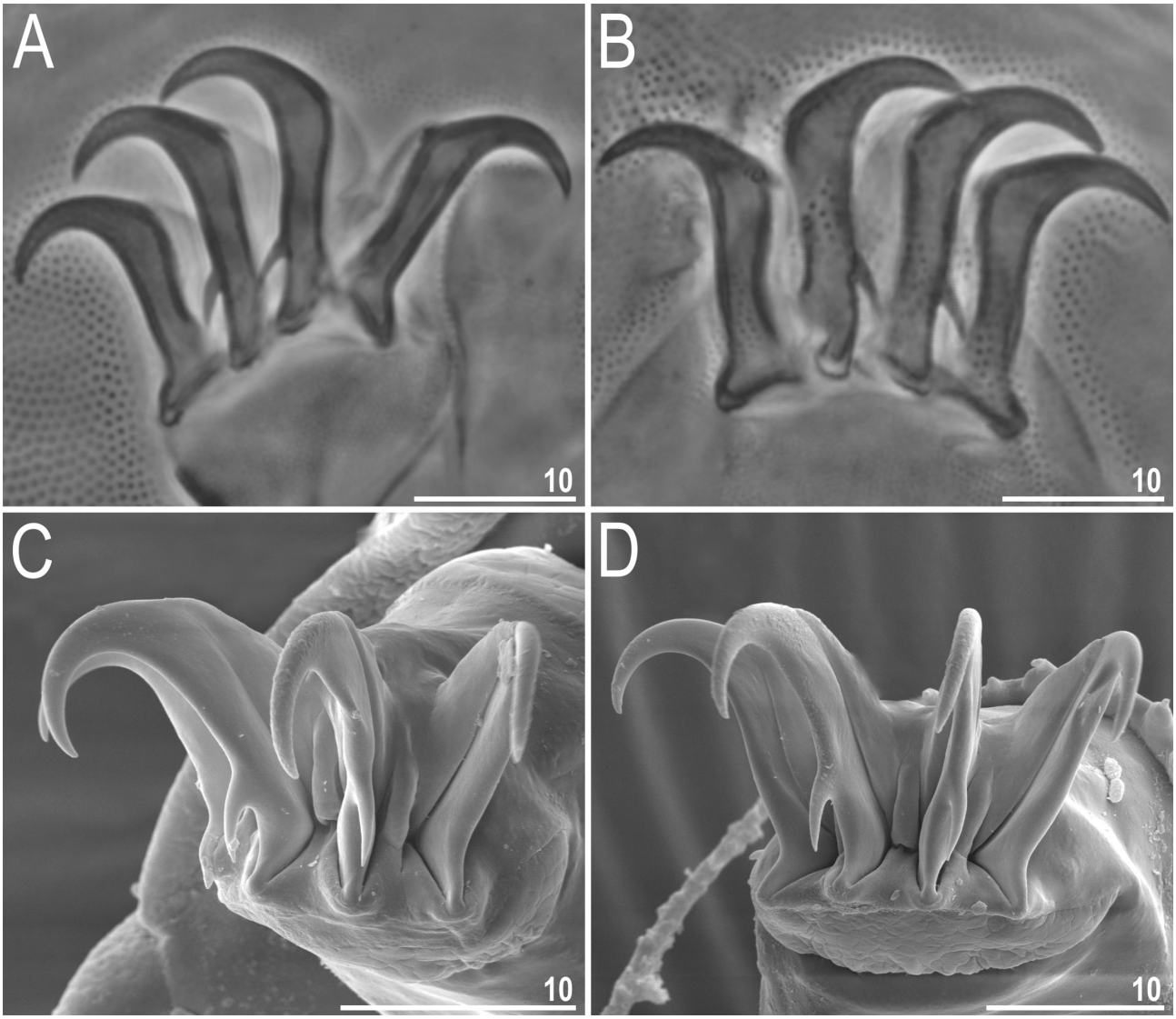

FIGURE 29. Claws of *Echiniscus draconis* **sp. nov.** (females): A—claws I (PCM), B—claws II (PCM), C—claws III (SEM), D—claws IV (SEM). Scale bars = 10 μm.

Juveniles (*i.e*. the second instar, measurements and statistics in Table 13). Phenotypically like adult females, beside of the lacking gonopore. Sculpturing fainter (Fig. 26C). Clearly smaller in the majority of morphometrically informative traits (scapular plate length, lengths of cephalic appendages and claws), including a gap in the body length (see Tables 12–13).

TABLE 12. Measurements [in µm] of selected morphological structures of the adult females of *Echiniscus draconis* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Holotype	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	15	277	–	400	*465*	–	*725*	334	*505*	32	*64*	382	*725*
Scapular plate length	15	52.7	–	84.7		–		66.7	–	8.0	–	52.7	–
Head appendages lengths													
Cirrus *internus*	13	9.9	–	21.2	*14.0*	–	*25.0*	13.5	*20.1*	3.5	*3.6*	10.6	*20.1*
Cephalic papilla	15	6.9	–	10.5	*10.5*	–	*16.3*	8.7	*13.2*	1.2	*1.9*	8.0	*15.2*
Cirrus *externus*	13	14.6	–	34.9	*20.1*	–	*50.3*	24.0	*35.6*	5.8	*8.0*	26.5	*50.3*
Clava	15	3.9	–	8.3	*5.6*	–	*12.7*	6.7	*10.2*	1.0	*1.8*	6.7	*12.7*
Cirrus *A*	12	48.5	–	77.9	*70.1*	–	*133.0*	65.9	*99.2*	9.7	*17.1*	70.1	*133.0*
Cirrus *A*/Body length ratio	12	15%	–	24%		–		19%	–	3%	–	18%	–
Body appendages lengths													
Spine *C*	14	21.8	–	51.2	*34.0*	–	*60.4*	30.5	*45.9*	6.9	*7.1*	24.7	*46.9*
Spine C^d	14	10.3	–	28.9	*14.7*	–	*41.9*	21.7	*32.5*	4.4	*7.0*	22.1	*41.9*
Spine *D*	15	30.4	–	75.1	*41.8*	–	*98.7*	50.0	*75.3*	11.6	*15.4*	47.1	*89.4*
Spine D^d	14	11.2	–	34.2	*17.4*	–	*46.2*	24.7	*36.5*	5.8	*7.1*	19.4	*36.8*
Spine on leg I length	13	3.3	–	5.5	*5.8*	–	*8.6*	4.5	*7.0*	0.5	*0.9*	4.5	*8.5*
Papilla on leg IV length	14	3.7	–	6.3	*6.0*	–	*9.3*	5.0	*7.4*	0.6	*1.1*	4.9	*9.3*
Number of teeth on the collar	15	10	–	15		–		12.3	–	1.5	–	12	–
Claw I heights													
Branch	14	14.1	–	20.3	*24.0*	–	*34.2*	18.0	*27.3*	1.5	*2.7*	18.0	*34.2*
Spur	14	2.6	–	4.2	*4.3*	–	*6.8*	3.5	*5.3*	0.4	*0.8*	3.6	*6.8*
Spur/branch height ratio	14	17%	–	23%		–		19%	–	2%	–	20%	–
Claw II heights													
Branch	13	13.4	–	22.5	*23.8*	–	*35.1*	17.6	*26.8*	2.1	*3.0*	18.5	*35.1*
Spur	13	2.7	–	4.2	*4.5*	–	*6.1*	3.4	*5.2*	0.4	*0.5*	3.2	*6.1*
Spur/branch height ratio	13	17%	–	23%		–		20%	–	2%	–	17%	–
Claw III heights													
Branch	13	13.7	–	22.0	*23.9*	–	*36.2*	18.0	*27.2*	2.0	*3.3*	19.1	*36.2*
Spur	12	2.9	–	3.9	*4.1*	–	*7.0*	3.5	*5.2*	0.3	*0.8*	3.7	*7.0*
Spur/branch height ratio	12	16%	–	21%		–		19%	–	2%	–	19%	–
Claw IV heights													
Branch	11	16.4	–	24.6	*27.1*	–	*35.0*	20.5	*29.8*	2.3	*2.3*	?	*?*
Spur	11	3.3	–	4.4	*4.8*	–	*6.7*	3.8	*5.5*	0.4	*0.6*	?	*?*
Spur/branch height ratio	11	16%	–	23%		–		18%	–	2%	–	?	–

TABLE 13. Measurements [in µm] of selected morphological structures of the juveniles and a male of *Echiniscus draconis* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		♂	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	5	163	–	257	*465*	–	*538*	207	*508*	41	*30*	242	*460*
Scapular plate length	5	31.3	–	48.9		–		41.0	–	8.5	–	52.7	–
Head appendages lengths													
Cirrus *internus*	5	4.4	–	8.8	*13.6*	–	*26.2*	7.4	*18.4*	1.8	*4.8*	11.1	*21.1*
Cephalic papilla	5	4.2	–	7.5	*13.0*	–	*21.1*	6.3	*15.6*	1.2	*3.2*	7.7	*14.6*
Cirrus *externus*	5	7.3	–	15.1	*22.6*	–	*40.3*	11.5	*28.6*	2.8	*7.5*	21.3	*40.4*
Clava	5	2.6	–	6.0	*8.0*	–	*19.2*	5.1	*12.7*	1.4	*4.0*	5.1	*9.7*
Cirrus *A*	4	28.7	–	50.8	*88.9*	–	*113.4*	40.4	*101.0*	10.1	*10.3*	53.2	*100.9*
Cirrus *A*/Body length ratio	4	18%	–	22%		–		20%	–	2%	–	22%	–
Body appendages lengths													
Spine *C*	5	7.1	–	20.1	*21.1*	–	*51.1*	14.6	*36.0*	5.7	*13.7*	24.3	*46.1*
Spine C^d	4	5.2	–	17.1	*10.6*	–	*38.2*	10.2	*23.4*	5.6	*11.7*	16.8	*31.9*
Spine *D*	4	14.3	–	36.9	*44.3*	–	*77.4*	26.5	*66.7*	9.9	*15.2*	32.5	*61.7*
Spine D^d	5	8.0	–	20.1	*16.4*	–	*53.7*	14.6	*36.5*	5.5	*14.3*	17.7	*33.6*
Spine on leg I length	5	1.9	–	4.1	*2.9*	–	*8.6*	2.9	*6.4*	0.8	*2.3*	4.2	*8.0*
Papilla on leg IV length	5	2.9	–	4.5	*8.0*	–	*10.9*	3.7	*8.9*	0.6	*1.2*	4.1	*7.8*
Number of teeth on the collar	5	7	–	12		–		9.2	–	1.9	–	13.0	–
Claw I heights													
Branch	5	12.0	–	14.3	*8.6*	–	*38.3*	13.0	*26.4*	0.8	*10.9*	15.3	*29.0*
Spur	4	1.6	–	2.7	*1.5*	–	*6.7*	2.1	*4.6*	0.5	*2.2*	3.2	*6.1*
Spur/branch height ratio	4	12%	–	19%		–		16%	–	3%	–	21%	–
Claw II heights													
Branch	3	10.7	–	13.6	*8.0*	–	*28.5*	12.1	*21.0*	1.5	*11.3*	14.0	*26.6*
Spur	3	1.5	–	2.4	*1.4*	–	*5.0*	2.0	*3.7*	0.5	*2.0*	2.8	*5.3*
Spur/branch height ratio	3	14%	–	18%		–		16%	–	2%	–	20%	–
Claw III heights													
Branch	4	10.7	–	13.9	*7.8*	–	*38.3*	12.1	*24.7*	1.3	*11.2*	14.5	*27.5*
Spur	4	2.1	–	2.5	*1.2*	–	*7.3*	2.3	*4.6*	0.2	*2.2*	3.7	*7.0*
Spur/branch height ratio	4	16%	–	23%		–		19%	–	3%	–	26%	–
Claw IV heights													
Branch	4	12.1	–	15.6	*9.2*	–	*38.7*	13.7	*27.9*	1.5	*12.9*	?	*?*
Spur	4	1.9	–	3.3	*2.2*	–	*8.0*	2.6	*5.7*	0.6	*2.5*	?	?
Spur/branch height ratio	4	15%	–	21%		–		19%	–	3%	–	?	–

Larvae (*i.e.* the first instar, measurements and statistics in Table 14). Smaller than juveniles (compare Tables 13–14). Sculpturing and trunk appendages formed as in juveniles (Fig. 26D). Lacking gonopore and anus.

Eggs. Up to six round, yellow eggs per exuvia were found.

DNA markers and phylogenetic position. *Echiniscus draconis* **sp. nov.** is the sister species of *E. imitans* **sp. nov.** (Fig. 117). The species closest in COI is *E. imitans* **sp. nov.** (p-distance = 9.1–9.7%), and in both ITS: *E. lichenorum* (ITS-1: 0.6–3.1%, ITS-2: 0.3–1.2%).

Type material. 48 ♀♀, 2 ♂♂, 4 juveniles and 2 larvae on slides ZA.056.01–2, ZA.060.01–7; holotype: mature ♀ on slide ZA.056.02. About 30 specimens on SEM stub 18.16.

TABLE 14. Measurements [in µm] of selected morphological structures of the larvae of *Echiniscus draconis* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD	
		µm			*sp*			µm	*sp*	µm	*sp*
Body length	5	154	–	164	*413*	–	*530*	160	*475*	4	*43*
Scapular plate length	5	31.0	–	38.1		–		33.8	–	2.9	–
Head appendages lengths											
Cirrus *internus*	5	5.0	–	7.8	*13.1*	–	*25.2*	6.2	*18.5*	1.2	4.5
Cephalic papilla	5	4.5	–	6.0	*12.9*	–	*19.4*	5.2	*15.5*	0.5	*2.5*
Cirrus *externus*	5	10.0	–	11.5	*29.1*	–	*37.1*	10.6	*31.5*	0.7	*3.4*
Clava	5	3.8	–	4.5	*10.9*	–	*13.7*	4.2	*12.4*	0.3	*1.2*
Cirrus *A*	5	22.1	–	37.4	*71.3*	–	*107.5*	31.1	*91.9*	5.7	*15.0*
Cirrus *A*/Body length ratio	5	13%	–	23%		–		20%	–	4%	–
Body appendages lengths											
Spine *C*	4	7.4	–	16.4	*19.4*	–	*47.1*	11.0	*32.9*	3.8	*11.5*
Spine C^d	5	5.6	–	11.3	*14.7*	–	*36.0*	8.4	*25.3*	2.2	8.4
Spine *D*	5	10.3	–	23.3	*29.6*	–	*74.2*	17.7	*53.2*	4.9	*17.8*
Spine D^d	5	7.2	–	21.0	*21.3*	–	*60.3*	11.6	*34.6*	5.5	*16.0*
Spine on leg I length	5	2.1	–	3.1	*5.8*	–	*9.0*	2.6	*7.9*	0.5	*1.5*
Papilla on leg IV length	5	2.3	–	3.4	*6.3*	–	*9.9*	2.8	*8.4*	0.5	*1.6*
Number of teeth on the collar	3	6	–	8		–		7.0	–	1.0	–
Claw I heights											
Branch	5	9.6	–	10.8	*27.3*	–	*32.0*	10.2	*30.3*	0.5	*1.8*
Spur	5	2.2	–	2.9	*7.0*	–	*8.6*	2.6	*7.7*	0.3	0.7
Spur/branch height ratio	5	23%	–	28%		–		26%	–	2%	–
Claw II heights											
Branch	5	9.1	–	10.4	*26.5*	–	*31.8*	9.8	*29.1*	0.5	*2.3*
Spur	5	2.0	–	3.1	*6.4*	–	*8.7*	2.6	*7.6*	0.4	*1.0*
Spur/branch height ratio	5	20%	–	31%		–		26%	–	5%	–
Claw III heights											
Branch	5	9.1	–	10.7	*27.6*	–	*30.7*	9.8	*29.1*	0.7	*1.4*
Spur	5	2.2	–	2.9	*6.3*	–	*8.3*	2.5	*7.3*	0.3	*0.7*
Spur/branch height ratio	5	21%	–	28%		–		25%	–	3%	–
Claw IV heights											
Branch	4	10.5	–	11.9	*29.4*	–	*35.5*	11.2	*32.5*	0.6	*2.8*
Spur	4	1.9	–	3.1	*5.6*	–	*8.6*	2.6	*7.6*	0.6	*1.3*
Spur/branch height ratio	4	18%	–	28%		–		23%	–	4%	–

Type locality. 33°24'10''S, 20°05'30''E, 760 m asl: Republic of South Africa, Western Cape, vicinity of Touws River; karoo, lichens from rocks (samples ZA.056 and ZA.060).

Etymology. From Latin *draconis* = dragon-like. The name refers to the Drakensberg, where, according to the local myths, dragons used to live. An adjective in the nominative singular.

Geographic distribution. The species is widely distributed and common in South Africa (Fig. 120F), likely endemic.

Remarks. Dioecious. Considerable genetic variability in the sequenced variable markers (COI: 0.4–1.2%, ITS-1: 0.9–2.9%, ITS-2: 0.3–1.5%; see also SM.2), together with a deeply divergent clade recovered in the phylogenetic analysis (Fig. 117), suggests that *E. draconis* **sp. nov.** may be a complex of poorly differentiated, young species.

Differential diagnosis. *Echiniscus egnatiae* is morphologically closest to *E. draconis* **sp. nov.**, since the

configuration of trunk appendages and sculpturing are alike, yet *E. egnatiae* can be separated from *E. draconis* **sp. nov.** by heteromorphic trunk spines (spines of similar lengths in *E. draconis* **sp. nov.** *vs* spines C^d clearly longer than other spines in *E. egnatiae*) and by claw morphology (robust claws, external claws IV smooth in *E. draconis* **sp. nov.** *vs* long, slender claws, external claws IV with minute spurs directed upwards in *E. egnatiae*). Finally, the related *E. imitans* **sp. nov.**, *E. lichenorum* and *E. similaris* **sp. nov.** have larger pores and appendages *B* are typically present, whereas pores are minute and appendages *B* are always absent in *E. draconis* **sp. nov.** The sculpture of *E. draconis* **sp. nov.** resembles that of the *E. merokensis* complex (Gąsiorek *et al*. 2019a), but the appendages *E*, which are characteristic for the complex (Claxton 1996, Fontoura *et al*. 2008), are always absent in *E. draconis* **sp. nov.**

Raw measurements. Supplementary Materials (SM.03) and Tardigrada Register (www.tardigrada.net/register/0084.htm).

10. Echiniscus gracilis sp. nov. Gąsiorek, Vončina, Morek & Michalczyk

urn:lsid:zoobank.org:act:4349A20B-D6DB-4342-BC4A-E445158508B9
Figures 30–34, Tables 15–17

Data source:
A total of 83 specimens (62 ♀♀, 4 ♂♂, 8 juveniles, and 9 specimens of unknown instar/sex):

- Sample ZA.022: 19 specimens (11 ♀♀, 1 ♂, 6 juveniles and 1 specimen of unknown sex on slides); found with *Echiniscus attenboroughi* **sp. nov.**, *E. dentatus* **sp. nov.**, *E. lichenorum*, *E. longispinous* and *E. setaceus* **sp. nov.**
- Sample ZA.023: 1 specimen (1 ♀♀ on a slide); found with *Echiniscus dentatus* **sp. nov.** and *E. irroratus* **sp. nov.**
- Sample ZA.025: 9 specimens (8 ♀♀ and 1 juvenile on slides); found with *E. dentatus* **sp. nov.**
- Sample ZA.096: 1 specimen (1 ♂ on a slide); found with *Echiniscus longispinosus* and E. *setaceus* **sp. nov.**
- Sample ZA.511: 3 specimens (3 ♀♀ on a slide); found with *Echiniscus longispinosus.*
- Sample ZA.513: 1 specimen (1 ♀ on a slide); found with *Echiniscus latruncularis* **sp. nov.**, *E. scabrospinosus*, and *E. setaceus* **sp. nov.**
- Sample ZA.552: 1 specimen (1 ♀ on a slide); found with *Echiniscus dentatus* **sp. nov.**
- Sample ZA.554: 32 specimens (22 ♀♀, 1 ♂, 1 juvenile and 1 specimen of unknown sex on slides, 3 specimens used for SEM and 4 used for DNA extraction); found with *Echiniscus dentatus* **sp. nov.**
- Sample ZA.555: 16 specimens (15 ♀♀ and 1 ♂ on slides); found with *Echiniscus dentatus* **sp. nov.**, *E. irroratus* **sp. nov.** and *E. latruncularis* **sp. nov.**

Description. Mature females (*i.e*. from the third instar onwards; measurements and statistics in Table 15). Small *Echiniscus* with light orange body and minute red eyes; body colour and eyes disappeared soon after mounting in Hoyer's medium. Small, dactyloid cephalic papillae (secondary clavae) and minute (primary) clavae (Fig. 30A–B); cirri growing out from bulbous cirrophores. Cirri *A* short. The body appendage configuration is *A*-*C*-*D*, with all trunk appendages formed as cirri of similar lengths (Fig. 30A–B, 31A, C). Asymmetries in the development of lateral cirri very rare.

Dorsal plates with a dense endocuticular layer (Fig. 31A, C) forming a uniform dark matrix under PCM (Fig. 30A–B). Pores intermixed with pseudopores of similar size, densely distributed in plates (Fig. 30A–B, 31A, C). The cephalic plate with an anterior chalice-shaped incision (Fig. 32). The cervical (neck) plate poorly developed as a thin darkish belt anterior to the scapular plate (Fig. 30A–B, 32). The scapular plate with a median longitudinal groove (Fig. 30A–B, 32), which is not visible under SEM, however in the same place a poorly outlined longitudinal poreless belt is present (Fig. 33A). Paired segmental plates with usual transverse stripes (Fig. 32, 33B), and both portions with identical sculpturing. The caudal (terminal) plate with one longitudinal and three transverse epicuticular ridges (variously developed) forming a distinct faceted/carinate pattern (Fig. 31A, 32, 33C). Caudal incisions weakly sclerotised. Median plates 1, 3 unipartite and similar to the posterior part of the bipartite m2, its anterior part is narrow and mostly unsculptured (Fig. 33B–C). Ventral cuticle with minute endocuticular pillars distributed throughout the whole venter, but genital plates present (Fig. 34A–B), with irregular surface under SEM (Fig. 34B). Sexpartite gonopore placed anteriorly to legs IV, and a trilobed anus between legs IV.

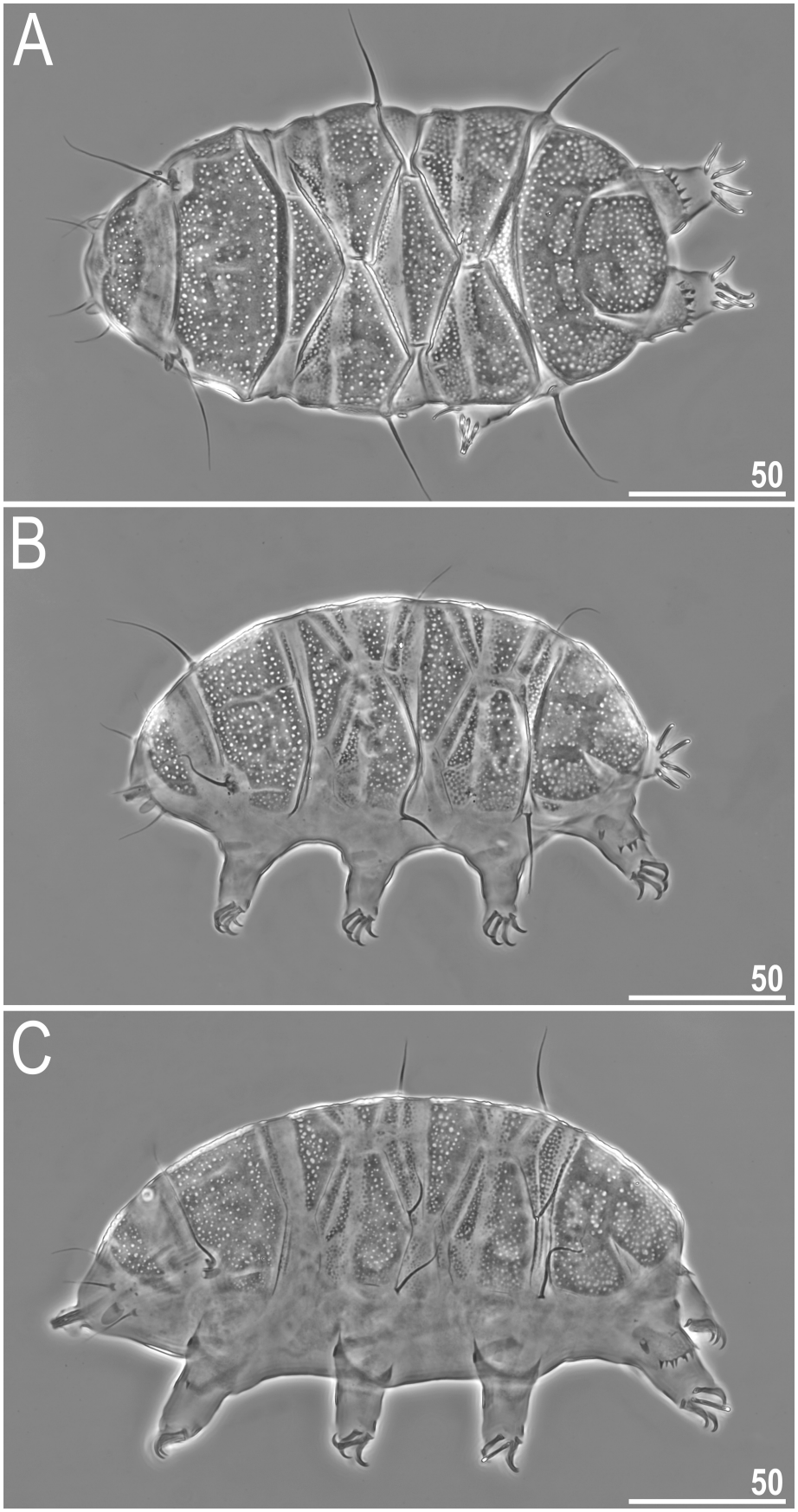

FIGURE 30. Habitus and intraspecific variability of *Echiniscus gracilis* **sp. nov.** (PCM): A—holotype, female in dorsal view, B—paratype, female in dorsolateral view, C—allotype, male in lateral view. Scale bars = 50 µm.

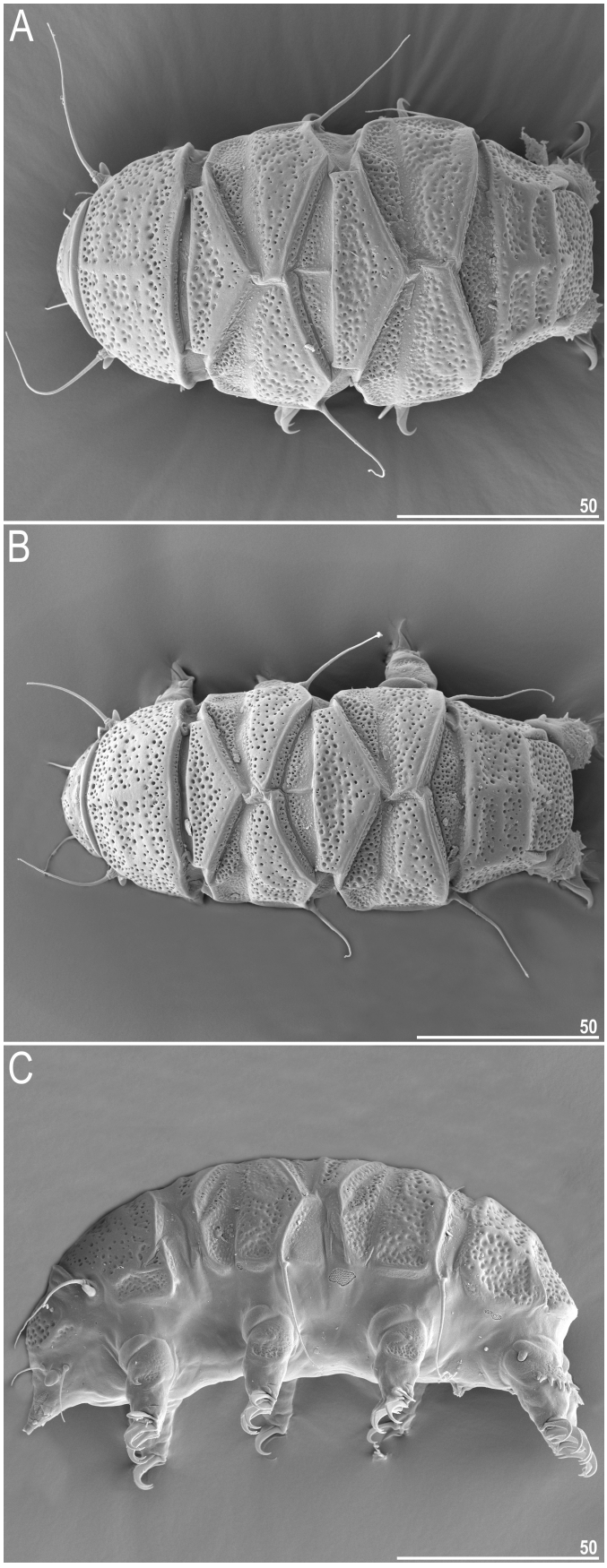

FIGURE 31. Habitus and intraspecific variability of *Echiniscus gracilis* **sp. nov.** (SEM): A—female, dorsal view, B—male, dorsal view, C—female, lateral view. Scale bars = 50 μm.

Legs long, with pedal plates invisible under PCM (Fig. 30B), but identifiable under SEM (Fig. 34D). Pulvini evident both under PCM and SEM (Fig. 30B, 31C). A minute spine on leg I and a tiny papilla on leg IV (Fig. 30B, 31C). Claws IV higher than claws I–III (Table 15). Claws slender (Fig. 34C–D). External claws on all legs smooth (Fig. 29) and the internal ones with delicate spurs positioned at *ca.* 25% of the claw height.

Mature males and sexually dimorphic traits (*i.e.* from the third instar onwards; measurements and statistics in Table 16). Sexual dimorphism rudimentary, expressed in a different body appendage formula *A-(C)-C*^{d}*-(D)-D*^{d} (Fig. 30C, 32), more slender body (Fig. 31B) and in the circular gonopore. Apart from this, very similar to females, as morphometric gaps in measurable traits were not found (see Tables 15–16).

TABLE 15. Measurements [in µm] of selected morphological structures of the adult females of *Echiniscus gracilis* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Holotype	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	16	168	–	198	*456*	–	*603*	179	*526*	8	*39*	187	*603*
Scapular plate length	16	29.4	–	41.5		–		34.2	–	3.0	–	31.0	–
Head appendages lengths													
Cirrus *internus*	13	11.4	–	16.1	*33.8*	–	*46.8*	13.4	*38.9*	1.5	*4.3*	14.5	*46.8*
Cephalic papilla	15	4.9	–	7.4	*14.0*	–	*22.4*	6.0	*17.6*	0.9	*2.5*	5.4	17.4
Cirrus *externus*	13	12.2	–	20.9	*31.9*	–	*62.0*	16.4	*48.6*	2.5	*7.8*	17.3	*55.8*
Clava	16	3.5	–	5.6	*10.1*	–	*16.8*	4.6	*13.6*	0.6	*2.1*	5.2	*16.8*
Cirrus *A*	15	30.5	–	44.4	*89.7*	–	*123.9*	36.5	*106.8*	3.3	*9.7*	38.4	*123.9*
Cirrus *A*/Body length ratio	15	17%	–	23%		–		20%	–	2%	–	21%	–
Body appendages lengths													
Cirrus *C*	16	14.4	–	36.9	*34.7*	–	*108.3*	31.5	*93.2*	5.4	*17.6*	33.3	*107.4*
Cirrus *D*	15	24.4	–	43.4	*68.5*	–	*122.8*	36.4	*106.3*	5.2	*14.2*	36.5	*117.7*
Spine on leg I length	14	1.7	–	3.9	*5.0*	–	*11.2*	2.7	*7.9*	0.7	*2.0*	2.5	*8.1*
Papilla on leg IV length	15	2.9	–	7.0	*7.8*	–	*16.9*	3.6	*10.4*	1.0	*2.0*	3.2	*10.3*
Number of teeth on the collar	16	3	–	10		–		6.8	–	1.6	–	8	–
Claw I heights													
Branch	16	10.1	–	12.1	*25.3*	–	*35.0*	10.9	*31.9*	0.6	*2.3*	10.5	*33.9*
Spur	12	1.9	–	2.6	*5.5*	–	*8.4*	2.2	*6.6*	0.2	*0.9*	2.6	*8.4*
Spur/branch height ratio	12	17%	–	25%		–		20%	–	2%	–	25%	–
Claw II heights													
Branch	16	8.7	–	12.4	*26.5*	–	*37.0*	10.7	*31.3*	0.9	*2.7*	10.7	*34.5*
Spur	12	2.0	–	3.4	*5.2*	–	*10.2*	2.4	*7.0*	0.4	*1.3*	2.3	*7.4*
Spur/branch height ratio	12	18%	–	34%		–		22%	–	4%	–	21%	–
Claw III heights													
Branch	16	8.4	–	11.9	*25.6*	–	*38.1*	10.9	*32.0*	0.8	*2.9*	10.7	34.5
Spur	14	1.5	–	2.7	*4.5*	–	*8.1*	2.1	*6.3*	0.4	*0.9*	2.5	*8.1*
Spur/branch height ratio	14	13%	–	23%		–		19%	–	3%	–	23%	–
Claw IV heights													
Branch	15	11.1	–	15.0	*32.1*	–	*44.1*	12.8	*37.5*	1.2	*3.6*	11.2	*36.1*
Spur	3	2.3	–	2.9	*6.9*	–	*9.5*	2.7	*8.2*	0.3	*1.3*	?	*?*
Spur/branch height ratio	3	19%	–	24%		–		21%	–	3%	–	?	–

TABLE 16. Measurements [in µm] of selected morphological structures of the adult males of *Echiniscus gracilis* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Allotype	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	sp
Body length	2	170	–	206	*545*	–	*631*	188	*588*	25	*61*	170	*545*
Scapular plate length	2	31.2	–	32.6		–		31.9	–	1.0	–	31.2	–
Head appendages lengths													
Cirrus *internus*	2	11.5	–	17.4	*36.9*	–	*53.4*	14.5	*45.1*	4.2	*11.7*	11.5	*36.9*
Cephalic papilla	2	5.7	–	8.3	*18.3*	–	*25.5*	7.0	*21.9*	1.8	*5.1*	5.7	*18.3*
Cirrus *externus*	2	17.4	–	19.8	*55.8*	–	*60.7*	18.6	*58.3*	1.7	*3.5*	17.4	*55.8*
Clava	2	4.2	–	6.3	*13.5*	–	*19.3*	5.3	*16.4*	1.5	*4.1*	4.2	*13.5*
Cirrus *A*	2	29.5	–	49.3	*94.6*	–	*151.2*	39.4	*122.9*	14.0	*40.1*	29.5	*94.6*
Cirrus *A*/Body length ratio	2	17%	–	24%		–		21%	–	5%	–	17%	–
Body appendages lengths													
Cirrus *C*	1	26.2	–	26.2	*80.4*	–	*80.4*	26.2	*80.4*	?	*?*	?	*?*
Cirrus C^d	2	26.2	–	33.4	*80.4*	–	*107.1*	29.8	*93.7*	5.1	*18.9*	33.4	*107.1*
Cirrus *D*	1	17.8	–	17.8	*54.6*	–	*54.6*	17.8	*54.6*	?	*?*	?	*?*
Cirrus D^d	2	31.2	–	32.3	*95.7*	–	*103.5*	31.8	*99.6*	0.8	*5.5*	32.3	*103.5*
Spine on leg I length	2	2.5	–	2.6	*8.0*	–	*8.0*	2.6	*8.0*	0.1	*0.0*	2.5	8.0
Papilla on leg IV length	2	3.6	–	5.3	*11.5*	–	*16.3*	4.5	*13.9*	1.2	*3.3*	3.6	*11.5*
Number of teeth on the collar	2	5	–	9		–		7.0	–	2.8	–	5	–
Claw I heights													
Branch	2	9.4	–	11.1	*30.1*	–	*34.0*	10.3	*32.1*	1.2	*2.8*	9.4	*30.1*
Spur	2	1.8	–	2.3	*5.5*	–	*7.4*	2.1	*6.4*	0.4	*1.3*	2.3	*7.4*
Spur/branch height ratio	2	16%	–	24%		–		20%	–	6%	–	24%	–
Claw II heights													
Branch	2	9.0	–	10.6	*28.8*	–	*32.5*	9.8	*30.7*	1.1	*2.6*	9.0	*28.8*
Spur	2	1.7	–	1.8	*5.4*	–	*5.5*	1.8	*5.5*	0.1	*0.1*	1.7	*5.4*
Spur/branch height ratio	2	17%	–	19%		–		18%	–	1%	–	19%	–
Claw III heights													
Branch	2	9.2	–	10.2	*29.5*	–	*31.3*	9.7	*30.4*	0.7	*1.3*	9.2	*29.5*
Spur	2	1.8	–	1.9	*5.8*	–	*5.8*	1.9	*5.8*	0.1	*0.0*	1.8	*5.8*
Spur/branch height ratio	2	19%	–	20%		–		19%	–	1%	–	20%	–
Claw IV heights													
Branch	2	10.4	–	13.0	*33.3*	–	*39.9*	11.7	*36.6*	1.8	*4.6*	10.4	*33.3*
Spur	2	1.9	–	2.0	*6.1*	–	*6.1*	2.0	*6.1*	0.1	*0.0*	1.9	*6.1*
Spur/branch height ratio	2	15%	–	18%		–		17%	–	2%	–	18%	–

Juveniles (*i.e*. the second instar, measurements and statistics in Table 17). Phenotypically like adult females, beside of the lacking gonopore and body appendage formula *A-(C)-*C^d*-(D)-*D^d. However, clearly smaller in some of the morphometrically informative traits (*e.g*. body length, scapular plate length, lengths of trunk appendages; see Tables 15 and 17).

Larvae. Unknown.

Eggs. Up to two round, yellow eggs per exuvia were found.

DNA markers and phylogenetic position. The closest relatives of *E. gracilis* **sp. nov.** are *E. capensis* **sp. nov.** and *E. irroratus* **sp. nov.**, the latter being a sister species (Fig. 117). The species closest in COI are *E. attenboroughi*

sp. nov. and *E. similaris* **sp. nov.** (p-distance = 14.5%), *E. irroratus* **sp. nov.** in ITS-1 (3.1%), and *E. capensis* **sp. nov.** in ITS-2 (1.2%).

Type material. 22 ♀♀, 1 ♂, 1 juvenile and 1 specimen of unknown sex on slides ZA.554.01, 3–8; holotype: mature ♀ on slide ZA.554.06, allotype: mature ♂ on slide ZA.554.04. Mounted together with 4 ♀♀ and 1 juvenile of *E. dentatus* **sp. nov.** Two specimens on SEM stub 19.06. Four individuals used for DNA extraction, all retrieved as hologenophores.

Type locality. 34°00'46.8"S, 18°59'54.06"E, 1090 m asl: Republic of South Africa, Western Cape, Jonkershoek Nature Reserve; fynbos, mosses and lichens from rocks (sample ZA.554).

TABLE 17. Measurements [in µm] of selected morphological structures of the juveniles of *Echiniscus gracilis* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD	
		µm			*sp*			µm	*sp*	µm	*sp*
Body length	4	117	–	145	*413*	–	*538*	131	*485*	12	*53*
Scapular plate length	4	24.3	–	31.2		–		27.3	–	3.2	–
Head appendages lengths											
Cirrus *internus*	3	6.8	–	15.0	*24.4*	–	*52.4*	9.8	*34.7*	4.5	*15.4*
Cephalic papilla	3	4.1	–	5.8	*13.1*	–	*20.3*	4.7	*16.9*	0.9	*3.6*
Cirrus *externus*	4	8.7	–	14.5	*27.9*	–	*50.7*	10.7	*39.7*	2.7	*10.2*
Clava	4	3.0	–	5.4	*9.6*	–	*22.2*	4.1	*15.3*	1.3	*5.6*
Cirrus *A*	4	20.8	–	33.7	*66.7*	–	*132.9*	26.9	*100.2*	7.1	*30.5*
Cirrus *A*/Body length ratio	4	16%	–	28%		–		21%	–	6%	–
Body appendages lengths											
Cirrus *C*	2	12.7	–	15.8	*44.4*	–	*65.0*	14.3	*54.7*	2.2	*14.6*
Cirrus C^d	4	13.8	–	28.2	*55.4*	–	*116.0*	22.4	*82.6*	6.1	*25.0*
Cirrus *D*	2	16.3	–	19.9	*57.0*	–	*81.9*	18.1	*69.4*	2.5	*17.6*
Cirrus D^d	4	15.8	–	30.7	*63.5*	–	*116.0*	24.3	*89.7*	6.6	*25.9*
Spine on leg I length	2	1.3	–	2.6	*5.2*	–	*9.1*	2.0	*7.2*	0.9	*2.7*
Papilla on leg IV length	3	2.5	–	3.8	*9.6*	–	*13.3*	3.1	*11.0*	0.7	*2.0*
Number of teeth on the collar	3	6	–	7		–		6.3	–	0.6	–
Claw I heights											
Branch	4	7.1	–	9.2	*23.7*	–	*34.6*	8.0	*29.7*	1.0	*4.7*
Spur	2	1.5	–	2.3	*4.8*	–	*9.2*	1.9	*7.0*	0.6	*3.1*
Spur/branch height ratio	2	20%	–	32%		–		26%	–	9%	–
Claw II heights											
Branch	4	6.9	–	9.6	*22.1*	–	*33.7*	7.9	*29.3*	1.3	*5.5*
Spur	2	1.9	–	1.9	*6.1*	–	*7.6*	1.9	*6.9*	0.0	*1.1*
Spur/branch height ratio	2	28%	–	28%		–		28%	–	0%	–
Claw III heights											
Branch	4	6.7	–	10.1	*21.5*	–	*35.3*	8.0	*29.7*	1.5	*6.3*
Spur	3	1.2	–	1.9	*3.8*	–	*7.6*	1.5	*5.9*	0.4	*1.9*
Spur/branch height ratio	3	18%	–	27%		–		21%	–	5%	–
Claw IV heights											
Branch	4	8.4	–	9.8	*26.9*	–	*40.3*	9.3	*34.4*	0.6	*5.7*
Spur	0		?			?		?	*?*	?	*?*
Spur/branch height ratio	0		?			–		?	–	?	–

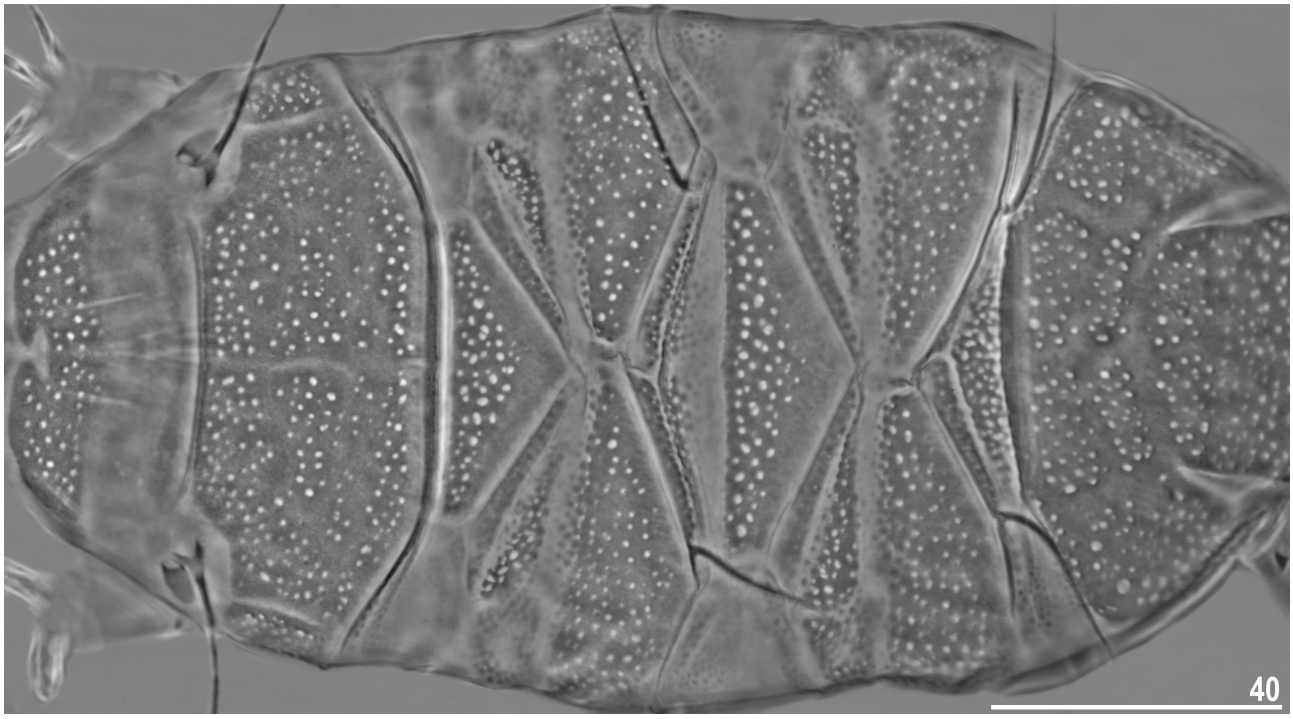

FIGURE 32. Dorsal sculpturing of *Echiniscus gracilis* **sp. nov.** in close-up (PCM, male). Scale bar = 40 μm.

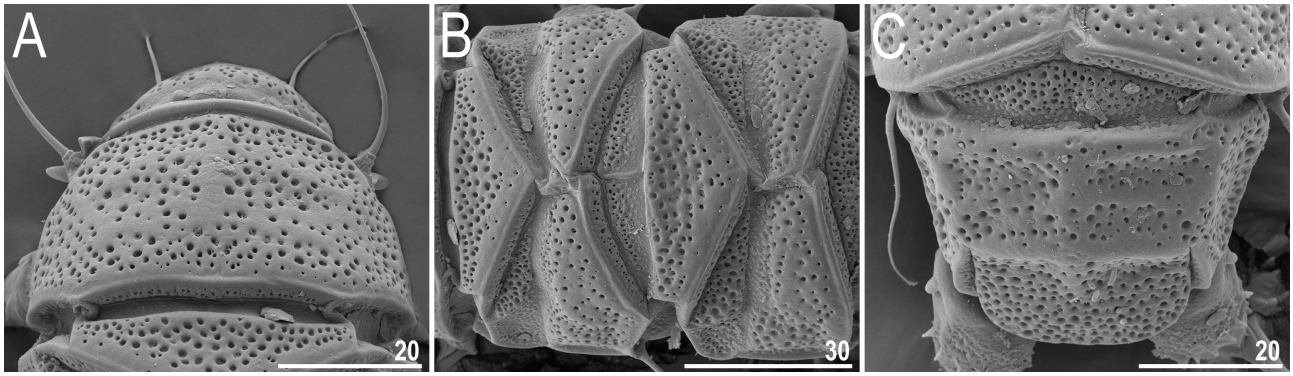

FIGURE 33. Dorsal sculpturing of *Echiniscus gracilis* **sp. nov.** (SEM, male): A—scapular plate, B—paired segmental and median plates, C—median plate 3 and caudal (terminal) plate. Scale bars in μm.

Etymology. From Latin *gracilis* = graceful, underlying elegantly regular dorsal sculpturing. An adjective in the nominative singular.

Geographic distribution. The species has a restricted distribution embracing Western Cape (Fig. 120F), thus it is most likely endemic to South Africa.

Remarks. Males most probably develop from juveniles, as we found a morphometric gap between juveniles and males (see Tables 16–17). A rare species, found mostly together with large populations of *E. dentatus* **sp. nov.** and *E. longispinosus*.

Differential diagnosis. *E. gracilis* **sp. nov.** is similar only to its closest congeners, *E. capensis* **sp. nov.** (see above) and *E. irroratus* **sp. nov.**, but can be distinguished from:

- *E. irroratus* **sp. nov.** by the body appendage configuration (*A-C-C^{d}-D-D^{d}* in *E. gracilis* **sp. nov.** *vs A-(B)-(C)-(D)-(D^{d})-(E)* in *E. irroratus* **sp. nov.**), and dorsal sculpturing (dark epicuticular granules absent in *E. gracilis* **sp. nov.** *vs* dark epicuticular granules present in *E. irroratus* **sp. nov.**).

Raw measurements. Supplementary Materials (SM.03) and Tardigrada Register (www.tardigrada.net/register/0085.htm).

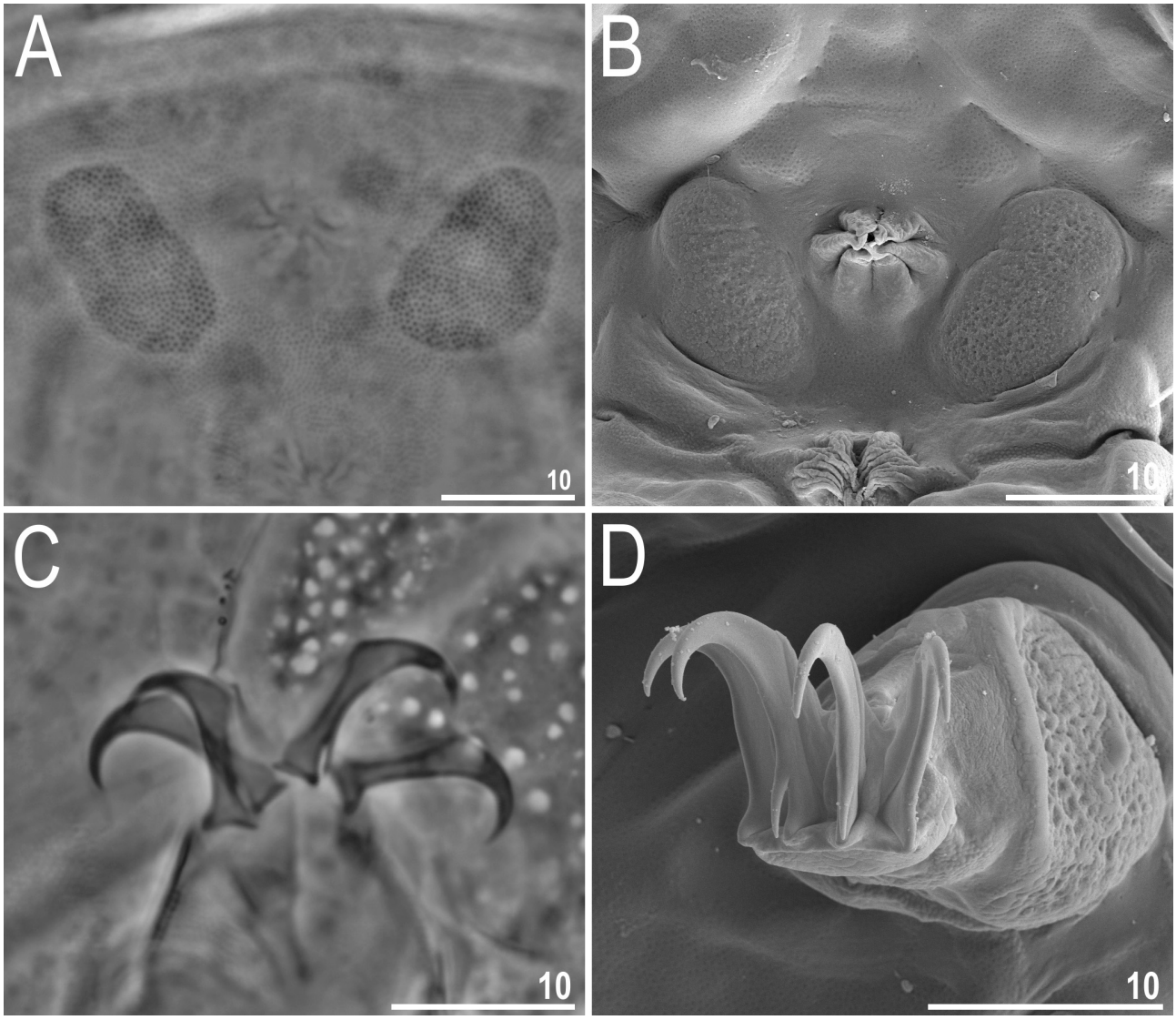

FIGURE 34. Ventral plates and claws of *Echiniscus gracilis* **sp. nov.** (females): A—genital plates (PCM), B—genital plates (SEM), C—claws II (PCM), D—claws III (SEM). Scale bars = 10 μm.

11. Echiniscus imitans sp. nov. Gąsiorek, Vončina, Morek & Michalczyk

urn:lsid:zoobank.org:act:7E5D422D-DCBE-44AA-97E8-B3939590AB14
Figures 35–39, Tables 18–20

Data source:

A total of 225 specimens (89 ♀♀, 18 ♂♂, 48 juveniles, 8 larvae, and 62 specimens of unknown instar/sex):

- Sample ZA.222: 3 specimens (3 ♀♀ on a slide); found with *Echiniscus blumi*, *E. draconis* **sp. nov.**, and *E. longispinosus*.
- Sample ZA.224: 1 specimen (1 ♀ on a slide); found with *Echiniscus oreas* **sp. nov.**, *E. regularis* **sp. nov.**, and *E. scabrospinosus*.
- Sample ZA.227: 167 specimens (46 ♀♀, 13 ♂♂, 42 juveniles and 8 larvae on slides, 50 specimens on SEM stub 18.18, and 8 specimens used for DNA extraction, including 5 hologenophores); found with *E. regularis* **sp. nov.**
- Sample ZA.247: 22 specimens (12 ♀♀, 3 ♂♂ and 3 juveniles on slides, and 4 specimens used for DNA extraction, including 4 hologenophores); found with *Echiniscus oreas* **sp. nov.** and *E. regularis* **sp. nov.**
- Sample ZA.248: 14 specimens (12 ♀♀, 1 ♂ and 1 juvenile on slides); found with *Echiniscus blumi*.

- Sample ZA.255: 3 specimens (2 ♀♀, 1 juvenile on a slide); found with *Echiniscus blumi* and *E. regularis* **sp. nov.**
- Sample ZA.431: 1 specimen (1 ♀ on a slide); found with *Echiniscus draconis* **sp. nov**., *E. lichenorum*, and *E. scabrocirrosus* **sp. nov.**
- Sample ZA.480: 14 specimens (12 ♀♀, 1 ♂ and 1 juvenile on slides); found with *Echiniscus draconis* **sp. nov.** and *E. scabrocirrosus* **sp. nov.**

Description. Mature females (*i.e*. from the third instar onwards; measurements and statistics in Table 18). Large *Echiniscus* with orange body and large red eyes; body colour and eyes disappeared soon after mounting in Hoyer's medium. Small, dactyloid cephalic papillae (secondary clavae) and (primary) clavae (Fig. 35A, 38A); cirri growing out from bulbous cirrophores. Cirri *A* short. The body appendage configuration is *A-B-C-C^d-D-D^d*, with all lateral appendages formed as very long cirri, and dorsal appendages somehow intermediate between long spines and stiff cirri (Fig. 35A, 36). Lateral trunk cirri with massive elevated bases. Dorsal appendages with a double structure (hollow): outer involucre and inner core (Fig. 35A, 37A, 39D–E). Asymmetries in the development of appendages rare.

Dorsal plates with a dense endocuticular layer forming a uniform dark matrix under PCM (Fig. 35A). Large pores densely and regularly distributed in plates (Fig. 35A, 36, 37A, 38F). *Striae* join the *capituli* of pillars in the following areas: the narrow stripe between the scapular plate and median plate 1 (Fig. 38B), in the anterior portions of the median plate 2 and paired segmental plates I–II (Fig. 38C–D), particularly minute in the transverse belts of segmental plates (Fig. 38E), and in the median plate 3 (Fig. 36A, 38C). The cephalic plate with an anterior triangular incision (Fig. 35A, 38A). The cervical (neck) plate poorly developed as a narrow, rectangular belt before the scapular plate (Fig. 35A, 36A, 38B). The scapular plate large, without median sutures or ridges (Fig. 38B), but with the usual lateral sutures (Fig. 35A, 36B). The caudal (terminal) plate with two short incisions (Fig. 35A), and occasional rudimental ridges forming facets (Fig. 36A). The caudal plate does not cover the entirety of the posterior body end, leaving an unplated surface as in *Cornechiniscus* (Fig. 6A). Ventral cuticle with large endocuticular pillars distributed throughout the whole venter; two quasirectangular genital plates with single pores present (Fig. 39A). Sexpartite gonopore placed between genital plates, and a trilobed anus between legs IV.

Legs short, massive and stout (Fig. 35A), with pedal plates invisible under PCM, but identifiable under SEM as semicircular areas of irregular cuticle (Fig. 36B). Pulvini present and easily identifiable. Spine on leg I and a papilla on leg IV present (Fig. 36B, 38A). Claws I–IV of equal heights, large and robust (Fig. 39B–C). External claws on all legs smooth. Internal claws with spurs of a moderate size positioned at *ca.* 25–30% of the claw height and strongly divergent from the branch.

Mature males and sexually dimorphic traits (*i.e*. from the third instar onwards; measurements and statistics in Table 19). Qualitatively like females (Fig. 35B). Sexual dimorphism rudimentary, expressed in smaller mean body size, shorter claws (compare Tables 18–19) and in the circular gonopore.

Juveniles (*i.e*. the second instar, measurements in Table 20). No gonopore and body appendage configuration *A-C-C^d-D-D^d*. A clear morphometric gap between adult females and juveniles (see Tables 18–20).

Larvae (*i.e*. the first instar, measurements and statistics in Table 20). Lacking gonopore and anus. Body appendage configuration *A-C-C^d-D-D^d* (Fig. 35C). Anterior portions of m2 and paired segmental plates weakly sculptured compared to older instars.

Eggs. Up to four round, yellow eggs per exuvia were found.

DNA markers and phylogenetic position. The sister species of *E. draconis* **sp. nov.** (Fig. 117, see also above). The species closest in COI is *E. draconis* **sp. nov.** (p-distance = 9.1–9.7%), and in both ITS—*E. lichenorum* (ITS-1: 1.7–2.3%, ITS-2: 0.9–1.2%).

Type material. 12 ♀♀, 3 ♂♂, and 3 juveniles on slides ZA.247.01–7; holotype: mature ♀ on slide ZA.247.04, allotype: mature ♂ on slide ZA.247.05. Four individuals used for DNA extraction, all retrieved as hologenophores.

Type locality. 29°45'13.7"S, 29°11'33"E, 1900 m asl: Republic of South Africa, KwaZulu-Natal, Drakensberg, Garden Castle Nature Reserve; shrubs at the river bank, lichens from rock (sample ZA.247).

Etymology. From Latin *imito* = to imitate, referring to the superficial similarity with *E. quadrispinosus*. A participle in the nominative singular.

Geographic distribution. Known only from South Africa, with a restricted mountainous distribution (Fig. 120I).

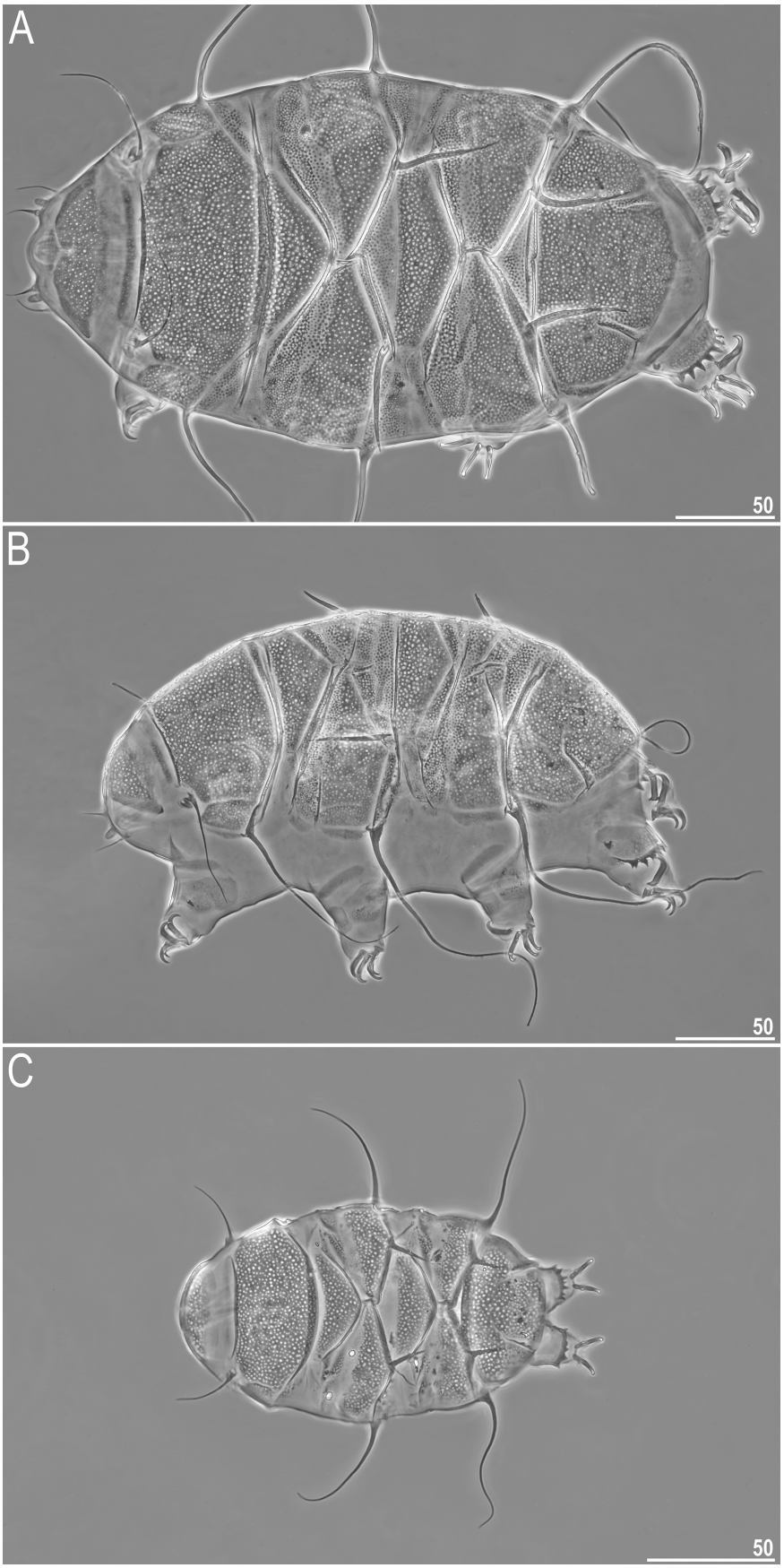

FIGURE 35. Habitus and intraspecific variability of *Echiniscus imitans* **sp. nov.** (PCM): A—holotype, female in dorsal view, B—allotype, male in lateral view, C—larva in dorsal view. Scale bars = 50 μm.

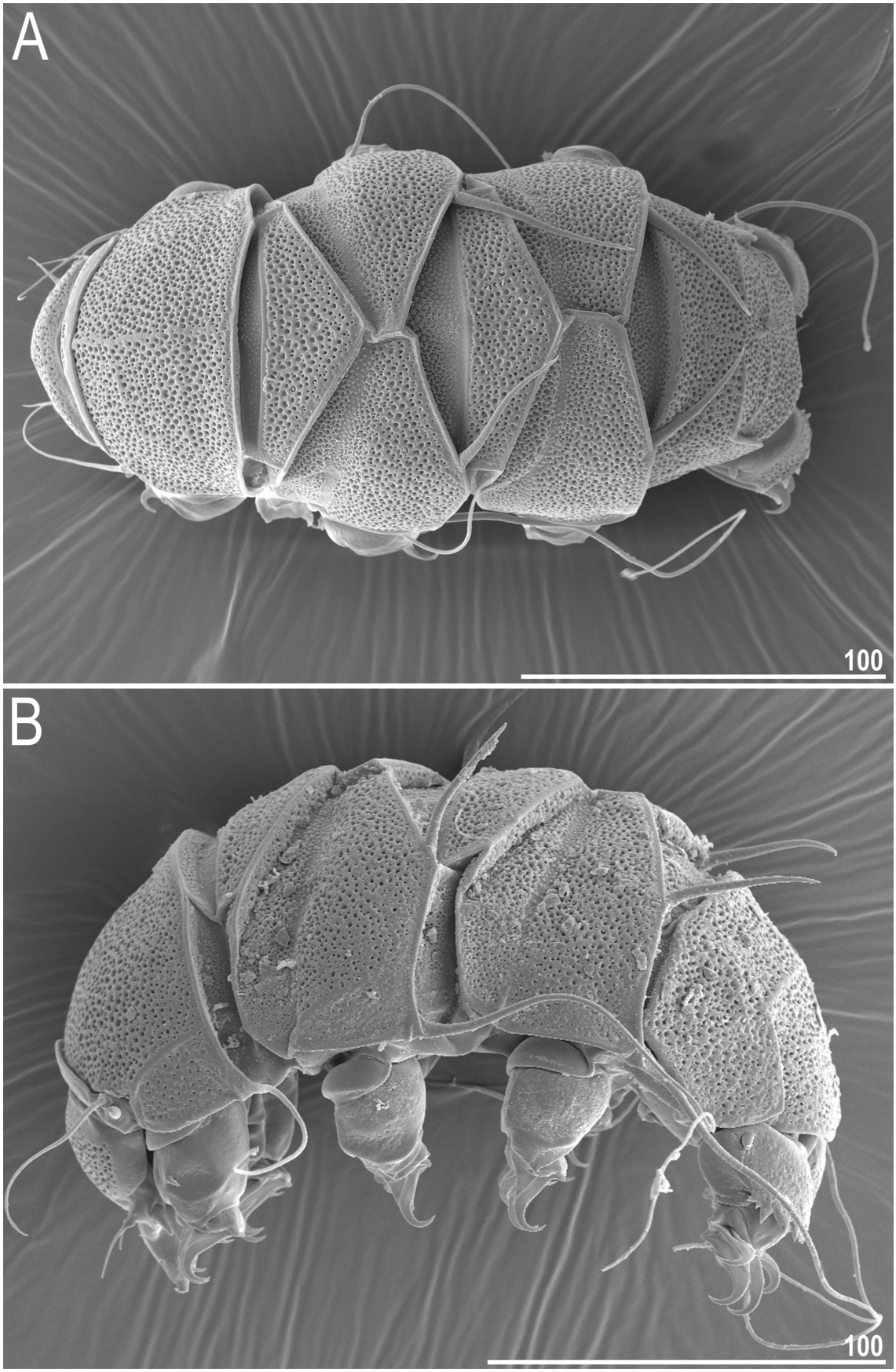

FIGURE 36. Habitus of *Echiniscus imitans* **sp. nov.** (SEM, females): A—female, dorsal view, B—female, lateral view. Scale bars = 100 μm.

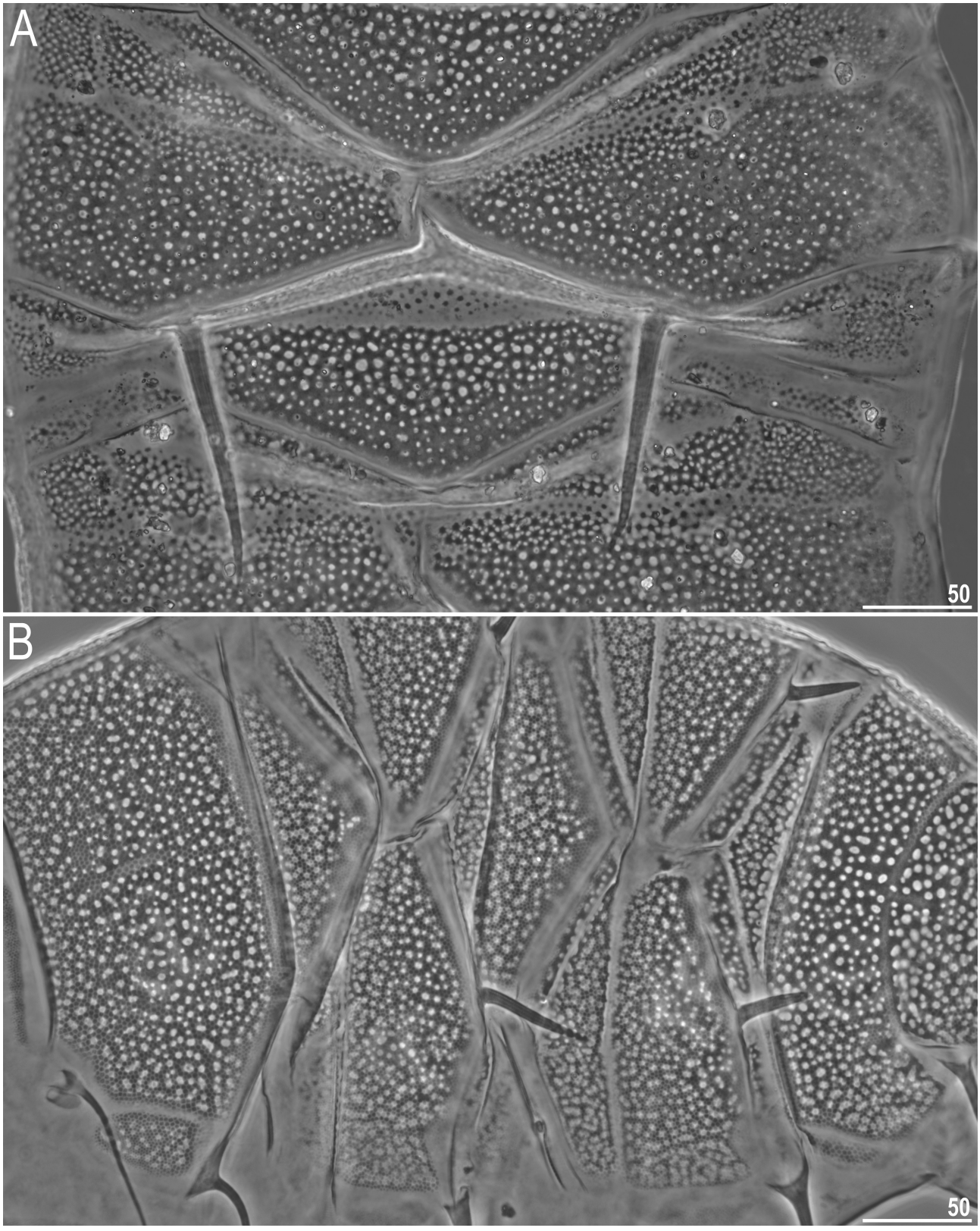

FIGURE 37. The comparison of the dorsal sculpturing of *Echiniscus imitans* **sp. nov.** (A) and *Echiniscus quadrispinosus* Richters, 1902 (B) (PCM, females). Scale bars = 50 μm.

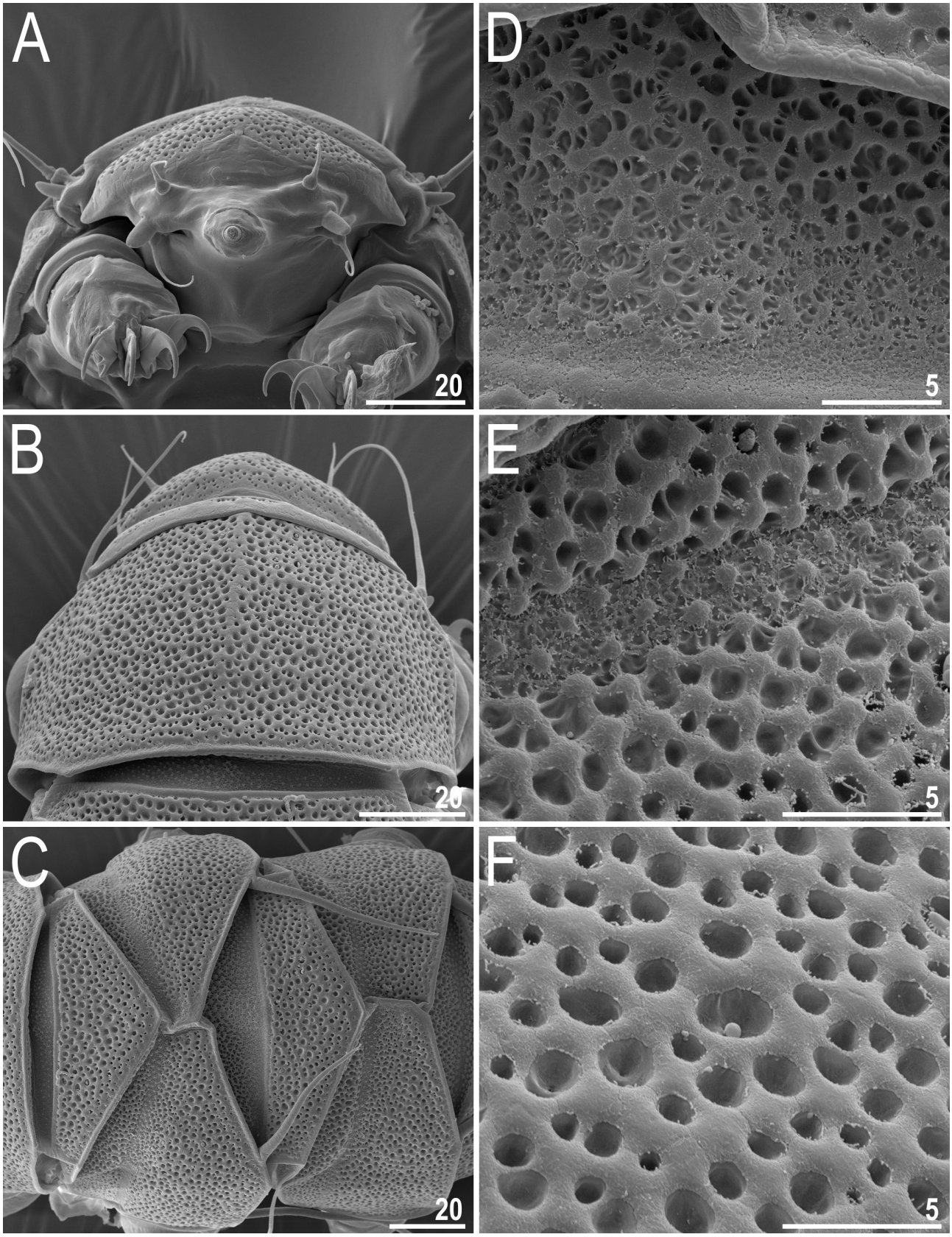

FIGURE 38. Head and dorsal sculpturing of *Echiniscus imitans* **sp. nov.** (SEM, females): A—cephalic appendages, cephalic plate and legs I, B—scapular plate, C—paired segmental and median plates, D—close-up on the anterior portion of the median plate 2, E—close-up on the transition zone (belt) between anterior and posterior portion of the segmental plate, F—close-up on the pores. Scale bars in μm.

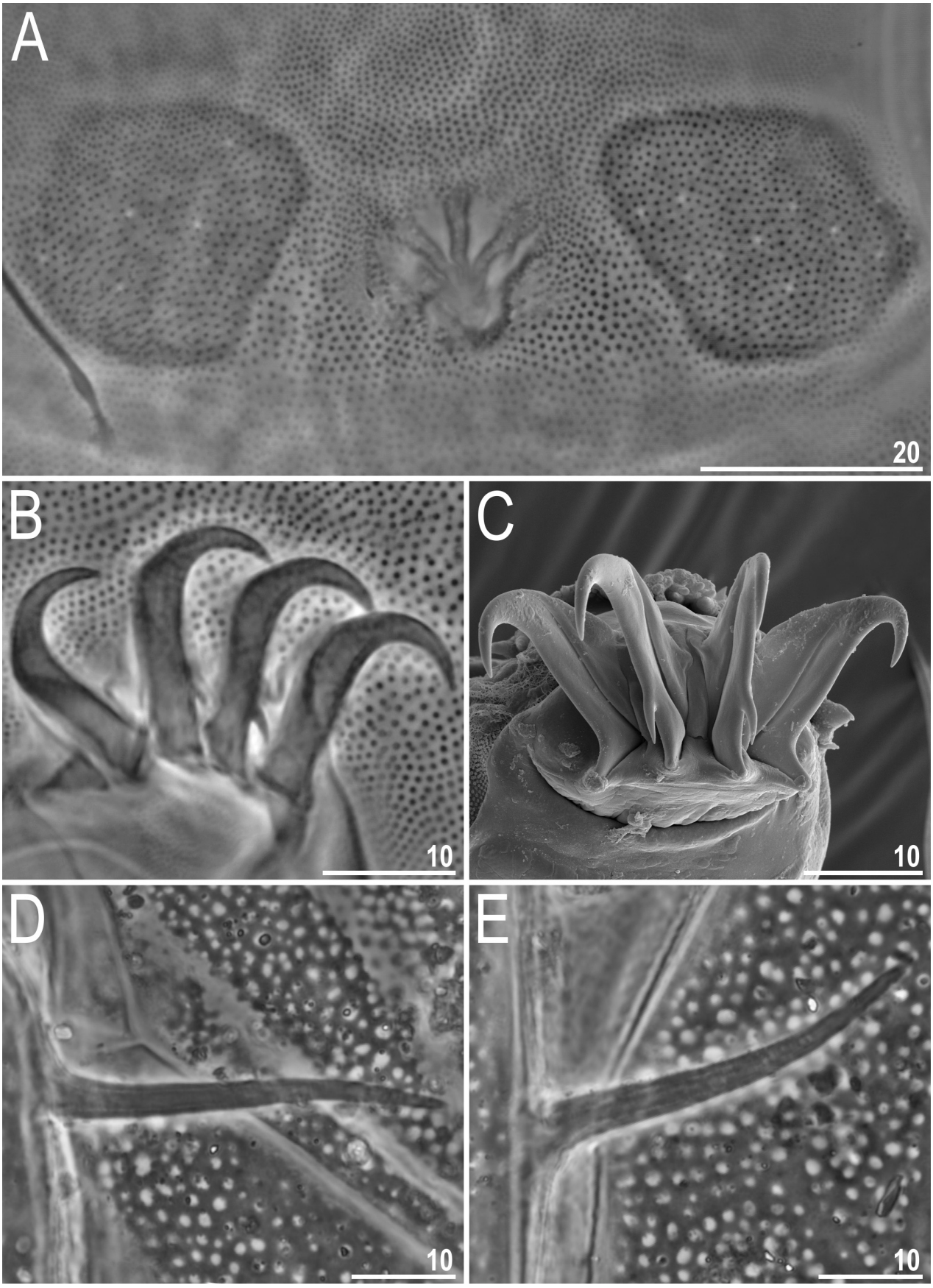

FIGURE 39. Ventral plates and claws of *Echiniscus imitans* **sp. nov.** (females): A—genital plates (PCM), B—claws III (PCM), C—claws IV (SEM), D—spine C^d, E—spine D^d. Scale bars in µm.

TABLE 18. Measurements [in µm] of selected morphological structures of the adult females of *Echiniscus imitans* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Holotype	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	20	282	–	370	*445*	–	*601*	339	*526*	22	*40*	347	*601*
Scapular plate length	20	47.9	–	76.8		–		64.8	–	6.5	–	57.7	–
Head appendages lengths													
Cirrus *internus*	20	11.3	–	21.1	*17.2*	–	*31.4*	16.2	*25.0*	2.3	*3.3*	16.8	*29.1*
Cephalic papilla	20	6.3	–	9.9	*10.4*	–	*15.9*	8.2	*12.7*	0.8	*1.3*	7.8	*13.5*
Cirrus *externus*	20	22.6	–	34.5	*25.3*	–	*51.5*	24.8	*38.6*	3.7	*6.4*	23.3	40.4
Clava	19	5.1	–	9.1	*6.6*	–	*15.0*	7.0	*10.8*	1.0	*1.9*	7.5	*13.0*
Cirrus *A*	19	47.3	–	76.5	*67.7*	–	*114.2*	60.1	*93.6*	6.8	*11.5*	63.6	*110.2*
Cirrus *A*/Body length ratio	19	13%	–	24%		–		18%	–	2%	–	18%	–
Body appendages lengths													
Cirrus *B*	19	21.2	–	165.0	*36.7*	–	*263.5*	121.5	*187.0*	31.5	*46.6*	21.2	*36.7*
Cirrus *C*	20	53.6	–	217.2	*92.9*	–	*358.5*	159.1	*246.2*	39.1	*60.2*	53.6	*92.9*
Cirrus C^d	20	32.5	–	148.8	*48.2*	–	*257.9*	52.5	*82.7*	23.7	*43.0*	148.8	*257.9*
Cirrus *D*	18	99.1	–	221.4	*148.4*	–	*348.1*	167.3	*258.5*	37.2	*54.4*	194.2	*336.6*
Cirrus D^d	20	28.5	–	55.3	*47.8*	–	*87.0*	42.2	*65.5*	7.2	*11.7*	50.2	*87.0*
Spine on leg I length	20	3.6	–	7.0	*5.9*	–	*10.1*	4.9	*7.6*	0.8	*1.2*	3.8	*6.6*
Papilla on leg IV length	17	4.3	–	6.7	*6.6*	–	*10.6*	5.4	*8.3*	0.7	*1.2*	4.4	*7.6*
Number of teeth on the collar	18	5	–	14		–		9.6	–	2.4	–	8	–
Claw I heights													
Branch	20	17.1	–	22.6	*24.1*	–	*36.2*	19.2	*29.8*	1.6	*3.2*	18.8	*32.6*
Spur	20	2.6	–	4.2	*3.7*	–	*6.2*	3.3	*5.2*	0.5	*0.8*	3.5	6.1
Spur/branch height ratio	20	13%	–	22%		–		17%	–	2%	–	19%	–
Claw II heights													
Branch	20	15.6	–	21.8	*25.4*	–	*32.6*	18.5	*28.7*	1.6	*1.9*	17.5	*30.3*
Spur	20	2.7	–	4.1	*4.6*	–	*6.5*	3.4	*5.3*	0.3	*0.4*	3.1	*5.4*
Spur/branch height ratio	20	16%	–	21%		–		18%	–	1%	–	18%	–
Claw III heights													
Branch	19	15.4	–	22.1	*25.5*	–	*33.6*	18.9	*29.4*	1.7	*2.2*	17.8	*30.8*
Spur	19	2.1	–	4.6	*4.4*	–	*7.9*	3.3	*5.2*	0.6	*0.8*	2.8	*4.9*
Spur/branch height ratio	19	14%	–	27%		–		18%	–	3%	–	16%	–
Claw IV heights													
Branch	20	16.2	–	25.0	*27.1*	–	*37.2*	21.4	*33.2*	2.5	*3.0*	21.2	*36.7*
Spur	13	3.1	–	4.7	*4.2*	–	*7.0*	3.7	*5.7*	0.5	*0.7*	3.5	*6.1*
Spur/branch height ratio	13	14%	–	19%		–		17%	–	1%	–	17%	–

TABLE 19. Measurements [in µm] of selected morphological structures of the adult males of *Echiniscus imitans* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Allotype	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	6	249	–	299	*488*	–	*568*	274	*529*	17	*29*	274	*488*
Scapular plate length	6	47.9	–	56.1		–		51.8	–	3.5	–	56.1	–
Head appendages lengths													
Cirrus *internus*	6	12.2	–	14.3	*21.7*	–	*28.1*	13.6	*26.3*	0.8	*2.4*	12.2	*21.7*
Cephalic papilla	6	6.7	–	7.7	*11.9*	–	*15.8*	7.0	*13.6*	0.4	*1.3*	6.7	*11.9*
Cirrus *externus*	6	16.2	–	19.5	*28.9*	–	*40.0*	18.3	*35.5*	1.1	*4.0*	16.2	*28.9*
Clava	6	5.2	–	6.9	*10.5*	–	*12.5*	6.1	*11.7*	0.7	*0.8*	6.9	*12.3*
Cirrus *A*	6	48.4	–	57.2	*90.0*	–	*106.8*	51.7	*99.8*	3.2	*5.5*	57.2	*102.0*
Cirrus *A*/Body length ratio	6	17%	–	21%		–		19%	–	2%	–	21%	–
Body appendages lengths													
Cirrus *B*	6	80.4	–	108.6	*162.8*	–	*207.5*	95.3	*183.7*	11.3	*16.9*	101.6	*181.1*
Cirrus *C*	6	126.1	–	151.4	*250.8*	–	*271.5*	135.2	*260.9*	9.2	*8.7*	151.4	*269.9*
Cirrus C^d	6	25.5	–	37.4	*45.5*	–	*76.6*	31.2	*60.6*	4.2	*10.4*	25.5	*45.5*
Cirrus *D*	5	121.7	–	174.3	*246.4*	–	*357.2*	149.1	*284.3*	19.1	*42.9*	155.4	*277.0*
Cirrus D^d	6	25.7	–	37.7	*52.0*	–	*77.3*	31.2	*60.2*	4.7	*9.2*	35.8	*63.8*
Spine on leg I length	6	3.3	–	4.0	*6.5*	–	*7.5*	3.6	*7.0*	0.3	*0.3*	4.0	*7.1*
Papilla on leg IV length	4	4.5	–	5.2	*8.4*	–	*10.2*	4.8	*9.3*	0.3	*0.8*	4.7	*8.4*
Number of teeth on the collar	4	7	–	11		–		8.5	–	1.9	–	?	–
Claw I heights													
Branch	6	11.4	–	15.8	*20.7*	–	*31.4*	14.5	*28.1*	1.6	*3.8*	15.8	*28.2*
Spur	6	2.6	–	3.9	*4.6*	–	*7.1*	3.1	*5.9*	0.5	*1.0*	2.6	*4.6*
Spur/branch height ratio	6	16%	–	34%		–		22%	–	6%	–	16%	–
Claw II heights													
Branch	6	14.0	–	16.6	*26.2*	–	*33.2*	15.2	*29.5*	1.0	*2.9*	14.7	*26.2*
Spur	6	2.1	–	3.3	*4.4*	–	*6.3*	2.8	*5.3*	0.4	*0.7*	2.8	*5.0*
Spur/branch height ratio	6	13%	–	23%		–		18%	–	4%	–	19%	–
Claw III heights													
Branch	6	13.8	–	16.2	*26.7*	–	*30.9*	15.0	*29.0*	0.9	*1.5*	15.8	*28.2*
Spur	6	2.5	–	3.5	*4.5*	–	*7.1*	2.8	*5.5*	0.4	*1.0*	2.5	*4.5*
Spur/branch height ratio	6	16%	–	24%		–		19%	–	3%	–	16%	–
Claw IV heights													
Branch	6	16.7	–	18.0	*30.3*	–	*35.2*	17.3	*33.4*	0.5	*2.0*	17.8	*31.7*
Spur	5	2.2	–	3.4	*4.5*	–	*7.1*	3.0	*5.7*	0.5	*1.0*	2.9	*5.2*
Spur/branch height ratio	5	13%	–	20%		–		17%	–	3%	–	16%	–

TABLE 20. Measurements [in µm] of selected morphological structures of the larvae and a juvenile of *Echiniscus imitans* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Juvenile	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	4	143	–	186	*502*	–	*610*	161	*546*	18	*47*	196	*491*
Scapular plate length	4	27.2	–	31.9		–		29.6	–	2.1	–	39.9	–
Head appendages lengths													
Cirrus *internus*	4	6.3	–	7.8	*21.6*	–	*28.7*	7.2	*24.5*	0.7	*3.3*	9.4	23.6
Cephalic papilla	4	4.3	–	4.8	*14.1*	–	*17.6*	4.7	*15.8*	0.2	*1.6*	7.2	*18.0*
Cirrus *externus*	4	8.8	–	10.2	*29.8*	–	*35.3*	9.6	*32.4*	0.7	*2.3*	12.3	*30.8*
Clava	4	3.4	–	4.3	*11.3*	–	*14.1*	3.7	*12.5*	0.4	*1.2*	5.2	*13.0*
Cirrus *A*	4	26.2	–	28.9	*88.1*	–	*101.0*	27.9	*94.7*	1.2	*5.4*	43.1	*108.0*
Cirrus *A*/Body length ratio	4	15%	–	19%		–		17%	–	1%	–	22%	–
Body appendages lengths													
Cirrus *C*	4	42.7	–	55.0	*157.0*	–	*192.3*	50.3	*170.3*	5.4	*15.3*	81.8	*205.0*
Cirrus C^d	4	13.2	–	16.7	*46.5*	–	*52.4*	14.4	*48.6*	1.6	*2.6*	26.9	*67.4*
Cirrus *D*	3	52.5	–	65.6	*193.0*	–	*215.1*	59.6	*206.7*	6.6	*11.9*	73.7	*184.7*
Cirrus D^d	4	11.5	–	12.8	*40.1*	–	*43.8*	12.2	*41.3*	0.6	*1.7*	25.0	*62.7*
Spine on leg I length	4	1.7	–	2.6	*6.3*	–	*8.5*	2.3	*7.7*	0.4	*1.0*	2.6	*6.5*
Papilla on leg IV length	3	2.7	–	3.6	*9.4*	–	*11.8*	3.0	*10.5*	0.5	*1.2*	?	*?*
Number of teeth on the collar	4	6	–	7		–		6.5	–	0.6	–	7.0	–
Claw I heights													
Branch	4	10.1	–	11.0	*33.9*	–	*38.5*	10.6	*36.1*	0.4	*2.1*	12.8	*32.1*
Spur	4	2.0	–	2.6	*6.3*	–	*9.1*	2.3	*7.8*	0.2	*1.2*	2.0	*5.0*
Spur/branch height ratio	4	19%	–	24%		–		22%	–	2%	–	16%	–
Claw II heights													
Branch	4	10.0	–	10.8	*33.9*	–	*37.8*	10.5	*35.7*	0.4	*1.9*	10.9	*27.3*
Spur	4	1.9	–	2.6	*6.6*	–	*9.6*	2.4	*8.1*	0.3	*1.2*	?	*?*
Spur/branch height ratio	4	18%	–	26%		–		23%	–	4%	–	?	–
Claw III heights													
Branch	4	9.8	–	10.6	*32.0*	–	*37.1*	10.1	*34.4*	0.4	*2.5*	13.1	*32.8*
Spur	4	2.2	–	3.1	*7.5*	–	*10.2*	2.5	*8.6*	0.4	*1.2*	?	?
Spur/branch height ratio	4	21%	–	31%		–		25%	–	4%	–	?	–
Claw IV heights													
Branch	4	11.2	–	11.8	*35.7*	–	*43.4*	11.5	*39.0*	0.3	*3.2*	12.9	*32.3*
Spur	3	2.4	–	2.6	*7.5*	–	*8.5*	2.5	*8.1*	0.1	*0.5*	?	*?*
Spur/branch height ratio	3	21%	–	23%		–		22%	–	1%	–	?	–

Remarks. Large populations of *E. imitans* **sp. nov.** were intermixed with other *Echiniscus* spp., typically with *E. blumi*, *E. draconis* **sp. nov.**, *E. oreas* **sp. nov.**, and *E. regularis* **sp. nov.** Meyer *et al*. (2018) recorded a representative of the *E. quadrispinosus* complex from Swaziland, but this had much more slender claws and long cirri *E* that distinguish it from *E. imitans* **sp. nov.**, suggesting that the specimen from Meyer *et al*. (2018) belongs to another new species.

Differential diagnosis. *E. imitans* **sp. nov.** is similar to several species, but it can be distinguished from:

- *E. blumi*, by the type of sculpturing (pores without marked rims in *E. imitans* **sp. nov.** *vs* pores with thick polygonal edges in *E. blumi*), and claw morphology (spurless claws IV in *E. imitans* **sp. nov.** *vs* claws IV with secondary and tertiary spurs in *E. blumi*);
- *E. knowltoni*, a Nearctic endemic (Schuster & Grigarick 1971), by the body appendage configuration (*A-B-C-C^d-D-D^d* in *E. imitans* **sp. nov.** *vs A-C-C^d-D-D^d* in *E. knowltoni*) and claw morphology (spurless claws IV in *E. imitans* **sp. nov.** *vs* claws IV with secondary spurs in *E. knowltoni*);
- *E. quadrispinosus*, by the body appendage configuration (*A-B-C-C^d-D-D^d* in *E. imitans* **sp. nov.** *vs A-B-C-C^d-D-D^d-E* in *E. quadrispinosus*) and dorsal plate sculpturing (endocuticular pillars absent in *E. imitans* **sp. nov.** *vs* endocuticular pillars present in *E. quadrispinosus*, compare Fig. 37A and 37B).

Raw measurements. Supplementary Materials (SM.03) and Tardigrada Register (www.tardigrada.net/register/0086.htm).

12. Echiniscus intricatus sp. nov. Gąsiorek, Vončina, Morek & Michalczyk

urn:lsid:zoobank.org:act:5B912B9D-FDD2-4871-9938-2E20B78C3A0F
Figures 40–43A–D, Tables 21–23

Data source:
A total of 186 specimens (97 ♀♀, 4 ♂♂, 31 juveniles, 7 larvae, and 47 specimens of unknown instar/sex):

- Sample ZA.130: 36 specimens (30 ♀♀, 2 ♂♂ and 4 juveniles on slides); found with *Echiniscus tetraspinosus* **sp. nov.**
- Sample ZA.201: 9 specimen (1 juvenile on a slide and 8 specimens used for DNA extraction); found with *Echiniscus oreas* **sp. nov.** and *E. tetraspinosus* **sp. nov.**
- Sample ZA.217: 1 specimen (1 ♀ on a slide); found with *Echiniscus blumi*.
- Sample ZA.218: 3 specimens (2 ♀♀ on slides, 1 specimen used for DNA extraction); found with *Echiniscus draconis* **sp. nov.**, *E. lichenorum*, and *E. tetraspinosus* **sp. nov.**
- Sample ZA.219: 106 specimens (45 ♀♀, 2 ♂♂, 18 juveniles and 7 larvae on slides, 20 specimens on SEM stub 18.18, 14 specimens used for DNA extraction); found with *Echiniscus oreas* **sp. nov.**
- Sample ZA.225: 28 specimens (16 ♀♀ and 8 juveniles on slides, and 4 specimens used for DNA extraction, including 3 hologenophores); found with *Echiniscus blumi* and *E. regularis* **sp. nov.**
- Sample ZA.238: 3 specimens (3 ♀♀ on a slide); found with *E. regularis* **sp. nov.**

Description. Mature females (*i.e*. from the third instar onwards; measurements and statistics in Table 21). Medium-sized *Echiniscus* with yellow, plump body and large red eyes; body colour and eyes disappeared soon after mounting in Hoyer's medium. Dactyloid cephalic papillae (secondary clavae) and much smaller (primary) clavae (Fig. 40A, C, 41C); cirri growing out from bulbous cirrophores. Cirri *A* very short. Trunk unappendaged.

Dorsal plates with a dense endocuticular layer forming a uniform dark matrix under PCM (Fig. 40A, C). Large pores densely and irregularly distributed in plates (Fig. 40A, C, 41, 42A–B). Anterior portions of paired segmental plates I–II and median plate 2, and the entire m3 with different sculpturing—solid, small granules surrounded by a delicate wrinkling (*striae* visible in anteriormost portions of pI–II (Fig. 40); circular pseudopores with thickened edges between granules (Fig. 42C)). The cephalic plate with an anterior chalice-like incision (Fig. 40A). The cervical (neck) plate poorly developed as a narrow, rectangular belt before the scapular plate (Fig. 40A, 41, 42A). The scapular plate large (Fig. 42A), with the usual lateral sutures poorly marked (Fig. 40A, 41C), and the median longitudinal ridge/suture weakly developed, mostly poreless (Fig. 40A). The caudal (terminal) plate with two short incisions (Fig. 40A, C, 41B). Ventral cuticle with minute endocuticular pillars distributed throughout the whole venter; ventral plates absent. Sexpartite gonopore placed anteriorly to legs IV, and a trilobed anus between legs IV.

Legs massive and stout, with sculptured pedal plates I–IV (Fig. 40C). Pulvini clearly visible. Spine on leg I placed at the border of the pedal plate and a tiny papilla on leg IV present (Fig. 40C, 41C). Claws I–IV of equal heights, large and robust (Fig. 43). All external claws on legs spurless. All internal claws with large spurs positioned at *ca.* 25–30% of the claw height and strongly divergent from the branch.

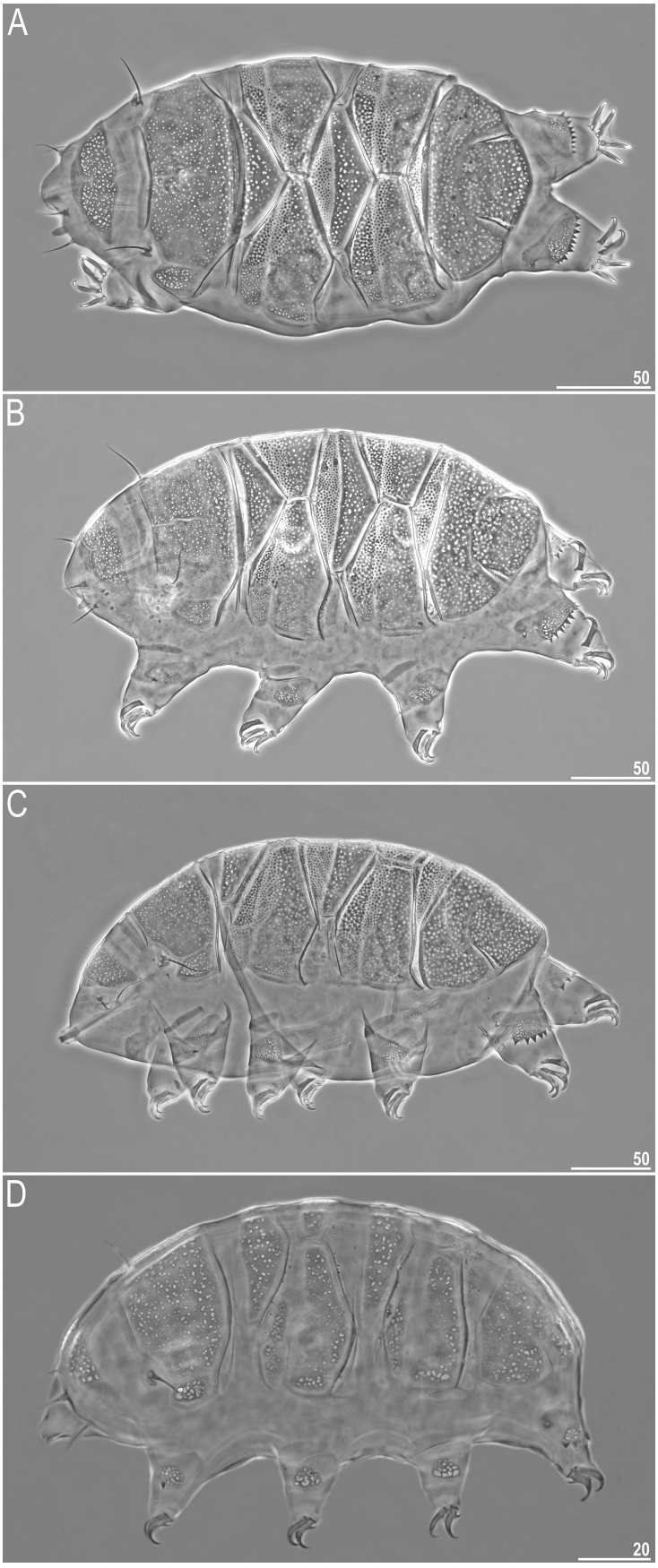

FIGURE 40. Habitus and intraspecific variability of *Echiniscus intricatus* **sp. nov.** (PCM): A—holotype, female in dorsal view, B—allotype, male in dorsolateral view, C—paratype, female in lateral view, D—paratype, larva in dorsolateral view. Scale bars in μm.

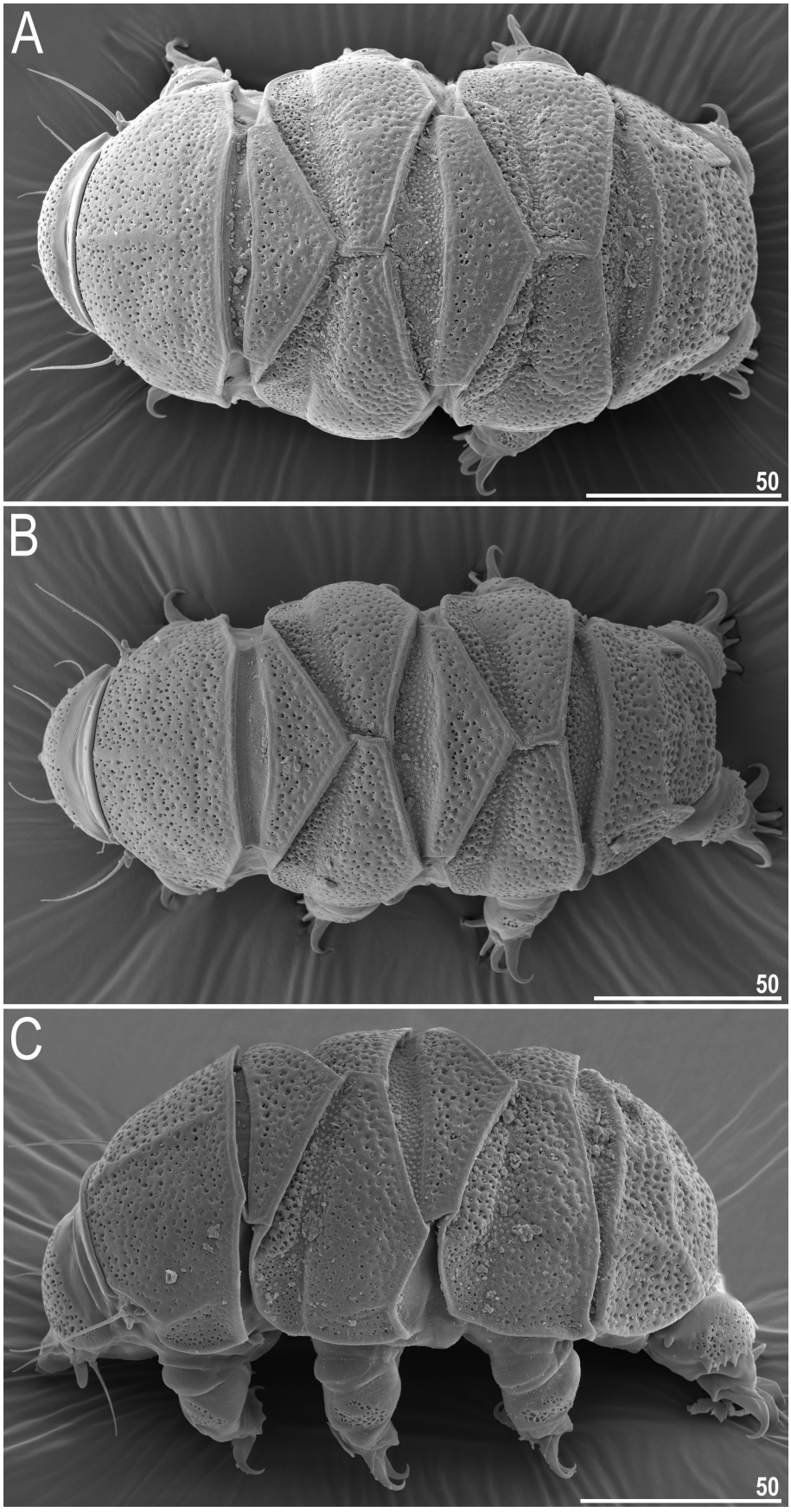

FIGURE 41. Habitus and intraspecific variability of *Echiniscus intricatus* **sp. nov.** (SEM, females): A, B—dorsal view, C—lateral view. Scale bars = 50 µm.

Mature males and sexually dimorphic traits (*i.e*. from the third instar onwards; measurements and statistics in Table 22). Qualitatively like females (Fig. 40B). Sexual dimorphism rudimentary, expressed in smaller body size (compare Tables 21–22) and in the circular gonopore.

Juveniles (*i.e*. the second instar, measurements and statistics in Table 22). No gonopore and a clear morphometric gap exists between adult females and juveniles (evidenced also in the scapular plate length; see Tables 21–22).

TABLE 21. Measurements [in µm] of selected morphological structures of the adult females of *Echiniscus intricatus* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Holotype	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	20	236	–	311	*479*	–	*621*	270	*548*	20	*38*	288	*520*
Scapular plate length	20	42.1	–	56.6		–		49.4	–	4.1	–	55.4	–
Head appendages lengths													
Cirrus *internus*	20	11.4	–	17.2	*23.7*	–	*35.5*	14.2	*28.8*	1.8	*3.1*	15.0	*27.1*
Cephalic papilla	20	5.8	–	8.8	*13.1*	–	*18.3*	7.7	*15.7*	0.7	*1.5*	7.4	*13.4*
Cirrus *externus*	20	14.4	–	26.6	*30.2*	–	*54.9*	20.5	*41.6*	3.6	*6.8*	20.8	*37.5*
Clava	20	4.4	–	7.0	*9.1*	–	*15.9*	5.9	*12.1*	0.8	*1.8*	6.4	11.6
Cirrus *A*	20	23.6	–	35.3	*48.6*	–	*71.2*	30.5	*62.0*	3.0	*5.8*	31.2	*56.3*
Cirrus *A*/Body length ratio	20	9%	–	13%		–		11%	–	1%	–	11%	–
Body appendages lengths													
Spine on leg I length	19	3.1	–	4.7	*6.3*	–	*9.7*	3.8	*7.8*	0.4	*0.9*	3.6	*6.5*
Papilla on leg IV length	20	2.7	–	4.2	*6.0*	–	*8.5*	3.6	*7.3*	0.4	*0.7*	3.8	*6.9*
Number of teeth on the collar	20	6	–	12		–		8.6	–	1.9	–	9	–
Claw I heights													
Branch	20	12.4	–	19.2	*26.0*	–	*36.3*	15.7	*31.8*	1.6	*2.5*	16.5	*29.8*
Spur	19	1.9	–	3.4	*3.9*	–	*6.5*	2.7	*5.4*	0.4	*0.8*	3.1	*5.6*
Spur/branch height ratio	19	12%	–	21%		–		17%	–	2%	–	19%	–
Claw II heights													
Branch	20	11.0	–	17.0	*23.1*	–	*33.4*	15.0	*30.4*	1.4	*2.2*	15.7	*28.3*
Spur	14	2.0	–	3.4	*4.1*	–	*6.8*	2.7	*5.4*	0.4	*0.8*	2.8	*5.1*
Spur/branch height ratio	14	13%	–	28%		–		18%	–	4%	–	18%	–
Claw III heights													
Branch	20	11.8	–	18.2	*24.7*	–	*34.5*	15.3	*31.1*	1.5	*2.5*	15.9	*28.7*
Spur	18	2.1	–	3.7	*3.9*	–	*6.9*	2.8	*5.6*	0.5	*0.8*	3.3	*6.0*
Spur/branch height ratio	18	13%	–	24%		–		18%	–	3%	–	21%	–
Claw IV heights													
Branch	20	13.2	–	19.2	*27.7*	–	*38.7*	17.2	*34.8*	1.5	*2.9*	18.3	*33.0*
Spur	8	2.8	–	4.0	*5.7*	–	*7.8*	3.5	*6.9*	0.4	*0.7*	4.0	*7.2*
Spur/branch height ratio	8	16%	–	28%		–		21%	–	4%	–	22%	–

Larvae (*i.e*. the first instar, measurements and statistics in Table 23). No gonopore and anus. A clear morphometric gap between juveniles and larvae. Central portions of the paired segmental plates I–II smooth, their anterior and posterolateral portions, and posterolateral portions of the scapular plate and pedal plates with larger and densely packed pores of irregular, not circular, shape (Fig. 40D).

Eggs. Up to four round, yellow eggs per exuvia were found.

TABLE 22. Measurements [in µm] of selected morphological structures of the juveniles and a male of *Echiniscus intricatus* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		♂	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	5	151	–	219	*467*	–	*528*	181	*495*	25	*24*	223	*558*
Scapular plate length	5	29.6	–	41.5		–		36.6	–	4.7	–	40.0	–
Head appendages lengths													
Cirrus *internus*	5	6.5	–	15.7	*22.0*	–	*41.3*	11.1	*29.9*	3.7	*7.7*	13.6	*34.0*
Cephalic papilla	5	3.4	–	8.7	*11.5*	–	*22.9*	6.3	*17.0*	2.0	*4.1*	8.7	*21.8*
Cirrus *externus*	5	11.2	–	21.2	*37.8*	–	*51.1*	16.5	*44.5*	3.7	*4.9*	14.1	*35.3*
Clava	5	3.6	–	7.1	*9.6*	–	*18.7*	4.9	*13.3*	1.5	*3.4*	4.0	*10.0*
Cirrus *A*	5	16.6	–	30.6	*55.9*	–	*80.5*	24.7	*66.7*	6.3	*10.6*	25.0	*62.5*
Cirrus *A*/Body length ratio	5	11%	–	17%		–		14%	–	2%	–	11%	–
Body appendages lengths													
Spine on leg I length	5	2.0	–	3.3	*6.8*	–	*8.0*	2.8	*7.6*	0.5	*0.5*	2.3	*5.8*
Papilla on leg IV length	5	2.3	–	3.6	*6.5*	–	*9.1*	2.9	*7.9*	0.5	*1.0*	3.5	*8.8*
Number of teeth on the collar	5	5.0	–	11.0	*16.9*	–	*27.8*	8.2	*22.0*	2.6	*4.7*	7.0	–
Claw I heights													
Branch	5	8.6	–	14.9	*26.1*	–	*39.2*	12.0	*32.4*	3.0	*5.1*	13.9	*34.8*
Spur	2	1.6	–	2.7	*5.4*	–	*6.5*	2.2	*6.0*	0.8	*0.8*	2.3	*5.8*
Spur/branch height ratio	2	19%	–	20%		–		19%	–	1%	–	17%	–
Claw II heights													
Branch	5	7.7	–	14.9	*26.0*	–	*39.2*	11.6	*31.4*	2.8	*5.0*	13.9	*34.8*
Spur	2	2.2	–	2.4	*5.6*	–	*6.3*	2.3	*5.9*	0.1	*0.5*	1.8	*4.5*
Spur/branch height ratio	2	16%	–	17%		–		17%	–	1%	–	13%	–
Claw III heights													
Branch	5	8.5	–	14.3	*28.7*	–	*37.6*	11.8	*32.1*	2.6	*4.1*	13.4	*33.5*
Spur	2	1.7	–	2.3	*5.7*	–	*5.8*	2.0	*5.8*	0.4	*0.0*	2.1	5.3
Spur/branch height ratio	2	16%	–	20%		–		18%	–	3%	–	16%	–
Claw IV heights													
Branch	5	8.9	–	16.2	*30.1*	–	*42.6*	13.4	*36.2*	3.3	*5.1*	13.4	*33.5*
Spur	2	2.3	–	2.4	*7.0*	–	*7.8*	2.4	*7.4*	0.1	*0.6*	?	*?*
Spur/branch height ratio	2	22%	–	26%		–		24%	–	3%	–	?	–

DNA markers and phylogenetic position. The phylogeny reconstruction inferred *E. belloporus* sister to *E. intricatus* **sp. nov.**, both constituting the sister clade of the *E. spinulosus* complex (Fig. 117). The species closest in COI is *E. draconis* **sp. nov.** (p-distance = 14.3–14.7%), in ITS-1—*E. oreas* **sp. nov.** (6.9–7.1%), and in ITS-2—*E. dentatus* **sp. nov.** (5.3–5.6%).

Type material. 45 ♀♀, 2 ♂♂, 18 juveniles and 7 larvae on slides ZA.219.01, 3–12; holotype: mature ♀ on slide ZA.219.04. Mounted together with 2 ♂♂, 5 juveniles and 1 larva of *E. oreas* **sp. nov.**, 20 ♀♀, 17 juveniles and 4 larvae of *E. regularis* **sp. nov.** About 20 specimens on a SEM stub 18.18. 14 individuals used for DNA extraction, 11 retrieved as hologenophores.

Type locality. 29°16'6.4''S, 29°30'45.5''E, 1770 m asl: Republic of South Africa, KwaZulu-Natal, Drakensberg, Giants Castle Game Reserve; montane grassland, lichens from rock (sample ZA.219).

Etymology. From Latin *intricatus* = complex, referring to an intricate dorsal sculpturing. An adjective in the nominative singular.

Geographic distribution. Only recorded from South Africa; uncommon (Fig. 120J).

Remarks. Populations of *E. intricatus* **sp. nov.** were always accompanied by other echiniscids, macrobiotids, milnesiids and ramazzottiids, with no obvious associations between the taxa.

Differential diagnosis. *Echiniscus intricatus* **sp. nov.** is similar to the unappendaged *E. bisculptus*, reported from Morocco (Maucci 1983), but the morphological disparities between them are evident: thin *striae* are localised only in the anteriormost portions of paired segmental plates I–II (Fig. 40) in *E. intricatus* **sp. nov.**, but they are large and present in all dorsal plates (Fig. 44) in *E. bisculptus*, a strong difference in the cirrus *A* length (up to 35 µm [<20% of the body length] in *E. intricatus* **sp. nov.** *vs* up to 81 µm [*ca*. 25% of the body length] in *E. bisculptus*), and the morphology of internal spurs (large spurs highly divergent from branches in *E. intricatus* **sp. nov.** *vs* tiny spurs adjacent to branches in *E. bisculptus*, compare Fig. 43A–D and 43E).

Raw measurements. Supplementary Materials (SM.03) and Tardigrada Register (www.tardigrada.net/register/0087.htm).

TABLE 23. Measurements [in µm] of selected morphological structures of the larvae of *Echiniscus intricatus* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD	
		µm			*sp*			µm	*sp*	µm	*sp*
Body length	2	136	–	150	*507*	–	*509*	143	*508*	10	*2*
Scapular plate length	2	26.7	–	29.6		–		28.2	–	2.1	–
Head appendages lengths											
Cirrus *internus*	2	5.2	–	5.3	*17.6*	–	*19.9*	5.3	*18.7*	0.1	*1.6*
Cephalic papilla	2	3.9	–	4.3	*13.2*	–	*16.1*	4.1	*14.6*	0.3	*2.1*
Cirrus *externus*	2	7.4	–	9.3	*25.0*	–	*34.8*	8.4	*29.9*	1.3	*7.0*
Clava	2	2.9	–	3.3	*10.9*	–	*11.1*	3.1	*11.0*	0.3	*0.2*
Cirrus *A*	2	15.1	–	15.1	*51.0*	–	*56.6*	15.1	*53.8*	0.0	*3.9*
Cirrus *A*/Body length ratio	2	10%	–	11%		–		11%	–	1%	–
Body appendages lengths											
Spine on leg I length	2	1.6	–	2.0	*5.4*	–	*7.5*	1.8	*6.4*	0.3	*1.5*
Papilla on leg IV length	2	2.3	–	2.4	*7.8*	–	*9.0*	2.4	*8.4*	0.1	*0.9*
Number of teeth on the collar	2	5	–	6		–		5.5	–	0.7	–
Claw I heights											
Branch	2	7.9	–	8.3	*28.0*	–	*29.6*	8.1	*28.8*	0.3	*1.1*
Spur	2	2.3	–	2.4	*7.8*	–	*9.0*	2.4	*8.4*	0.1	*0.9*
Spur/branch height ratio	2	28%	–	30%		–		29%	–	2%	–
Claw II heights											
Branch	2	7.9	–	8.3	*28.0*	–	*29.6*	8.1	*28.8*	0.3	*1.1*
Spur	2	2.0	–	2.4	*6.8*	–	*9.0*	2.2	*7.9*	0.3	*1.6*
Spur/branch height ratio	2	24%	–	30%		–		27%	–	4%	–
Claw III heights											
Branch	2	7.8	–	8.2	*27.7*	–	*29.2*	8.0	*28.5*	0.3	*1.1*
Spur	2	2.1	–	2.4	*7.1*	–	*9.0*	2.3	*8.0*	0.2	*1.3*
Spur/branch height ratio	2	26%	–	31%		–		28%	–	4%	–
Claw IV heights											
Branch	2	9.0	–	9.3	*31.4*	–	*33.7*	9.2	*32.6*	0.2	*1.6*
Spur	2	2.5	–	2.6	*8.4*	–	*9.7*	2.6	*9.1*	0.1	*0.9*
Spur/branch height ratio	2	27%	–	29%		–		28%	–	1%	–

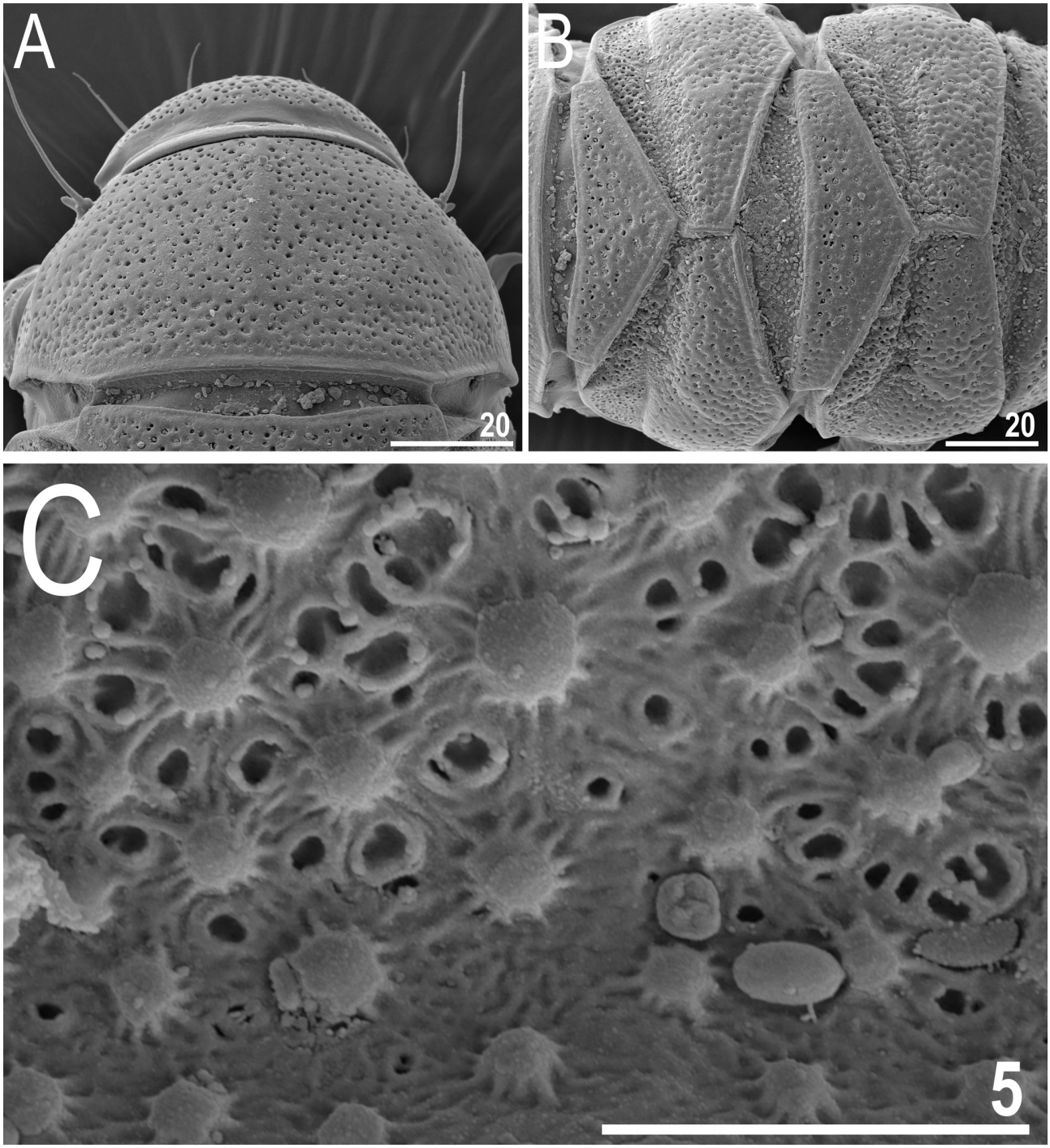

FIGURE 42. Dorsal sculpturing of *Echiniscus intricatus* **sp. nov.** (SEM, females): A—scapular plate, B—paired segmental and median plates, C—close-up on the sculpture of anterior portion of the median plate 2. Scale bars in μm.

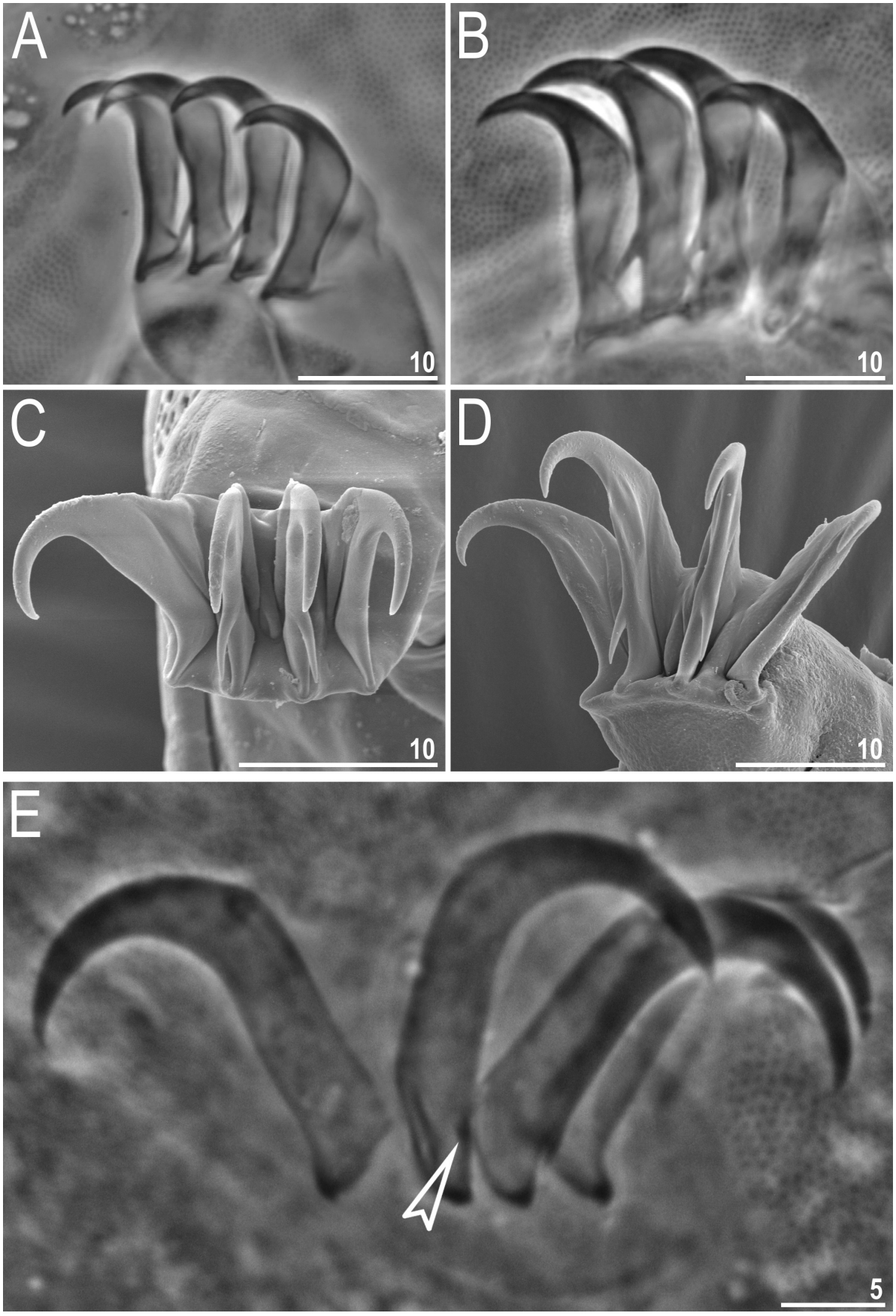

FIGURE 43. Claws of *Echiniscus intricatus* **sp. nov.** (females): A—claws I (PCM), B—claws IV (PCM), C—claws II (SEM), D—claws IV (SEM), E—claws II of *Echiniscus bisculptus* (female, PCM). Arrowhead indicates lack of spur. Scale bars = 10 μm.

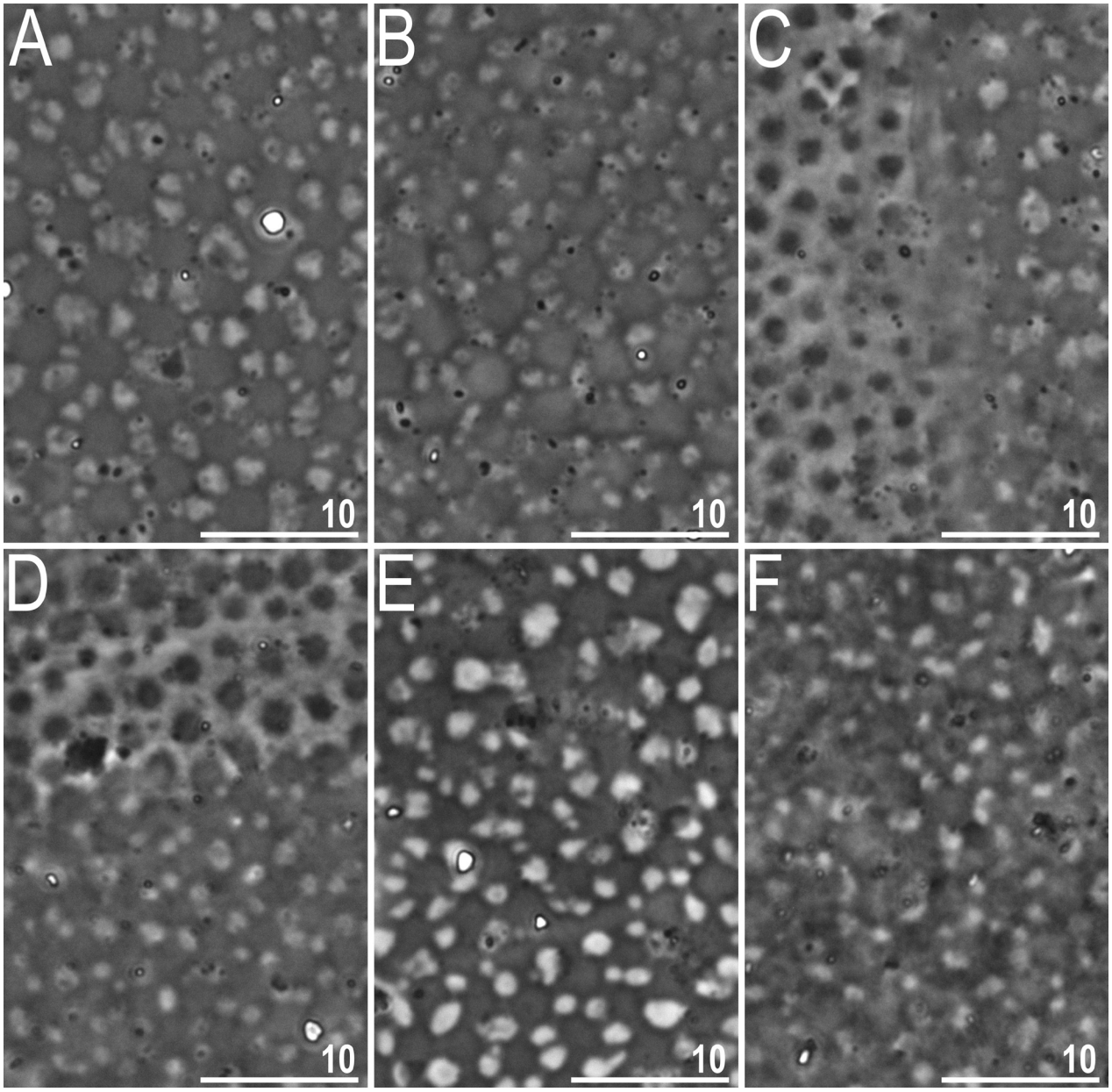

FIGURE 44. Dorsal sculpturing of *Echiniscus bisculptus* Maucci, 1983 (PCM, females): A, B—scapular plate, C—paired segmental plate I, D—median plate 2, E, F—caudal (terminal) plate. Scale bars = 10 μm.

13. Echiniscus irroratus sp. nov. Gąsiorek, Vončina, Morek & Michalczyk

urn:lsid:zoobank.org:act:2C8AC5EF-9A2E-4084-B722-F9B18F639720
Figures 45–48, Table 24

Data source:

A total of 24 specimens (18 ♀♀, 2 ♂♂, 2 juveniles, and 2 specimens of unknown instar/sex):

- Sample ZA.022: 1 specimen (1 ♀ on a slide); found with *Echiniscus attenboroughi* **sp. nov.**, *E. dentatus* **sp. nov.**, *E. gracilis* **sp. nov.**, *E. lichenorum*, *E. longispinosus*, and *E. setaceus* **sp. nov.**
- Sample ZA.023: 5 specimens (4 ♀♀ and 1 juvenile on slides); found with *E. dentatus* **sp. nov.** and *E. gracilis* **sp. nov.**
- Sample ZA.502: 3 specimens (2 ♀♀ and 1 specimen of unknown sex on slides); found with *Cornechiniscus madagascariensis*, *Echiniscus dentatus* **sp. nov.**, *E. latruncularis* **sp. nov**., and *E. setaceus* **sp. nov.**
- Sample ZA.504: 7 specimens (5 ♀♀ and 1 ♂ on slides, and 1 specimen used for DNA extraction); found with

Echiniscus dentatus **sp. nov.**

- Sample ZA.518: 2 specimens (1 ♀ and 1 juvenile on a slide); found with *Echiniscus dentatus* **sp. nov.**, *E. scabrospinosus*, *Pseudechiniscus (Pseudechiniscus)* cf. *ehrenbergi*, and *P. (Meridioniscus) wallacei* **sp. nov.**
- Sample ZA.511: 1 specimen (1 ♀ on a slide); found with *Echiniscus gracilis* **sp. nov.** and *E. longispinosus*.
- Sample ZA.551: 1 specimen (1 ♀ on a slide); found with *Echiniscus dentatus* **sp. nov.**.
- Sample ZA.555: 3 specimens (2 ♀♀ on a slide, and 1 ♂ on SEM stub 19.06); found with *E. dentatus* **sp. nov.**, *E. gracilis* **sp. nov.**, and *E. latruncularis* **sp. nov.**
- Sample ZA.558: 1 specimen (1 ♀ on a slide); found with *E. dentatus* **sp. nov.** and *E. longispinosus*.

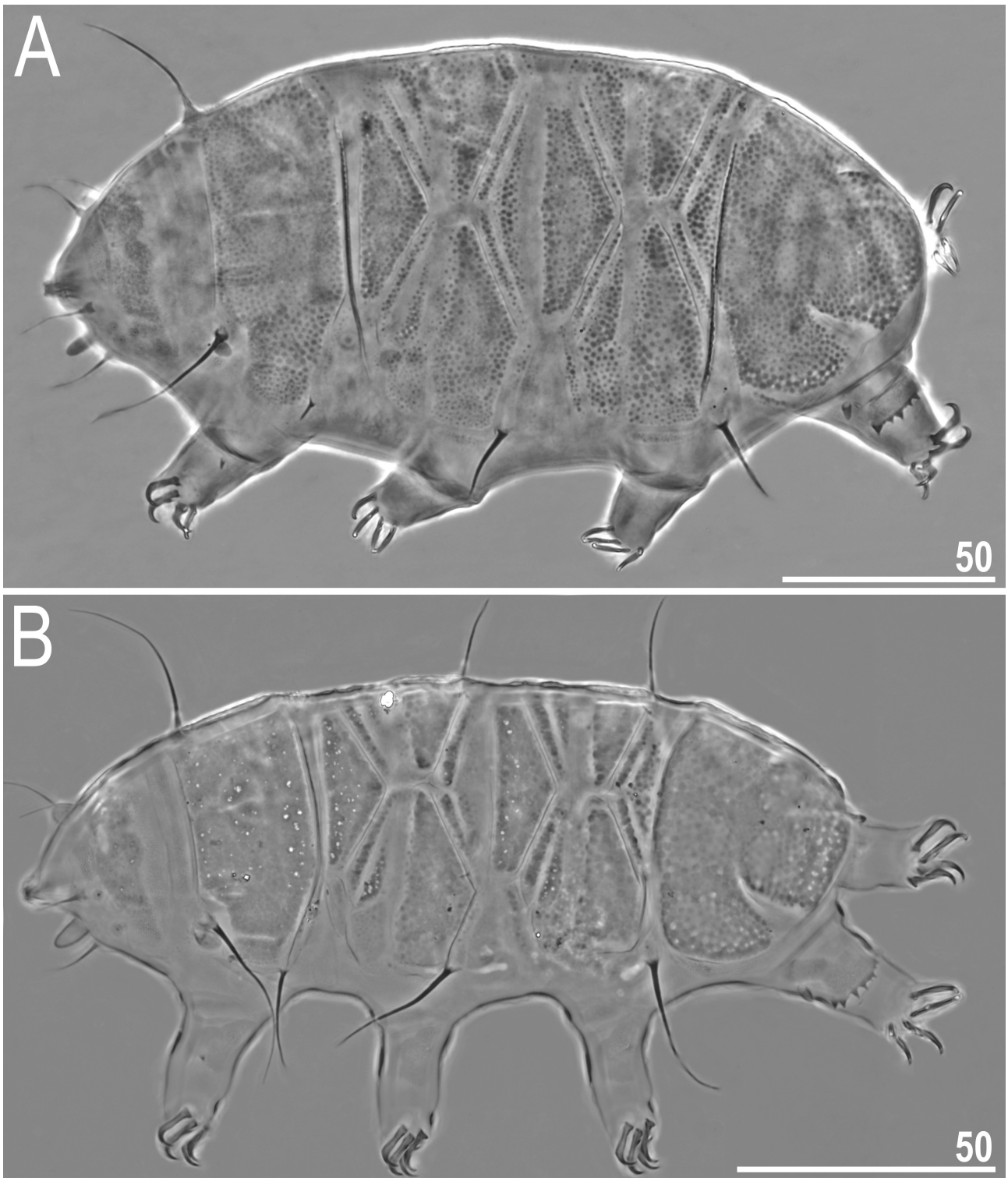

FIGURE 45. Habitus of *Echiniscus irroratus* **sp. nov.** (PCM): A—holotype, female in dorsal view, B—allotype, male in dorsolateral view. Scale bars = 50 µm.

Description. Mature females (*i.e*. from the third instar onwards; measurements and statistics in Table 24). Small *Echiniscus* with hyaline yellow body, and minute red eyes; body colour and eyes disappeared soon after mounting in Hoyer's medium. Dactyloid cephalic papillae (secondary clavae) and (primary) clavae (Fig. 45A, 46); cirri growing out from bulbous cirrophores. Cirri *A* short. Body appendage formula highly unstable: *A-(B)-(C)-(D)-(D^{d})-(E)*, with trunk appendages formed as short cirri (Fig. 46), very often lacking asymmetrically (Fig. 47). Two specimens unappendaged (Fig. 46C). One specimen with supernumerary spines on the posterior margins of paired segmental plates I–II (Fig. 46A).

Dorsal plates with dominant epicuticular multangular and circular granules visible as large dark dots under PCM (Fig. 45A, 46, 47), which may be faint (Fig. 46A); pores either absent (Fig. 45A) or sparse and distributed in all plates (Fig. 46A–B), but in some specimens mainly in the scapular plate (Fig. 46C, 47). The cephalic plate with an anterior chalice-like incision (Fig. 46A–B). The cervical (neck) plate poorly developed as a narrow, rectangular belt before the scapular plate. The scapular plate with poorly developed median longitudinal groove and lateral sutures (Fig. 46A–B), sometimes the median groove absent (Fig. 45A, 46C, 47). Median plate 1 and the posterior portion of the m2 equal in size, and of the same shape and sculpturing; sculpturing on the anterior portion of m2 and m3 identically poorly developed. Anterior and posterior portions of paired segmental plates I–II dissimilar in size, but of similar sculpturing. The caudal (terminal) plate with two short incisions and variously developed facets: either absent (Fig. 45A, 47) or evident (Fig. 46A–B). Ventral cuticle with minute endocuticular pillars distributed throughout the whole venter; ventral plates present: a pair in the subcephalic row and a pair of genital plates. Sex-partite gonopore placed between genital plates, and a trilobed anus between legs IV.

Pedal plates absent, pulvini present and clearly visible (Fig. 46A, C). Minute spine on leg I and a tiny papilla on leg IV present (Fig. 45A, 46A, C). Claws IV slightly higher than claws I–III. All external claws spurless. Internal claws heteromorphic: claws I–III with smaller spurs positioned at *ca.* 25% of the claw, but claws IV with large, highly divergent spurs positioned at *ca.* 30% of the claw (Fig. 48C–D).

Mature males and sexually dimorphic traits (*i.e*. from the third instar onwards). Smaller and with a more elongated body than females (body length 159 µm, scapular plate length 25.0 µm in the only male mounted on a microscope slide; Fig. 45B). Cephalic appendages lengths: *cirrus internus* 9.6 µm, cephalic papilla 7.4 µm, *cirrus externus* 15.9 µm, (primary) clava 6.4 µm. Body appendage configuration *A-B-C-D*, all appendages in the form of cirri: *A* 35.5 µm, *B* 20.6 µm, *C* 27.7 µm, *D* 32.1 µm. Epicuticular granules poorly visible, pores scarce. Subcephalic plates large and oval (Fig. 48A); much smaller and trapezoid genital plates (Fig. 48B). Leg appendages lengths: spine I 1.1. µm, papilla IV 3.3 µm. Dentate collar IV with nine teeth. Claw heights: 7.6–10.7 µm; internal spurs: 1.9–2.4 µm. Gonopore circular.

Juveniles (*i.e*. the second instar). No gonopore, but qualitatively look like females.

Larvae. Unknown.

Eggs. Unknown.

DNA markers and phylogenetic position. The closest relatives of *E. irroratus* **sp. nov.** are *E. capensis* **sp. nov.** and *E. gracilis* **sp. nov.**, the latter being a sister species (Fig. 117). The species closest in ITS is *E. gracilis* **sp. nov.** (ITS-1: p-distance = 3.1%, ITS-2: 1.8%).

Type material. 7 ♀♀, 1 ♂, 1 specimen of unknown sex on slides ZA.502.09, ZA.504.01–2, 4, 6; holotype: mature ♀ on slide ZA.504.04. Mounted together with 5 ♀♀ of *E. dentatus* **sp. nov.** One individual used for DNA extraction.

Type locality. 33°59'44.4"S, 18°58'52.2"E, 480 m asl: Republic of South Africa, Western Cape, Jonkershoek Nature Reserve; fynbos in a river bank, mosses and lichens from rocks partially submerged by water (samples ZA.502 and ZA.504).

Etymology. From Latin *irroro* = to sprinkle, referring to the sculpture of the species, whose cuticle is sprinkled by regular granules. A participle in the nominative singular.

Geographic distribution. Only recorded from South Africa, uncommon and restricted to the Western Cape (Fig. 120H).

Remarks. Small populations or single specimens of *E. irroratus* **sp. nov.** were almost always accompanied by the much commoner *E. dentatus* **sp. nov.**

Differential diagnosis. See above for the distinction between *E. irroratus* **sp. nov.** and the two most similar species: *E. capensis* **sp. nov.** and *E. gracilis* **sp. nov.**

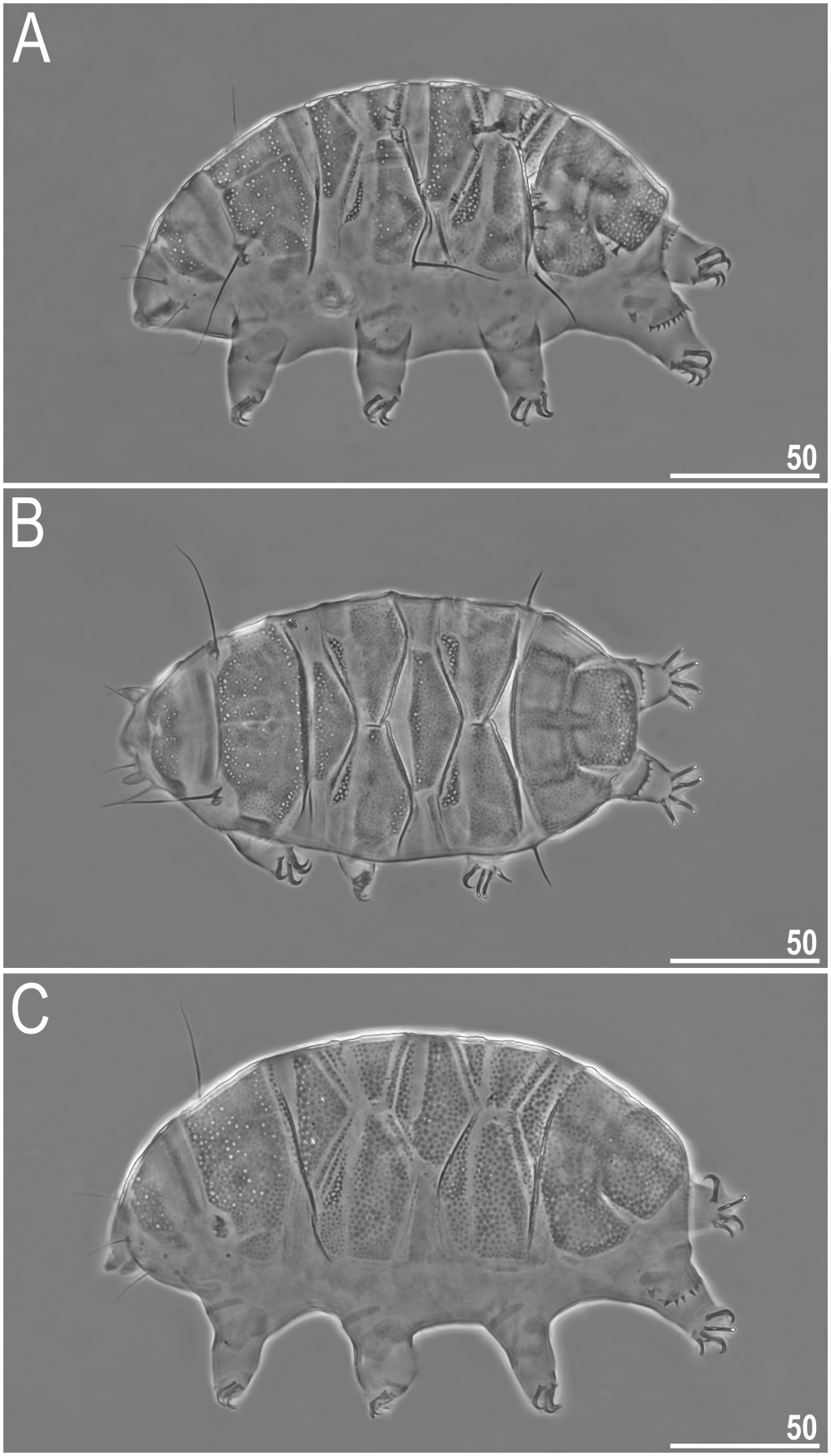

FIGURE 46. Intraspecific variability of *Echiniscus irroratus* **sp. nov.** (PCM, females): A—lateral view (numerous additional spicules present along the margins of paired segmental plates), B—dorsal view (exclusively short cirri *D* present), C—dorsolateral view (trunk appendages absent). Scale bars = 50 μm.

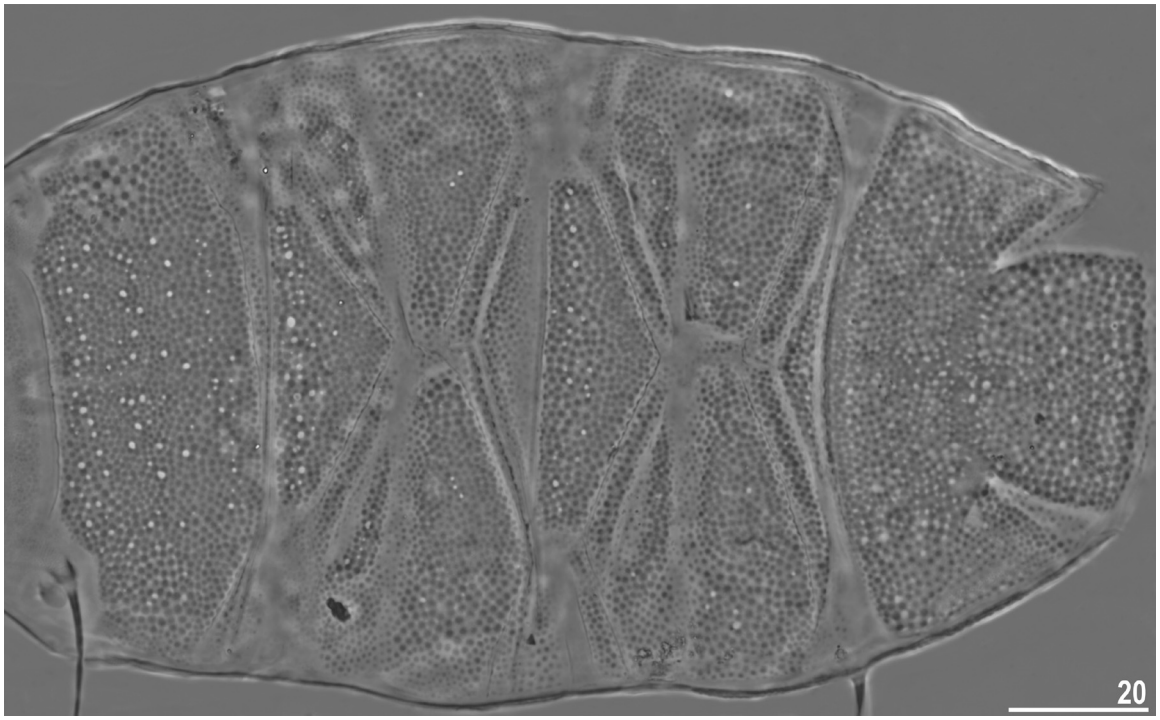

FIGURE 47. Dorsal sculpturing of *Echiniscus irroratus* **sp. nov.** in close-up (PCM, female). Scale bar = 20 μm.

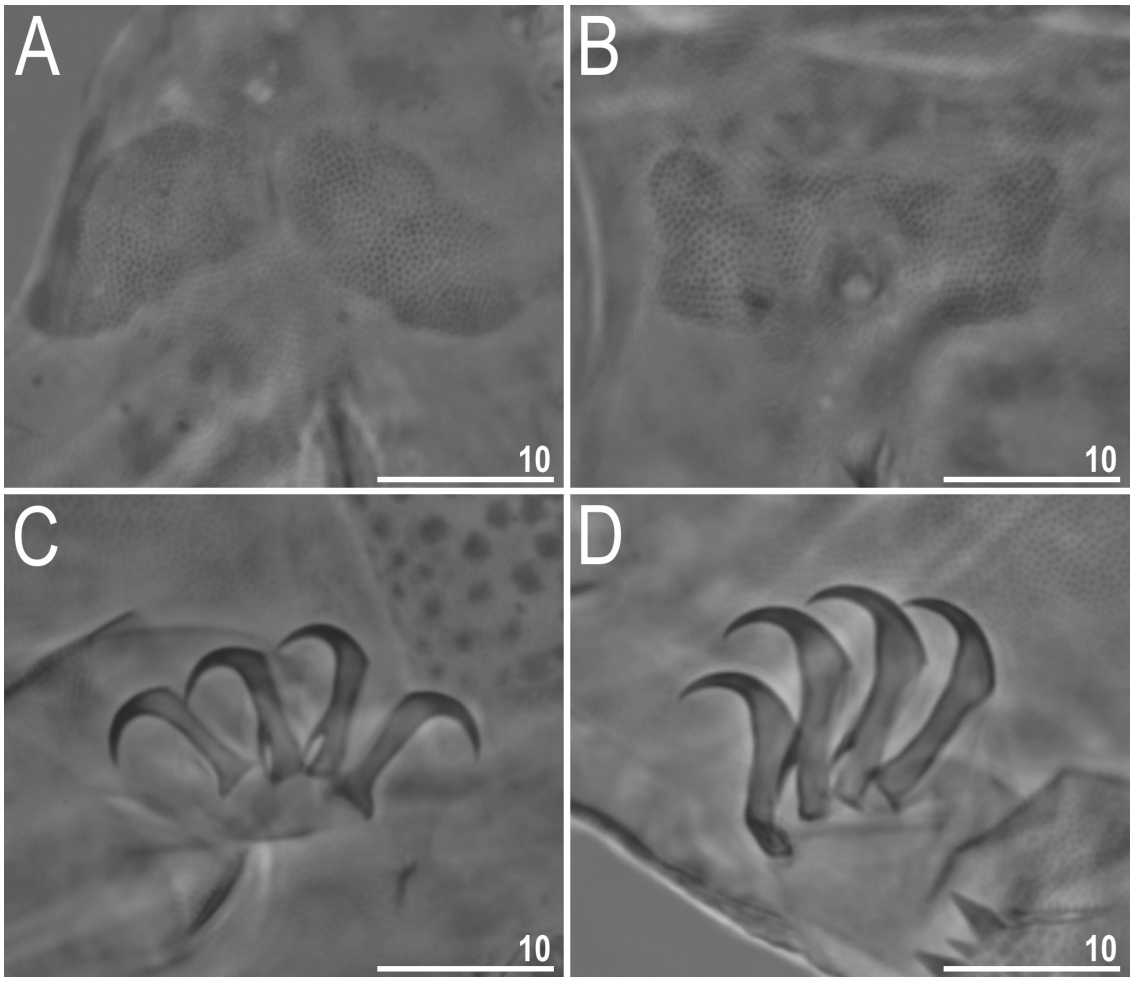

FIGURE 48. Ventral plates and claws of *Echiniscus irroratus* **sp. nov.** (PCM): A—subcephalic plates (male), B—genital plates (male), C—claws II (female), D—claws IV (female). Scale bars = 10 μm.

Raw measurements. Supplementary Materials (SM.03) and Tardigrada Register (www.tardigrada.net/register/0088.htm).

TABLE 24. Measurements [in µm] of selected morphological structures of the adult females of *Echiniscus irroratus* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Holotype	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	7	175	–	207	*492*	–	*673*	190	*591*	13	*56*	202	*673*
Scapular plate length	7	29.9	–	35.6		–		32.2	–	2.4	–	30.0	–
Head appendages lengths													
Cirrus *internus*	7	11.0	–	16.9	*35.7*	–	*53.3*	13.8	*43.0*	2.2	*7.0*	16.0	*53.3*
Cephalic papilla	7	6.3	–	7.9	*17.7*	–	*24.1*	6.9	*21.7*	0.6	*2.6*	7.0	*23.3*
Cirrus *externus*	7	15.0	–	21.4	*42.1*	–	*67.3*	17.7	*55.3*	2.6	*8.7*	20.2	*67.3*
Clava	7	4.1	–	5.4	*12.9*	–	*16.7*	4.8	*14.8*	0.4	*1.4*	5.0	*16.7*
Cirrus *A*	7	36.6	–	50.0	*105.7*	–	*146.0*	40.8	*126.8*	4.8	*13.5*	43.8	*146.0*
Cirrus *A*/Body length ratio	7	18%	–	29%		–		22%	–	3%	–	22%	–
Body appendages lengths													
Cirrus *B*	1	5.2	–	5.2	*15.9*	–	*15.9*	5.2	*15.9*	?	*?*	?	*?*
Cirrus *C*	4	18.6	–	30.0	*56.7*	–	*99.0*	23.9	*73.8*	5.8	*19.4*	?	*?*
Cirrus *D*	7	20.1	–	30.6	*61.3*	–	*101.7*	25.0	*77.9*	4.3	*13.7*	30.5	101.7
Cirrus D^d	2	2.1	–	3.3	*6.6*	–	*9.4*	2.7	*8.0*	0.8	*2.0*	?	*?*
Cirrus *E*	4	1.8	–	5.7	*6.0*	–	*18.8*	3.1	*9.9*	1.8	*6.0*	?	*?*
Spine on leg I length	7	1.4	–	2.3	*4.4*	–	*6.7*	2.0	*6.1*	0.3	*0.8*	1.8	*6.0*
Papilla on leg IV length	7	3.4	–	4.4	*9.6*	–	*14.5*	3.9	*12.3*	0.4	*1.9*	3.9	*13.0*
Number of teeth on the collar	7	9	–	14		–		11.3	–	1.8	–	10	–
Claw I heights													
Branch	7	8.6	–	11.3	*27.7*	–	*34.7*	9.8	*30.4*	1.0	*2.7*	10.4	*34.7*
Spur	6	2.3	–	3.3	*7.2*	–	*10.9*	2.8	*8.7*	0.3	*1.3*	?	*?*
Spur/branch height ratio	6	26%	–	33%		–		29%	–	3%	–	?	–
Claw II heights													
Branch	7	8.0	–	11.0	*26.5*	–	*33.7*	9.4	*29.3*	1.1	*2.6*	10.1	*33.7*
Spur	7	2.2	–	2.7	*6.9*	–	*8.6*	2.4	*7.6*	0.2	*0.7*	2.4	*8.0*
Spur/branch height ratio	7	23%	–	31%		–		26%	–	3%	–	24%	–
Claw III heights													
Branch	7	7.8	–	11.0	*26.1*	–	*33.3*	9.4	*29.1*	1.1	*2.6*	10.0	*33.3*
Spur	7	2.3	–	2.6	*6.5*	–	*8.6*	2.4	*7.5*	0.1	*0.7*	2.4	*8.0*
Spur/branch height ratio	7	23%	–	29%		–		26%	–	3%	–	24%	–
Claw IV heights													
Branch	7	10.0	–	12.3	*33.2*	–	*41.0*	11.3	*35.2*	0.9	*2.8*	12.3	*41.0*
Spur	5	2.3	–	3.2	*7.2*	–	*10.6*	2.8	*8.6*	0.3	*1.3*	2.7	9.0
Spur/branch height ratio	5	22%	–	30%		–		24%	–	3%	–	22%	–

14. Echiniscus latruncularis sp. nov. Gąsiorek, Vončina, Morek & Michalczyk

urn:lsid:zoobank.org:act:1AF47BCA-C0E6-43E8-BD4C-DA004B9DDF2B

Figures 49–52, Tables 25–27

Data source:

A total of 44 specimens (16 ♀♀, 14 ♂♂, 7 juveniles, and 7 specimens of unknown instar/sex):

- Sample ZA.502: 16 specimens (4 ♀♀, 5 ♂♂ and 1 juvenile on slides, 3 specimens used for DNA analyses, and 3 specimen used for SEM analysis on stub 19.02); found with *Cornechiniscus madagascariensis*, *Echiniscus dentatus* **sp. nov.**, *E. irroratus* **sp. nov.**, and *E. setaceus* **sp. nov.**
- Sample ZA.513: 6 specimens (3 ♀♀, 1 ♂ and 2 juveniles on slides); found with *Echiniscus gracilis* **sp. nov.**, *E. scabrospinosus*, and *E. setaceus* **sp. nov.**
- Sample ZA.542: 3 specimens (1 ♀, 1 ♂ and 1 juvenile on slides); found with *Echiniscus longispinosus* and *E. setaceus* **sp. nov.**
- Sample ZA.543: 1 specimen (1 ♀ on a slide); found with *Echiniscus longispinosus*.
- Sample ZA.544: 1 specimen (1 juvenile on a slide).
- Sample ZA.545: 9 specimens (2 ♀♀, 5 ♂♂ and 1 juvenile on slides, and 1 specimen used for DNA extraction and secured as a hologenophore).
- Sample ZA.553: 7 specimens (4 ♀♀, 2 ♂♂ and 1 juvenile on slides).
- Sample ZA.555: 1 specimen (1 ♀ on a slide); found with *Echiniscus dentatus* **sp. nov.**, *E. gracilis* **sp. nov.**, and *E. irroratus* **sp. nov.**

Description. Mature females (*i.e*. from the third instar onwards; measurements and statistics in Table 25). Large *Echiniscus* with dark orange, massive body (Fig. 49, 51, 52A) and large red eyes; body colour and eyes disappeared soon after mounting in Hoyer's medium. Dactyloid cephalic papillae (secondary clavae) and (primary) clavae (Fig. 49); cirri growing out from bulbous cirrophores. Cirri *A* short. Body appendage formula highly unstable: *A-(B)-C-C^{d}-D-(D^{d})-E*, with trunk appendages formed as extremely long, but stiff spines (Fig. 49, 51) of roughly equal lengths (Fig. 49B–C), or with spines *C* and *C^{d}* being the longest (Fig. 49A, 51, 52A). Trunk spine asymmetries common in the position *B* (Fig. 51).

Dorsal plates with pseudopores in the form of wide bright depressions intermingled with multangular elements of endocuticle connected by *striae* (Fig. 49, 51–52). Endocuticular elements have a tendency towards merging into larger, solid matrix (Fig. 49B), so plate surface becomes mostly uniform and smooth (Fig. 49C). This pattern is delusively similar to that characteristic for *Claxtonia vincula* (Horning *et al*. 1978, Pilato *et al*. 2005). The anterior portion of the median plate 2 and the posteriormost portion of m3 solely with epicuticular granules (Fig. 51, 52B). The cephalic plate with a poorly marked T-shaped anterior incision (Fig. 49A). The cervical (neck) plate poorly developed as a very narrow, discontinuous belt anterior to the scapular plate. The scapular plate with well-delimited, small rectangular lateral portions (Fig. 49, 52A). Anterior and posterior portions of paired segmental plates I–II dissimilar in size, but with identical sculpturing (Fig. 52C). The caudal (terminal) plate with two short, unsclerotised incisions and facets poorly visible under PCM (Fig. 49), but well-identifiable under SEM (Fig. 51). Ventral cuticle with minute endocuticular pillars distributed throughout the whole venter; ventral plates absent. Sexpartite gonopore placed anteriorly to legs IV, and a trilobed anus between legs IV.

Pedal plates I–III absent (Fig. 52A) or developed as dark irregular fields in the central portions of legs (Fig. 49B–C), but pedal plate IV present and weakly sculptured (Fig. 49A–B); pulvini present and clearly visible (Fig. 49B–C, 52A). A minute triangular spine on leg I and a papilla on leg IV (Fig. 49B–C, 50C, 51, 52A). Claws robust (Fig. 50C). Claws I–IV of similar heights. All external claws spurless. All internal claws with large, acute spurs positioned at *ca.* 30% of the claw (Fig. 48A–B).

Mature males and sexually dimorphic traits (*i.e*. from the third instar onwards; measurements and statistics in Table 26). Smaller and slenderer than females (Fig. 50A–B, see Tables 25–26). Body appendage configuration *A-B-C-C^{d}-D-D^{d}-E*. Peculiar dimorphism of males: some of them (type A) with tumescent primary and secondary clavae, large papillae IV, and long, massive limbs (Fig. 50A), whereas others (type B, commoner) with cephalic and leg appendages developed similarly to females, and thinner limbs (Fig. 50B). Claws shorter than in females (Fig. 50C, see Tables 25–26). Gonopore circular.

Juveniles (*i.e*. from the second instar onwards; measurements and statistics in Table 27). Smaller than adults, but qualitatively similar. Gonopore absent.

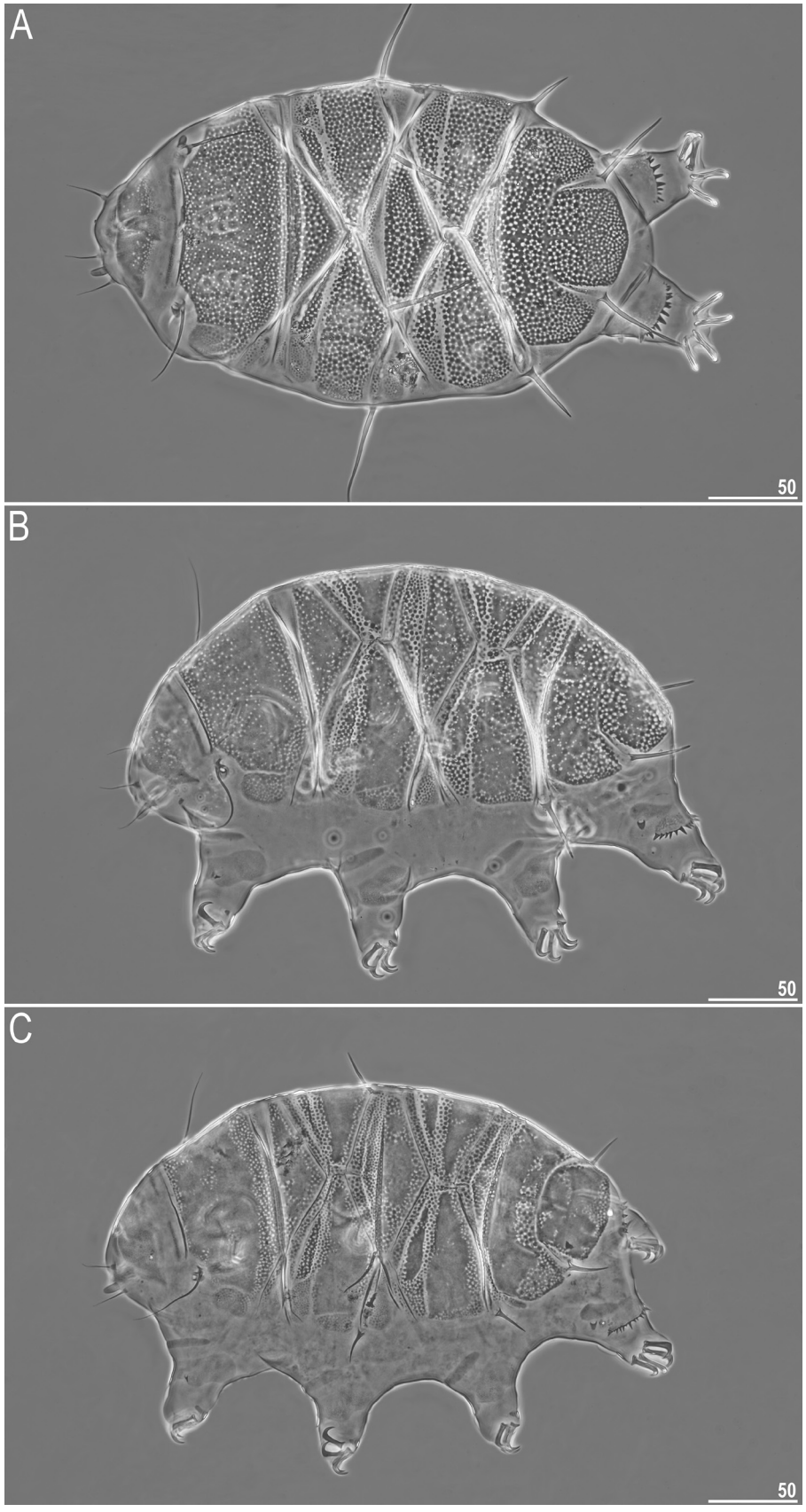

FIGURE 49. Habitus and intraspecific variability of females of *Echiniscus latruncularis* **sp. nov.** (PCM): A—holotype in dorsal view (typically formed sculpture), B—paratype in dorsolateral view (epicuticular matrix merged into uniform layer in many parts of dorsal plates), C—paratype in dorsolateral view (epicuticular matrix merged into uniform layer in most parts of dorsal plates, forming solid surface especially in the central portions of plates). Scale bars = 50 μm.

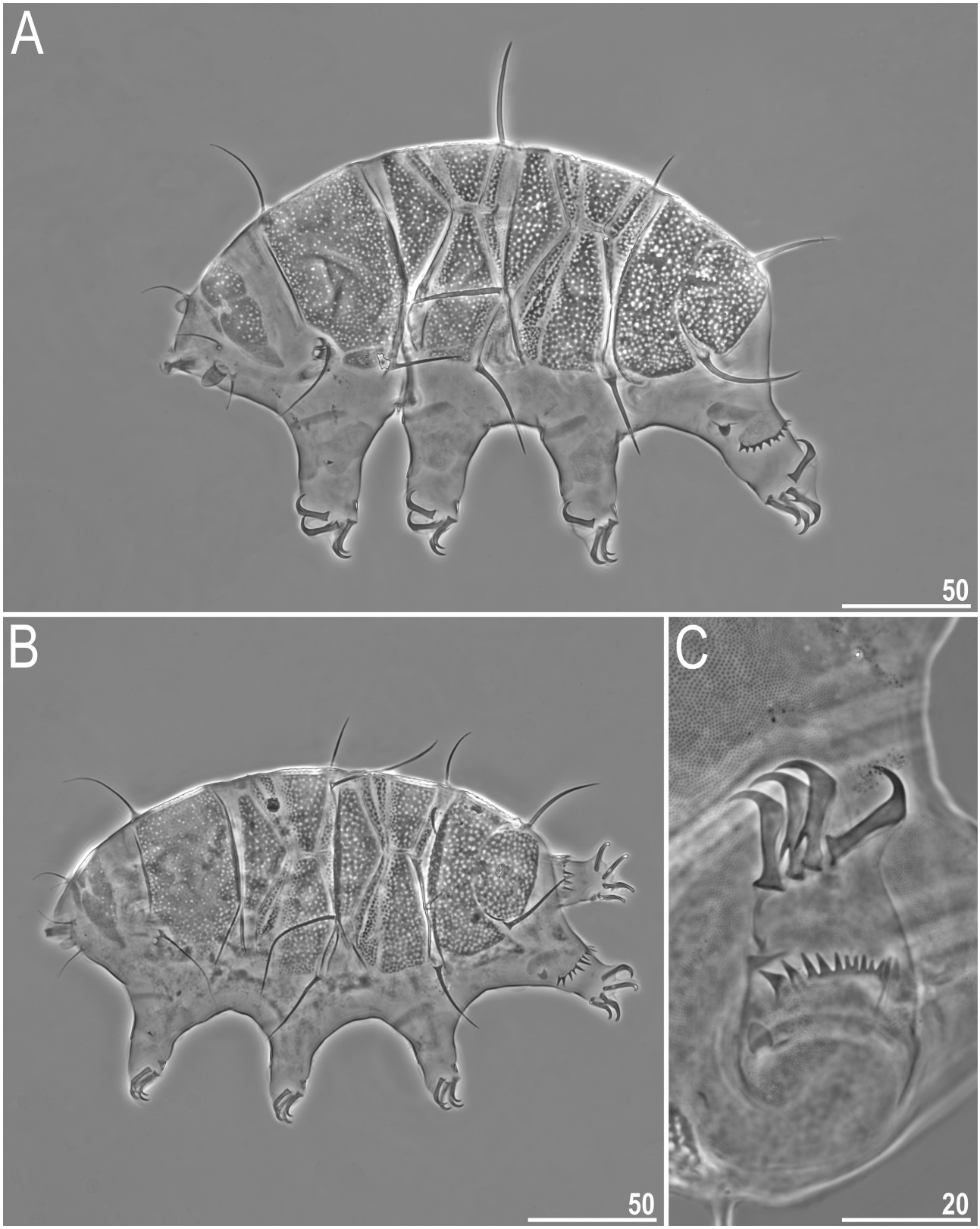

FIGURE 50. Habitus and dimorphism of males of *Echiniscus latruncularis* **sp. nov.** (PCM): A—allotype in dorsolateral view (♂ of the type *A* with cephalic papillae and papillae IV tumescent), B—paratype in dorsolateral view (♂ of the type *B* with cephalic papillae and papillae IV developed as in ♀), C—claws IV. Scale bars in μm.

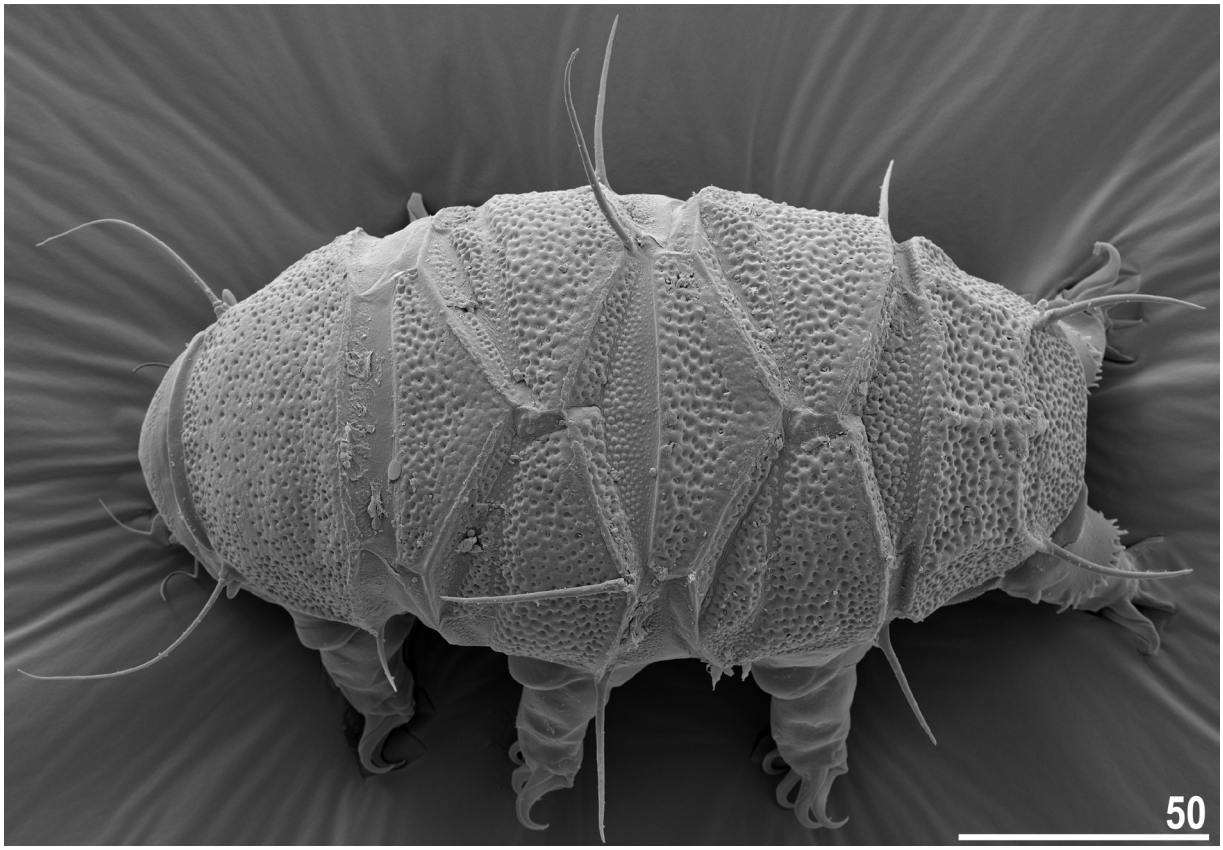

FIGURE 51. Habitus of *Echiniscus latruncularis* **sp. nov.** (SEM, female in dorsal view). Scale bar = 50 μm.

Larvae. Unknown.

Eggs. Unknown.

DNA markers and phylogenetic position. The species is the sister taxon of *E. scabrocirrosus* **sp. nov.** within the South-African endemic clade (Fig. 117). The species closest in COI is *E. attenboroughi* **sp. nov.** (p-distance = 11.7–11.9%), in ITS-1 and ITS-2—*E. scabrocirrosus* **sp. nov.** (1.4–2.3% and 0.9%, respectively).

Type material. 4 ♀♀, 5 ♂♂, 1 juvenile on slides ZA.502.04–8; holotype: mature ♀ on slide ZA.502.08, allotype: mature ♂ on slide ZA.502.07. Three specimens on a SEM stub 19.02. Three individuals used for DNA extraction.

Type locality. 33°59'44.4"S, 18°58'52.2"E, 480 m asl: Republic of South Africa, Western Cape, Jonkershoek Nature Reserve; fynbos in a river bank, mosses and lichens from rocks partially submerged by water (sample ZA.502).

Etymology. From Latin *latrunculi* = chess. A well-developed sculpture in this species (Fig. 49A) resembles a checkered chess board. An adjective in the nominative singular.

Geographic distribution. Only recorded from South Africa, rare and restricted to the Western Cape (Fig. 120C).

Remarks. Found always in a small number of specimens, together with populations of other echiniscids and macrobiotids.

Differential diagnosis. *E. latruncularis* **sp. nov.** is similar to *E. laterosetosus* and *E. polygonalis* by the dense polygonal dorsal sculpturing (Ito 1993), however both species exhibit long lateral cirri and secondary spurs on external claws IV, absent in the new species. Two species resemble *E. latruncularis* **sp. nov.** by the appendage formula, but they differ from the new species:

- *E. dikenli*, recorded from Turkey (Maucci 1972), by the appendage *E* morphology (stiff spine in *E. latruncularis* **sp. nov.** *vs* filamentous cirrus in *E. dikenli*), and dorsal plate sculpturing (pseudopores in the form of wide depressions mixed with polygonal elements of endocuticle in *E. latruncularis* **sp. nov.** *vs* pores of the *spinulosus* type in *E. dikenli*);

- *E. elaeinae*, a likely New Zealand endemic (Pilato *et al*. 2005), by dorsal plate sculpturing (pseudopores in the form of wide depressions intermingled with multangular elements of endocuticle in *E. latruncularis* **sp. nov.** *vs* reticulum of the *E. granulatus* type in *E. elaeinae*), and the morphology of internal spurs (robust and positioned at *ca.* 30% of the claw height in *E. latruncularis* **sp. nov.** *vs* thin and positioned at *ca.* 25% of the claw height in *E. elaeinae*).

Raw measurements. Supplementary Materials (SM.03) and Tardigrada Register (www.tardigrada.net/register/0089.htm).

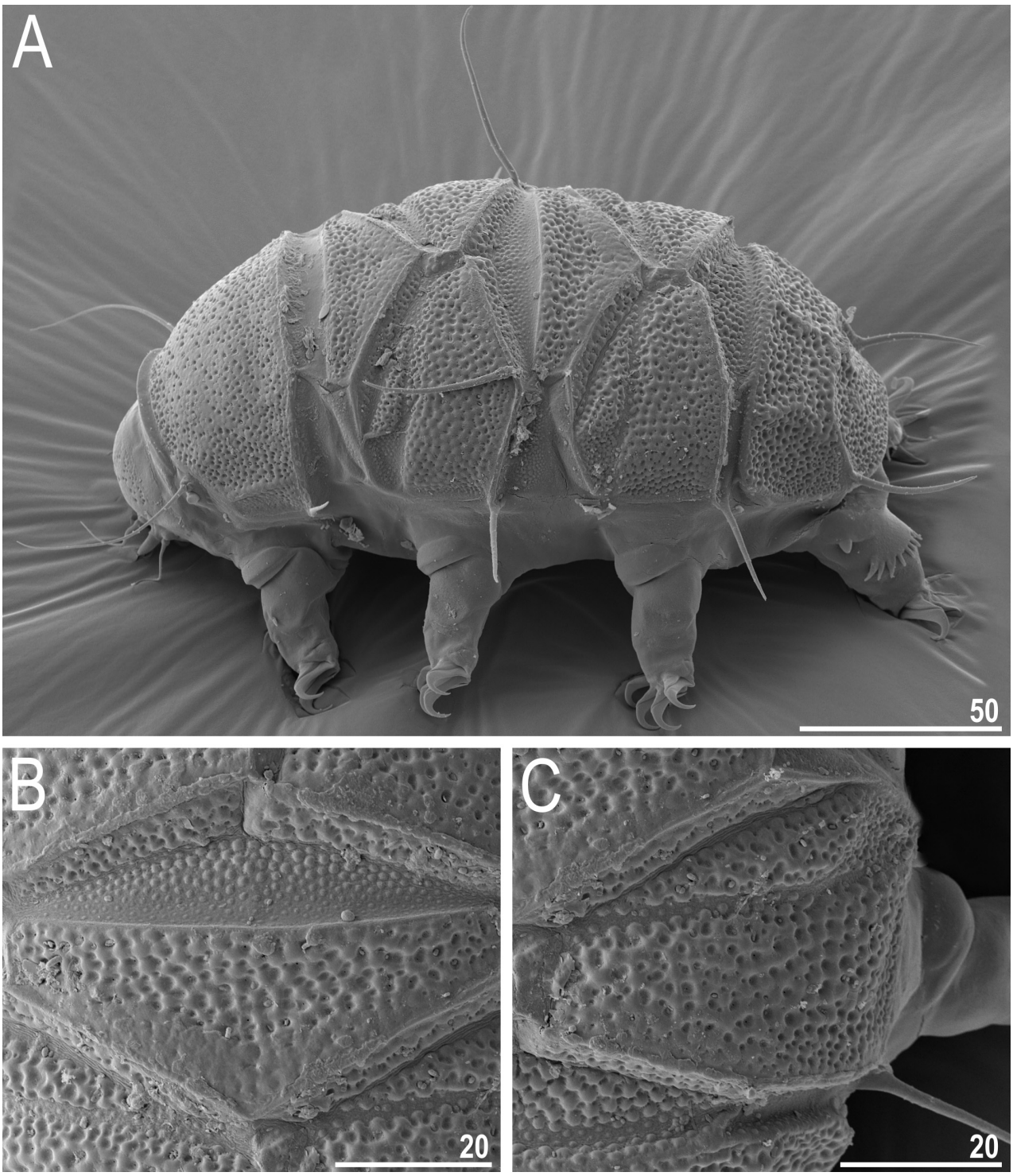

FIGURE 52. Dorsal sculpturing of *Echiniscus latruncularis* **sp. nov.** (SEM, female): A—dorsolateral view, B—median plate 2, C—segmental plate II. Scale bars in μm.

TABLE 25. Measurements [in µm] of selected morphological structures of the adult females of *Echiniscus latruncularis* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Holotype	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	10	257	–	358	*441*	–	*508*	305	*463*	30	*21*	314	*508*
Scapular plate length	10	57.7	–	75.8		–		65.8	–	5.8	–	61.9	–
Head appendages lengths													
Cirrus *internus*	9	15.9	–	26.2	*23.5*	–	*37.4*	20.5	*31.1*	2.9	*4.1*	20.3	*32.8*
Cephalic papilla	10	8.6	–	12.3	*12.9*	–	*17.9*	10.2	*15.5*	1.3	*2.0*	11.1	17.9
Cirrus *externus*	9	23.7	–	30.9	*38.0*	–	*41.7*	26.5	*40.1*	2.5	*1.5*	24.0	*38.8*
Clava	9	5.6	–	10.4	*8.0*	–	*14.4*	8.1	*12.4*	1.3	*2.1*	8.5	*13.7*
Cirrus *A*	9	46.5	–	70.2	*69.0*	–	*100.1*	52.5	*79.6*	7.4	*9.0*	46.5	*75.1*
Cirrus *A*/Body length ratio	9	15%	–	21%		–		17%	–	2%	–	15%	–
Body appendages lengths													
Appendage *B*	6	29.7	–	52.8	*46.8*	–	*75.3*	37.0	*54.7*	8.1	*10.6*	?	*?*
Appendage *C*	8	25.4	–	75.5	*44.0*	–	*111.5*	45.3	*68.8*	15.5	*22.2*	54.0	*87.2*
Appendage C^d	8	42.6	–	79.8	*59.9*	–	*113.8*	58.6	*87.5*	11.7	*16.9*	50.3	*81.3*
Appendage *D*	9	30.9	–	62.7	*49.2*	–	*89.4*	38.5	*58.2*	9.9	*12.9*	34.1	*55.1*
Appendage D^d	4	12.9	–	30.1	*20.8*	–	*39.7*	21.2	*30.2*	8.8	*10.6*	?	*?*
Appendage *E*	8	30.2	–	56.3	*42.5*	–	*83.2*	42.6	*65.0*	9.7	*13.2*	49.2	*79.5*
Spine on leg I length	9	2.6	–	5.7	*4.2*	–	*9.2*	4.3	*6.6*	1.0	*1.5*	5.7	*9.2*
Papilla on leg IV length	9	4.9	–	6.8	*7.7*	–	*10.7*	5.8	*8.9*	0.7	*1.1*	6.6	*10.7*
Number of teeth on the collar	8	10	–	12		–		11.3	–	0.9	–	12	–
Claw I heights													
Branch	8	17.0	–	21.2	*25.8*	–	*33.2*	18.6	*28.6*	1.4	*2.5*	18.9	*30.5*
Spur	8	3.1	–	6.2	*5.0*	–	*8.2*	4.5	*6.9*	0.9	*1.1*	5.0	*8.1*
Spur/branch height ratio	8	18%	–	29%		–		24%	–	4%	–	26%	–
Claw II heights													
Branch	7	16.8	–	20.3	*25.7*	–	*30.0*	18.2	*27.6*	1.3	*1.5*	?	*?*
Spur	7	3.9	–	5.1	*5.7*	–	*7.5*	4.5	*6.8*	0.5	*0.6*	?	*?*
Spur/branch height ratio	7	21%	–	29%		–		25%	–	3%	–	?	–
Claw III heights													
Branch	7	16.3	–	21.8	*25.6*	–	*33.8*	19.1	*29.2*	2.0	*2.8*	20.9	*33.8*
Spur	7	3.9	–	5.6	*5.6*	–	*8.0*	4.4	*6.7*	0.6	*0.8*	4.1	*6.6*
Spur/branch height ratio	7	20%	–	26%		–		23%	–	3%	–	20%	–
Claw IV heights													
Branch	6	18.0	–	22.9	*30.1*	–	*34.6*	20.5	*31.4*	1.7	*1.7*	?	*?*
Spur	6	4.6	–	5.7	*7.4*	–	*9.6*	5.3	*8.2*	0.4	*0.8*	?	*?*
Spur/branch height ratio	6	24%	–	28%		–		26%	–	1%	–	?	–

TABLE 26. Measurements [in µm] of selected morphological structures of the adult males of *Echiniscus latruncularis* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Allotype	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	10	195	–	268	*456*	–	*532*	231	*509*	19	*25*	232	*481*
Scapular plate length	10	37.8	–	50.7		–		45.5	–	3.9	–	48.1	–
Head appendages lengths													
Cirrus *internus*	6	9.1	–	24.0	*19.1*	–	*53.6*	18.1	*38.0*	5.9	*13.0*	123.0	*255.7*
Cephalic papilla	10	7.0	–	11.5	*18.5*	–	*24.4*	9.6	*21.1*	1.3	*1.9*	10.4	*21.6*
Cirrus *externus*	6	17.1	–	26.2	*41.6*	–	*56.8*	22.7	*49.5*	3.5	*6.3*	20.0	*41.6*
Clava	10	6.1	–	9.4	*12.8*	–	*21.2*	7.7	*17.0*	1.0	*2.5*	8.7	*18.1*
Cirrus *A*	9	30.6	–	53.2	*64.3*	–	*106.5*	42.1	*92.4*	6.6	*14.9*	40.3	*83.8*
Cirrus *A*/Body length ratio	9	14%	–	22%		–		18%	–	3%	–	17%	–
Body appendages lengths													
Appendage *B*	9	20.8	–	35.7	*46.2*	–	*82.4*	29.7	*64.5*	4.6	*12.1*	27.8	57.8
Appendage *C*	9	33.4	–	55.0	*82.4*	–	*122.8*	43.2	*94.4*	6.2	*12.0*	41.3	*85.9*
Appendage C^d	10	40.1	–	63.7	*89.1*	–	*133.8*	50.1	*110.8*	7.2	*17.9*	44.3	*92.1*
Appendage *D*	9	24.0	–	46.0	*47.3*	–	*96.6*	32.4	*72.4*	6.4	*13.8*	32.6	*67.8*
Appendage D^d	8	9.6	–	20.6	*19.3*	–	*45.8*	11.7	*26.5*	3.7	*8.2*	?	*?*
Appendage *E*	8	33.2	–	47.6	*73.8*	–	*107.4*	39.6	*87.9*	5.1	*11.0*	44.8	*93.1*
Spine on leg I length	10	2.9	–	4.6	*6.0*	–	*10.3*	3.4	*7.6*	0.5	*1.3*	2.9	*6.0*
Papilla on leg IV length	9	4.2	–	5.9	*9.7*	–	*13.8*	5.2	*11.5*	0.5	*1.3*	5.3	*11.0*
Number of teeth on the collar	8	5	–	13		–		10.9	–	2.5	–	13	–
Claw I heights													
Branch	7	12.7	–	16.6	*27.4*	–	*34.9*	14.5	*31.9*	1.3	*3.0*	16.6	*34.5*
Spur	7	3.1	–	4.0	*7.5*	–	*8.7*	3.7	*8.1*	0.4	*0.5*	4.0	*8.3*
Spur/branch height ratio	7	23%	–	29%		–		26%	–	2%	–	24%	–
Claw II heights													
Branch	6	12.1	–	15.4	*27.2*	–	*32.7*	14.0	*30.5*	1.2	*2.1*	15.4	*32.0*
Spur	6	2.7	–	4.6	*6.7*	–	*9.1*	3.8	*8.1*	0.7	*1.0*	3.2	6.7
Spur/branch height ratio	6	21%	–	31%		–		27%	–	4%	–	21%	–
Claw III heights													
Branch	5	11.4	–	17.1	*27.8*	–	*35.6*	14.6	*32.5*	2.1	*3.4*	17.1	*35.6*
Spur	5	3.0	–	4.2	*6.9*	–	*9.4*	3.5	*7.8*	0.5	*1.0*	3.4	*7.1*
Spur/branch height ratio	5	20%	–	28%		–		24%	–	4%	–	20%	–
Claw IV heights													
Branch	4	16.2	–	19.4	*32.0*	–	*41.1*	17.9	*38.4*	1.3	*4.3*	19.4	*40.3*
Spur	4	3.8	–	4.4	*8.1*	–	*9.1*	4.1	*8.7*	0.3	*0.4*	3.9	*8.1*
Spur/branch height ratio	4	20%	–	27%		–		23%	–	3%	–	20%	–

TABLE 27. Measurements [in µm] of selected morphological structures of the juveniles of *Echiniscus latruncularis* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD	
		µm			*sp*			µm	*sp*	µm	*sp*
Body length	5	140	–	186	*417*	–	*550*	168	*484*	20	*53*
Scapular plate length	5	31.2	–	38.0		–		34.8	–	3.0	–
Head appendages lengths											
Cirrus *internus*	4	10.5	–	11.0	*27.6*	–	*32.8*	10.8	*30.3*	0.3	*2.3*
Cephalic papilla	5	5.4	–	8.6	*16.3*	–	*22.6*	6.5	*18.7*	1.2	*2.5*
Cirrus *externus*	4	11.0	–	18.3	*34.1*	–	*48.2*	14.2	*39.5*	3.1	*6.1*
Clava	5	5.4	–	8.5	*14.7*	–	*27.2*	6.3	*18.3*	1.3	*5.1*
Cirrus *A*	4	27.3	–	37.7	*73.0*	–	*99.2*	30.7	*86.0*	4.8	*11.6*
Cirrus *A*/Body length ratio	4	16%	–	20%		–		17%	–	2%	–
Body appendages lengths											
Appendage *B*	4	13.8	–	30.1	*42.7*	–	*80.5*	21.4	*59.3*	7.0	*16.1*
Appendage *C*	4	19.9	–	29.6	*55.3*	–	*91.6*	23.1	*68.4*	4.4	*16.9*
Appendage C^d	2	30.7	–	37.8	*87.5*	–	*117.0*	34.3	*102.2*	5.0	*20.9*
Appendage *D*	2	18.5	–	21.0	*52.7*	–	*65.0*	19.8	*58.9*	1.8	*8.7*
Appendage D^d	5	7.5	–	11.3	*23.2*	–	*32.2*	9.1	*26.2*	1.7	*3.7*
Appendage *E*	3	21.6	–	38.9	*66.9*	–	*104.0*	28.5	*83.7*	9.2	*18.8*
Spine on leg I length	2	2.5	–	3.0	*7.1*	–	*9.3*	2.8	*8.2*	0.4	*1.5*
Papilla on leg IV length	5	2.8	–	4.0	*9.0*	–	*11.1*	3.4	*9.8*	0.6	*1.0*
Number of teeth on the collar	3	10	–	12		–		10.7	–	1.2	–
Claw I heights											
Branch	4	9.1	–	9.9	*25.7*	–	*30.7*	9.6	*28.2*	0.3	*2.2*
Spur	4	2.1	–	2.3	*6.1*	–	*6.8*	2.2	*6.6*	0.1	*0.3*
Spur/branch height ratio	4	22%	–	24%		–		23%	–	1%	–
Claw II heights											
Branch	3	8.7	–	11.8	*26.2*	–	*31.1*	10.1	*28.4*	1.6	*2.5*
Spur	3	2.3	–	2.6	*6.7*	–	*7.4*	2.5	*7.0*	0.2	*0.4*
Spur/branch height ratio	3	22%	–	26%		–		25%	–	2%	–
Claw III heights											
Branch	4	8.8	–	12.1	*25.1*	–	*31.8*	9.9	*27.9*	1.5	*2.9*
Spur	4	2.1	–	2.6	*5.6*	–	*7.1*	2.3	*6.4*	0.2	*0.6*
Spur/branch height ratio	4	21%	–	25%		–		23%	–	2%	–
Claw IV heights											
Branch	3	11.3	–	15.0	*33.3*	–	*39.5*	12.7	*35.9*	2.0	*3.2*
Spur	3	2.6	–	3.6	*8.0*	–	*9.5*	3.1	*8.9*	0.5	*0.7*
Spur/branch height ratio	3	23%	–	27%		–		25%	–	2%	–

15. Echiniscus lichenorum Maucci, 1983

Figures 53–56, Tables 28–30

Data source:

A total of 205 specimens (126 ♀♀, 3 ♂♂, 12 juveniles, 5 larvae, and 59 specimens of unknown instar/sex):

- Sample ZA.010: 53 specimens (37 ♀♀, 1 ♂ and 1 larva on slides, 10 specimens on SEM stub 17.10, and 4 specimens used for DNA extraction)
- Sample ZA.011: 1 specimen (1 ♀ on a slide).
- Sample ZA.015: 50 specimens (25 ♀♀, 4 juveniles and 1 specimen of unknown sex on slides, and 20 specimens on SEM stub 19.07); found with *Echiniscus attenboroughi* **sp. nov.**, *E. draconis* **sp. nov.**, *E. setaceus* **sp. nov.**, and *E. virginicus*.
- Sample ZA.020: 7 specimens (4 ♀♀ and 3 juveniles on slides); found with *Echiniscus dentatus* **sp. nov.**, *E. draconis* **sp. nov.**, *E. longispinosus*, and *E. setaceus* **sp. nov.**
- Sample ZA.022: 1 specimen (1 ♀ on a slide); found with *Echiniscus attenboroughi* **sp. nov.**, *E. dentatus* **sp. nov.**, *E. gracilis* **sp. nov.**, *E. longispinosus*, and *E. setaceus* **sp. nov.**
- Sample ZA.040: 15 specimens (8 ♀♀, 2 ♂♂ and 1 larva on slides, 4 specimens used for DNA extraction).
- Sample ZA.093: 3 specimens (3 ♀♀ on slides); found with *Echiniscus marginatus*.
- Sample ZA.096: 1 specimen (1 ♀ on a slide); found with *Echiniscus gracilis* **sp. nov.**, *E. longispinosus*, and *E. setaceus* **sp. nov.**
- Sample ZA.097: 2 specimens (2 ♀♀ on a slide); found with *Echiniscus scabrospinosus*.
- Sample ZA.098: 21 specimens (18 ♀♀, 1 juvenile and 2 larvae on slides); found with *Echiniscus draconis* **sp. nov.**, *E. marginatus*, and *E. scabrospinosus*.
- Sample ZA.218: 2 specimens (2 ♀♀ on a slide); found with *Echiniscus draconis* **sp. nov.**, *E. intricatus* **sp. nov.**, and *E. tetraspinosus* **sp. nov.**
- Sample ZA.240: 9 specimens (8 ♀♀ and 1 larva on slides).
- Sample ZA.360: 1 specimen (1 ♀ on a slide); found with *Echiniscus draconis* **sp. nov.**, *E. longispinosus*, and *E. scabrospinosus*.
- Sample ZA.431: 7 specimens (6 ♀♀ and 1 juvenile on slides); found with *Echiniscus draconis* **sp. nov.**, *E. imitans* **sp. nov.**, and *E. scabrospinosus*.
- Sample ZA.450: 32 specimens (10 ♀♀ and 2 juveniles on slides, and 20 frozen specimens); found with *Echiniscus draconis* **sp. nov.**
- New Iberian records: Spain, Andalucía, Sierra de Hornachuelos, Las Herrerías: Sample ES.156: 37°50’48.42”N, 5°15’44.22”W, 286 m asl, moss+lichen from a tree in a lucid mixed cork oak-oak forest (24 specimens: 13 ♀♀, 1 ♂, 4 juveniles on slides, and 6 specimens used for DNA extraction); Sample ES.162: 37°50’30.96”N, 5°15’44.52”W, 290 m asl, lichen from a tree in the same forest (8 specimens: 3 ♀♀, 1 ♂, 1 juvenile on slides, and 3 specimens used for DNA extraction); Sample ES.166: 37°50’55.32”N, 5°15’42.78”W, 254 m asl, lichen from a tree branch in the same forest (10 specimens: 8 ♀♀ on slides and 2 specimens used for DNA extraction); coll. 18.04.2018, Piotr Gąsiorek & Witold Morek.

Literature:

- Original description: Maucci (1983).

Description. Mature females (*i.e.* from the third instar onwards; measurements and statistics in Table 28). Medium-sized *Echiniscus* with dark orange, massive body (Fig. 53A, 54) and large red eyes; body colour and eyes disappeared soon after mounting in Hoyer’s medium. Dactyloid cephalic papillae (secondary clavae) and (primary) clavae (Fig. 53A); cirri growing out from bulbous cirrophores. Cirri *A* short. Body appendage formula *A-B-C-C^{d}-D-D^{d}*, with trunk appendages formed as long spines (usually dorsal) or reduced cirri (typically lateral), highly stable (Fig. 53A, 54) and extremely rarely asymmetric. Lateral appendages with broad triangular bases, dorsal ones with evident double structure, its outer layer thick and dark.

Dorsal plates resembling the *E. quadrispinosus*-type sculpture, *i.e.* a network of dense (dark under PCM) cuticular matrix with pores of various sizes and shapes (Fig. 53A and 54). The sculpture, however, may exhibit considerable variation depending on the size and proportions of cuticular matrix and pores. Specifically, sometimes the

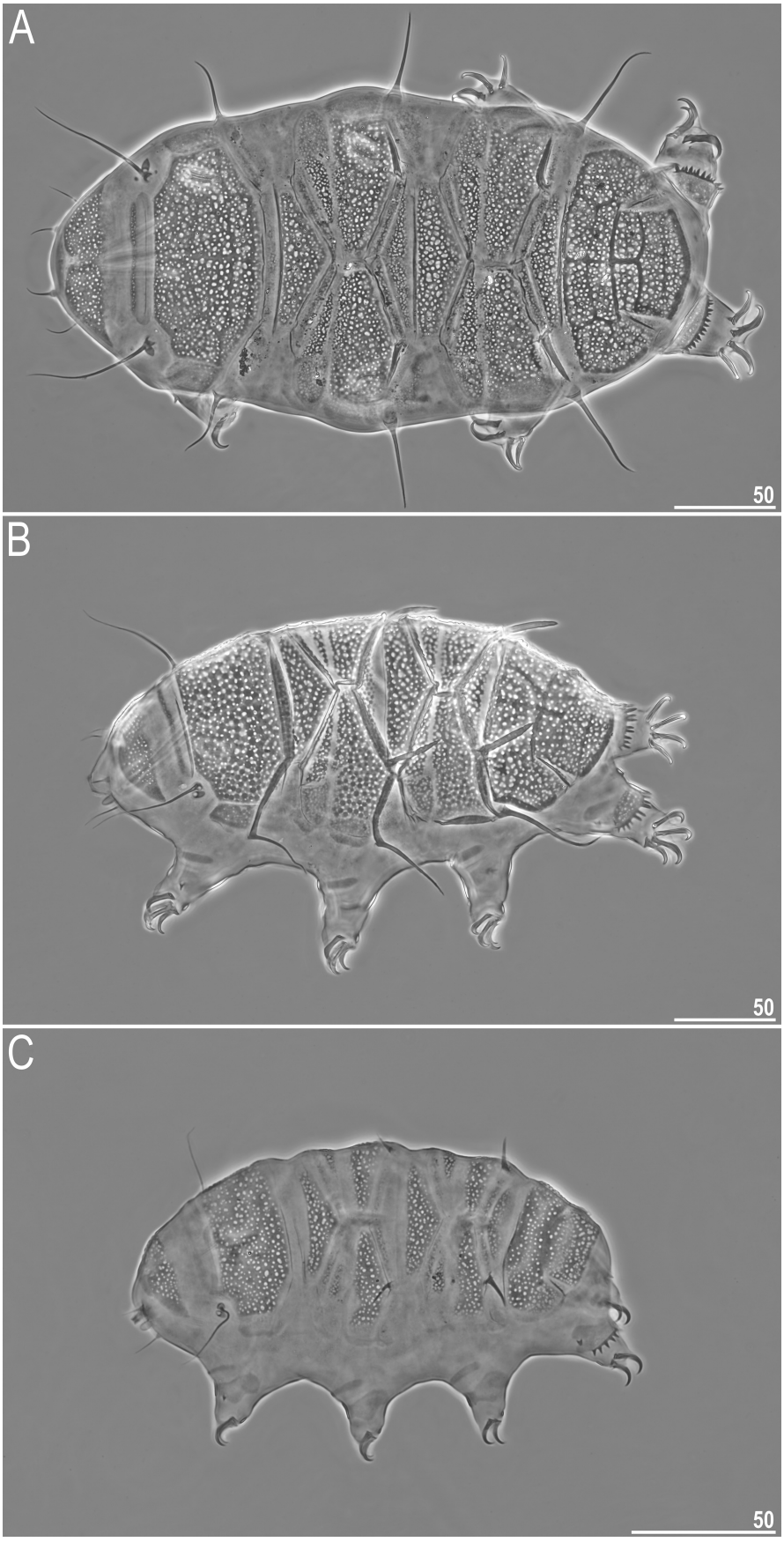

FIGURE 53. Habitus and intraspecific variability of *Echiniscus lichenorum* Maucci, 1983 (PCM): A—female, dorsal view, B—male, dorsolateral view, C—larva, dorsolateral view. Scale bars = 50 μm.

knots of the reticulum form granules that are connected via *striae* (pores in such cases are the spaces between the *striae*; Fig. 53B and 54A). In some specimens, the granules are more evident and tightly arranged with small and sparse pores present in between the granules where endocuciular matrix is absent (Fig. 55A). The cephalic plate with an anterior incision. The cervical (neck) plate sculptured only in its anteriormost portion, thick and adjacent to the scapular plate (Fig. 53A). The scapular plate large, with well-delimited, small rectangular lateral portions delimited by poreless sutures (Fig. 53A, 55A); a median and two transverse weakly porous and weakly outlined ridges/sutures, the transverse ridges join laterally (Fig. 53A). Anterior and posterior portions of paired segmental plates I–II dissimilar in size, but with identical sculpturing (Fig. 53A, 54, 55A). The caudal (terminal) plate with two short, sclerotised incisions and facets formed by a median, two lateral and three transverse weakly porous ridges/sutures (Fig. 53A, 54A). Ventral cuticle with minute endocuticular pillars distributed throughout the whole venter; ventral plates absent. Sexpartite gonopore placed anteriorly to legs IV, and a trilobed anus between legs IV.

Pedal plates I–III absent, but pedal plate IV present (sculptured and with the dentate collar; Fig. 53A, 54B, 55D); pulvini present. A spine on leg I and a papilla on leg IV present (Fig. 54B). Claws large and with relatively small internal spurs compared to the size of the branch, positioned at *ca.* 20–25% of the claw (Fig. 55B–D). Claws IV longer than claws I–III. All external claws spurless.

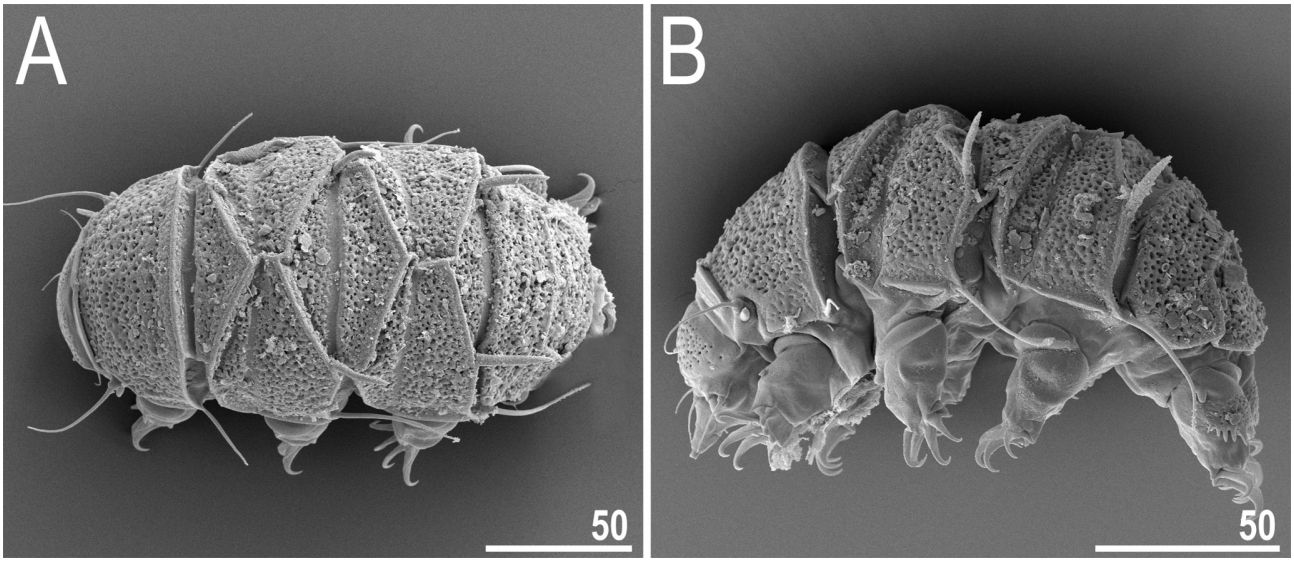

FIGURE 54. Habitus of *Echiniscus lichenorum* (SEM): A—female, dorsal view, B—female, lateral view. Scale bars = 50 µm.

Mature males and sexually dimorphic traits (*i.e.* from the third instar onwards; measurements and statistics in Table 29). Smaller and slenderer than females (Fig. 53B, compare Tables 28–29). Claws I–III shorter than in females. Gonopore circular.

Juveniles (*i.e.* from the second instar onwards). No gonopore. Qualitatively similar to adults, but with less developed dorsal sculpture. Exemplary morphometric data for a single specimen: body length 188 µm, scapular plate length 39.1 µm; cephalic appendages: *cirrus internus* 8.4 µm, cephalic papilla 4.3 µm, (primary) clava 5.3 µm, cirrus *A* 35.7 µm; trunk appendages: spine *B* 18.0 µm, spine *C* 22.0 µm, spine C^d 17.7 µm, spine *D* 32.2 µm; claws 11.1–15.5 µm, spurs 1.7–2.0 µm.

Larvae (*i.e.* the first instar; measurements and statistics in Table 30). Gonopore and anus absent. Clearly smaller than subsequent life stages. Body appendage formula *A*-C^d-D^d (Fig. 53C).

Eggs. Up to three eggs per exuvia were found.

DNA markers and phylogenetic position. *Echiniscus lichenorum* is the sister species of *E. similaris* **sp. nov.** (Fig. 117). The species closest in COI is *E. similaris* **sp. nov.** (p-distance = 1.2–1.8%), and in ITS—*E. draconis* **sp. nov.** (ITS-1: 0.6–3.1%, ITS-2: 0.3–1.2%). Intraspecific p-distances are as follows: COI—2.0%, ITS-1—0.3–0.6%, ITS-2—0.3%.

Etymology. From Latin *lichenorum* = associated with lichens. Maucci (1983) isolated the first specimens belonging to this species from lichen thalli. In South Africa, this species also exhibits strong lichenophilous preferences (~90% of samples with *E. lichenorum* were lichens).

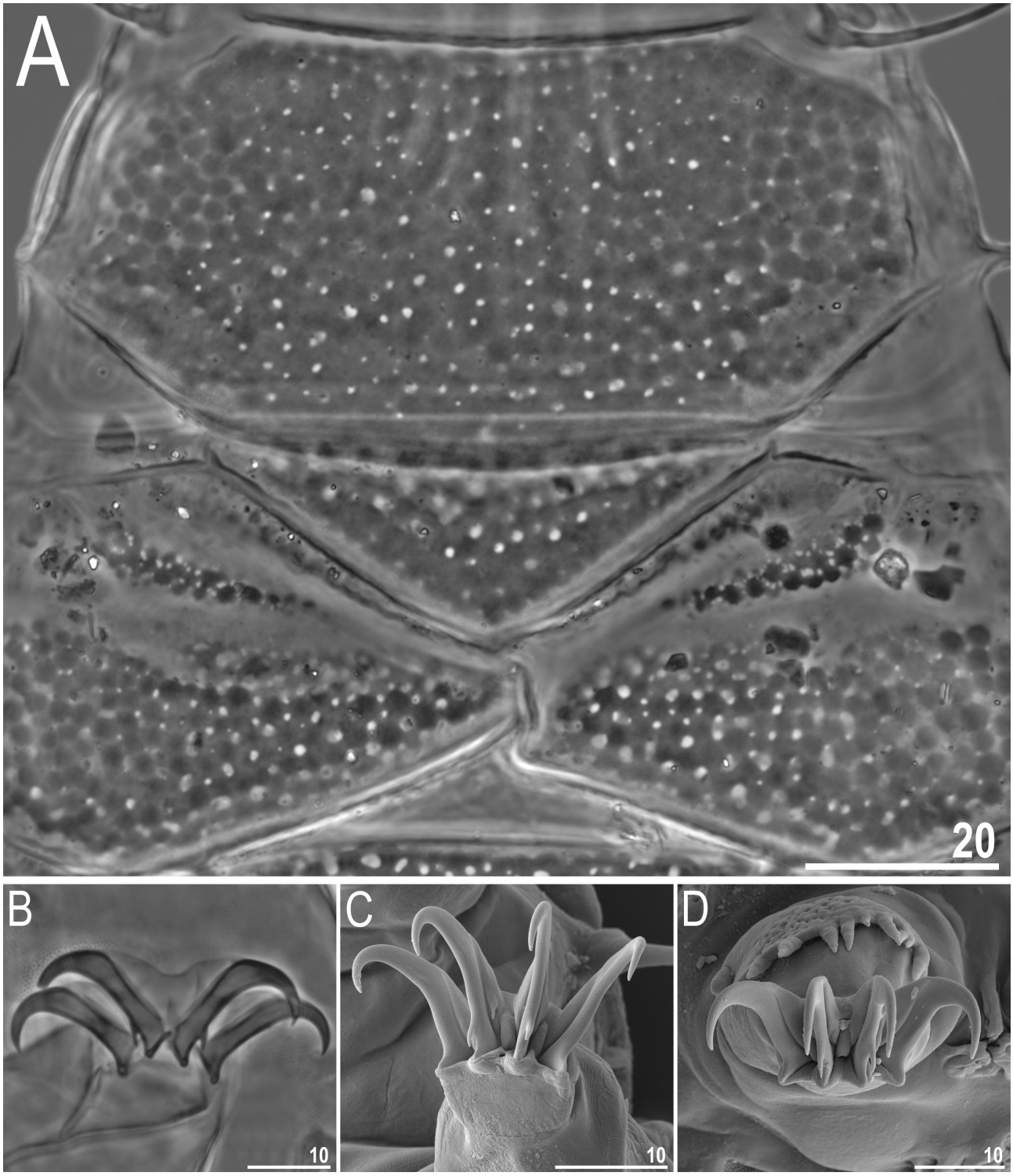

FIGURE 55. Morphology of *Echiniscus lichenorum* (females): A—dorsal sculpturing in close-up (PCM), B—claws I (PCM), C—claws I (SEM), D—claws IV (SEM). Scale bars = 50 μm.

Geographic distribution. The species is relatively common and widely distributed in South Africa (Fig. 120K). Our African and Spanish findings are the first records of *E. lichenorum* outside the *locus typicus* in Portugal (Maucci 1983).

Remarks. Usually large populations are mixed with other echiniscids, macrobiotids, and milnesiids. Given that this is only the second record of the species, we clarified the description by supplying it with missing details, and precisely describing the intraspecific variability within the Iberian and Afrotropical populations, also by consulting

the type series (paratype C.T.10398; Fig. 56). Consequently, we ascertained that it is a *bona species*, disaffirming the suspicion of invalidity in Gąsiorek *et al*. (2019a). The disjunctive distribution requires further investigation (see Discussion).

TABLE 28. Measurements [in µm] of selected morphological structures of the adult females of *Echiniscus lichenorum* mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD	
		µm			*sp*			µm	*sp*	µm	*sp*
Body length	17	226	–	300	*485*	–	*607*	271	*541*	22	*39*
Scapular plate length	17	44.8	–	58.7		–		50.1	–	4.4	–
Head appendages lengths											
Cirrus *internus*	13	7.8	–	14.1	*14.0*	–	*29.4*	10.7	*20.8*	2.4	*4.3*
Cephalic papilla	17	5.5	–	8.2	*9.9*	–	*16.9*	7.2	*14.4*	0.7	*1.7*
Cirrus *externus*	15	10.0	–	25.6	*20.9*	–	*51.5*	18.2	*36.0*	4.7	*8.6*
Clava	16	3.7	–	7.3	*6.5*	–	*15.6*	5.7	*11.3*	1.1	*2.4*
Cirrus *A*	14	25.6	–	60.3	*46.0*	–	*128.3*	52.7	*106.9*	8.6	*19.8*
Cirrus *A*/Body length ratio	14	9%	–	25%		–		20%	–	4%	–
Body appendages lengths											
Cirrus *B*	17	15.6	–	33.4	*31.6*	–	*69.3*	24.9	*49.7*	5.1	*9.2*
Cirrus *C*	17	23.5	–	51.6	*48.1*	–	*98.3*	35.3	*70.4*	9.4	*17.1*
Spine C^d	16	12.7	–	27.2	*22.8*	–	*59.3*	19.8	*40.1*	4.5	*9.4*
Cirrus *D*	16	32.3	–	53.3	*65.5*	–	*110.0*	43.4	*87.1*	6.2	*11.1*
Spine D^d	17	11.1	–	31.5	*19.9*	–	*61.0*	23.7	*47.6*	4.5	*9.7*
Spine on leg I length	14	3.0	–	12.2	*5.4*	–	*22.6*	4.1	*8.1*	2.4	*4.3*
Papilla on leg IV length	16	3.0	–	9.0	*5.5*	–	*17.2*	4.0	*8.0*	1.4	*2.7*
Number of teeth on the collar	17	4	–	15		–		9.4	–	2.6	–
Claw I heights											
Branch	15	14.4	–	17.9	*27.8*	–	*37.3*	16.4	*32.8*	0.9	*2.7*
Spur	10	2.2	–	4.4	*4.4*	–	*9.2*	2.9	*5.6*	0.6	*1.3*
Spur/branch height ratio	10	14%	–	27%		–		17%	–	4%	–
Claw II heights											
Branch	17	13.1	–	17.2	*26.8*	–	*36.4*	15.5	*31.1*	1.1	*2.8*
Spur	9	2.0	–	2.9	*3.6*	–	*6.3*	2.4	*4.6*	0.4	*0.9*
Spur/branch height ratio	9	12%	–	18%		–		15%	–	2%	–
Claw III heights											
Branch	16	14.1	–	17.8	*27.4*	–	*39.7*	15.9	*31.9*	1.0	*2.9*
Spur	6	2.1	–	2.9	*4.3*	–	*5.9*	2.6	*4.8*	0.3	*0.7*
Spur/branch height ratio	6	13%	–	17%		–		16%	–	2%	–
Claw IV heights											
Branch	16	14.1	–	21.6	*30.5*	–	*44.4*	19.3	*38.7*	1.7	*4.3*
Spur	2	2.7	–	2.8	*4.8*	–	*5.0*	2.8	*4.9*	0.1	*0.2*
Spur/branch height ratio	2	14%	–	15%		–		15%	–	1%	–

TABLE 29. Measurements [in µm] of selected morphological structures of the adult males of *Echiniscus lichenorum* mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD	
		µm			*sp*			µm	*sp*	µm	*sp*
Body length	3	181	–	209	*476*	–	*540*	199	*518*	16	*37*
Scapular plate length	3	33.6	–	43.5		–		38.6	–	5.0	–
Head appendages lengths											
Cirrus *internus*	3	8.1	–	8.9	*20.2*	–	*26.5*	8.6	*22.5*	0.4	*3.4*
Cephalic papilla	3	6.2	–	6.5	*14.9*	–	*18.5*	6.3	*16.6*	0.2	*1.8*
Cirrus *externus*	3	14.5	–	17.2	*35.2*	–	*51.2*	15.7	*41.3*	1.4	*8.7*
Clava	3	5.0	–	6.2	*12.9*	–	*15.5*	5.5	*14.2*	0.6	*1.3*
Cirrus *A*	3	42.9	–	46.2	*106.2*	–	*127.7*	44.1	*115.3*	1.8	*11.1*
Cirrus *A*/Body length ratio	3	21%	–	24%		–		22%	–	1%	–
Body appendages lengths											
Cirrus *B*	2	20.5	–	20.8	*47.8*	–	*53.0*	20.7	*50.4*	0.2	*3.6*
Cirrus *C*	3	19.9	–	23.5	*51.4*	–	*59.8*	21.2	*55.1*	2.0	*4.3*
Spine C^d	3	17.8	–	19.8	*43.7*	–	*53.0*	18.9	*49.3*	1.0	*4.9*
Cirrus *D*	2	29.6	–	34.0	*76.5*	–	*78.2*	31.8	*77.3*	3.1	*1.2*
Spine D^d	3	20.1	–	23.5	*47.8*	–	*60.7*	21.5	*56.1*	1.8	*7.2*
Spine on leg I length	3	2.9	–	4.3	*8.6*	–	*11.1*	3.7	*9.6*	0.7	*1.3*
Papilla on leg IV length	3	3.1	–	4.6	*8.0*	–	*11.6*	3.9	*10.1*	0.8	*1.9*
Number of teeth on the collar	3	8	–	10		–		8.7	–	1.2	–
Claw I heights											
Branch	3	11.4	–	14.0	*32.2*	–	*35.9*	13.1	*34.0*	1.5	*1.9*
Spur	2	1.9	–	2.2	*5.1*	–	*5.7*	2.1	*5.4*	0.2	*0.4*
Spur/branch height ratio	2	16%	–	17%		–		16%	–	1%	–
Claw II heights											
Branch	3	9.4	–	12.2	*28.0*	–	*31.0*	11.2	*29.0*	1.6	*1.7*
Spur	0		?			?		?	*?*	?	*?*
Spur/branch height ratio	0		?			–		?	–	?	–
Claw III heights											
Branch	3	9.8	–	14.5	*29.2*	–	*34.6*	12.6	*32.4*	2.5	*2.9*
Spur	2	2.0	–	2.5	*5.2*	–	*5.7*	2.3	*5.5*	0.4	*0.4*
Spur/branch height ratio	2	15%	–	17%		–		16%	–	2%	–
Claw IV heights											
Branch	3	14.5	–	16.7	*38.4*	–	*43.2*	15.9	*41.4*	1.2	*2.6*
Spur	0		?			?		?	*?*	?	*?*
Spur/branch height ratio	0		?			–		?	–	?	–

TABLE 30. Measurements [in µm] of selected morphological structures of the larvae of *Echiniscus lichenorum* mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD	
		µm			*sp*			µm	*sp*	µm	*sp*
Body length	3	153	–	173	*560*	–	*605*	164	*582*	10	*22*
Scapular plate length	3	27.3	–	29.8		–		28.2	–	1.4	–
Head appendages lengths											
Cirrus *internus*	3	5.6	–	7.5	*18.8*	–	*27.5*	6.6	*23.5*	1.0	*4.4*
Cephalic papilla	3	4.0	–	4.9	*14.7*	–	*16.4*	4.4	*15.4*	0.5	*0.9*
Cirrus *externus*	3	8.2	–	10.7	*30.0*	–	*38.8*	9.5	*33.6*	1.3	*4.6*
Clava	3	2.6	–	4.2	*9.5*	–	*15.2*	3.6	*12.7*	0.9	*2.9*
Cirrus *A*	3	20.0	–	30.0	*73.3*	–	*108.7*	25.7	*91.0*	5.1	*17.7*
Cirrus *A*/Body length ratio	3	13%	–	18%		–		16%	–	2%	–
Body appendages lengths											
Spine C^d	3	5.4	–	9.4	*19.8*	–	*32.6*	7.9	*28.0*	2.2	*7.1*
Spine D^d	3	10.9	–	12.7	*39.9*	–	*43.5*	11.9	*42.0*	0.9	*1.9*
Spine on leg I length	3	1.8	–	2.2	*6.5*	–	*7.4*	2.0	*7.1*	0.2	*0.5*
Papilla on leg IV length	3	1.4	–	3.7	*5.1*	–	*12.4*	2.4	*8.3*	1.2	*3.8*
Number of teeth on the collar	3	4	–	6		–		5.3	–	1.2	–
Claw I heights											
Branch	3	8.7	–	9.5	*31.9*	–	*34.1*	9.2	*32.6*	0.4	*1.3*
Spur	2	1.6	–	2.0	*5.9*	–	*6.7*	1.8	*6.3*	0.3	*0.6*
Spur/branch height ratio	2	18%	–	21%		–		20%	–	2%	–
Claw II heights											
Branch	3	8.7	–	9.4	*31.5*	–	*31.9*	9.0	*31.8*	0.4	*0.2*
Spur	3	1.7	–	2.3	*6.2*	–	*7.7*	1.9	*6.7*	0.3	*0.9*
Spur/branch height ratio	3	19%	–	24%		–		21%	–	3%	–
Claw III heights											
Branch	3	8.6	–	9.6	*31.2*	–	*33.3*	9.1	*32.2*	0.5	*1.1*
Spur	2	1.6	–	2.1	*5.9*	–	*7.0*	1.9	*6.5*	0.4	*0.8*
Spur/branch height ratio	2	18%	–	22%		–		20%	–	3%	–
Claw IV heights											
Branch	3	10.6	–	11.0	*36.9*	–	*39.9*	10.8	*38.4*	0.2	*1.5*
Spur	1	2.0	–	2.0	*6.7*	–	*6.7*	2.0	*6.7*	?	*?*
Spur/branch height ratio	1	18%	–	18%		–		18%	–	?	–

Differential diagnosis. *E. lichenorum* is similar to *E. quadrispinosus*, but three traits allow for a sound differentiation of the two species: the sculpturing (endocuticular pillars absent in *E. lichenorum vs* endocuticular pillars present in *E. quadrispinosus*), the presence of the appendage *E* (absent in *E. lichenorum vs* present in *E. quadrispinosus*), and the morphology of lateral appendages (long spines or reduced cirri in *E. lichenorum vs* long, filamentous cirri in *E. quadrispinosus*).

Raw measurements. Supplementary Materials (SM.03) and Tardigrada Register (www.tardigrada.net/register/0090.htm).

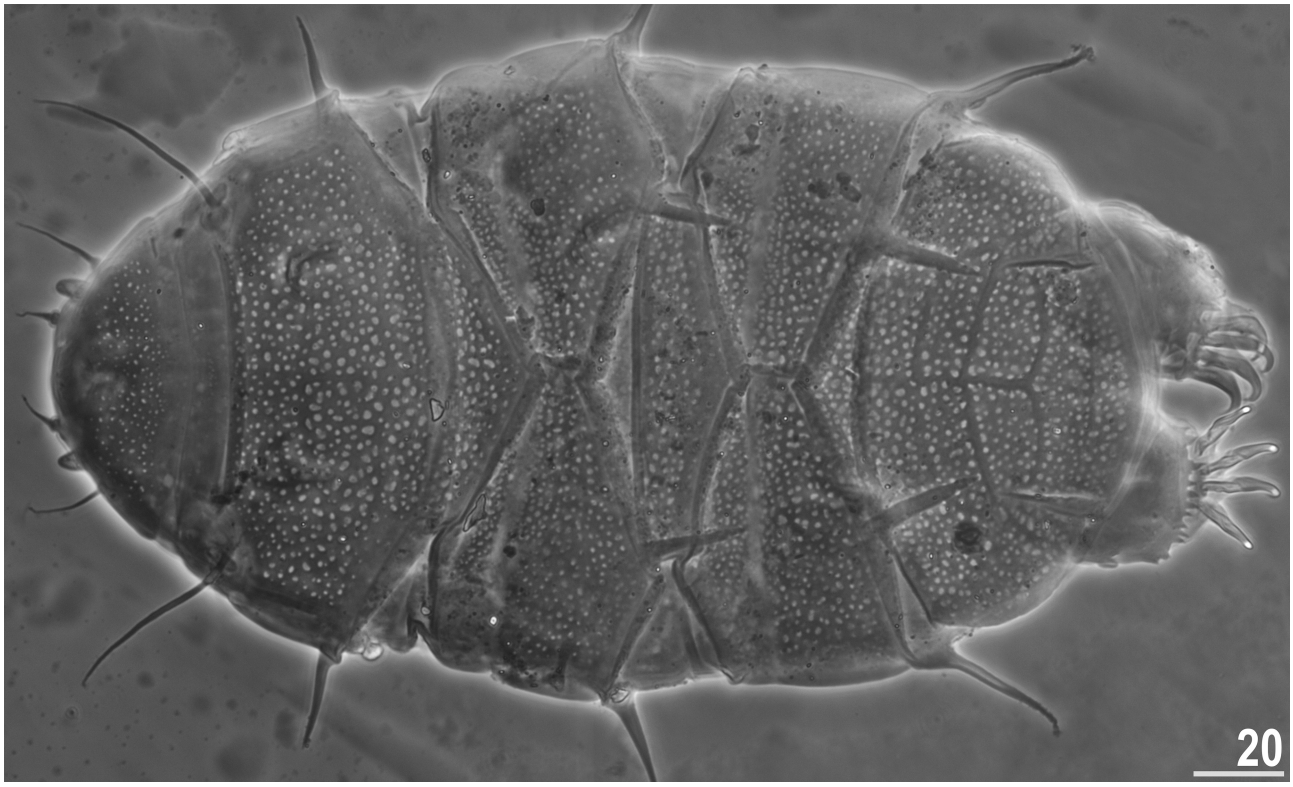

FIGURE 56. Paratype of *Echiniscus lichenorum* (PCM, dorsal view). Scale bar = 20 µm.

16. Echiniscus longispinosus Murray, 1907

Figures 57–61, Tables 31–34

Data source:

A total of 736 specimens (490 ♀♀, 13 ♂♂, 30 juveniles, 4 larvae, and 199 specimens of unknown instar/sex):

- Sample ZA.016: 131 specimens (129 ♀♀ and 2 larvae on slides).
- Sample ZA.020: 1 specimen (1 ♀ on a slide); found with *Echiniscus dentatus* **sp. nov.**, *E. draconis* **sp. nov.**, *E. lichenorum*, and *E. setaceus* **sp. nov.**
- Sample ZA.022: 8 specimens (6 ♀♀, 1 juvenile and 1 specimen of unknown sex on slides); found with *Echiniscus attenboroughi* **sp. nov.**, *E. dentatus* **sp. nov.**, *E. gracilis* **sp. nov.**, *E. lichenorum*, and *E. setaceus* **sp. nov.**
- Sample ZA.027: 1 specimen (1 juvenile on a slide).
- Sample ZA.090: 27 specimens (27 ♀♀ on slides).
- Sample ZA.091: 5 specimens (5 ♀♀ on slides).
- Sample ZA.092: 16 specimens (16 ♀♀ on slides).
- Sample ZA.094: 17 specimens (17 ♀♀ on slides).
- Sample ZA.095: 75 specimens (75 ♀♀ on slides).
- Sample ZA.096: 3 specimens (3 ♀♀ on slides); found with *Echiniscus gracilis* **sp. nov.** and *E. setaceus* **sp. nov.**
- Sample ZA.152: 2 specimens (2 ♀♀ on a slide); found with *Echiniscus oreas* **sp. nov.** and *E. virginicus*.
- Sample ZA.205: 1 specimen (1 ♀ on a slide); found with *Pseudechiniscus (Pseudechiniscus)* cf. *ehrenbergi*.
- Sample ZA.222: 1 specimen (1 ♀ on a slide); found with *Echiniscus blumi*, *E. draconis* **sp. nov.**, and *E. imitans* **sp. nov.**
- Sample ZA.235: 1 specimen (1 ♀ on a slide); found with *Echiniscus regularis*.
- Sample ZA.257: 13 specimens (9 ♀♀, 2 ♂♂ and 2 juveniles on slides); found with *Echiniscus blumi* and *E. oreas* **sp. nov.**
- Sample ZA.258: 4 specimens (1 ♀, 2 ♂♂ and 1 juvenile on slides); found with *Echiniscus blumi*, *E. oreas* **sp.**

nov., and *Pseudechiniscus (Pseudechiniscus)* cf. *ehrenbergi*.

- Sample ZA.260: 1 specimen (1 ♀ on a slide); found with *Doryphoribius bindae*, *Echiniscus baius*, *E. oreas* **sp. nov.**, *E. pellucidus*, *E. scabrospinosus*, and *E. virginicus*.
- Sample ZA.263: 2 specimens (2 ♀♀ on a slide); found with *Echiniscus regularis* **sp. nov.**, *Pseudechiniscus (Pseudechiniscus)* cf. *ehrenbergi,* and *P. (Meridioniscus) wallacei* **sp. nov.**
- Sample ZA.270: 1 specimen (1 juvenile on a slide).
- Sample ZA.273: 2 specimens (2 ♀♀ on slides).
- Sample ZA.274: 199 specimens (81 ♀♀, 11 juveniles, 1 larva and 2 specimens of unknown sex on slides, 100 specimens on SEM stubs 18.11–12, and 4 specimens used for DNA extraction).
- Sample ZA.331: 4 specimens (3 ♀♀, 1 juvenile on slides).
- Sample ZA.336: 1 specimen (1 ♀ on a slide).
- Sample ZA.339: 9 specimens (6 ♀♀, 2 juveniles, 1 larva on slides).
- Sample ZA.360: 1 specimen (1 ♀ on a slide); found with *Echiniscus draconis* **sp. nov.**, *E. lichenorum*, and *E. scabrospinosus*.
- Sample ZA.433: 3 specimens (3 ♂♂ on a slide).
- Sample ZA.438: 61 specimens (8 ♀♀, 2 juveniles and 1 specimen of unknown sex on slides, and 50 frozen specimens).
- Sample ZA.461: 50 specimens (13 ♀♀, 2 juveniles and 5 specimens of unknown sex on slides, and 30 frozen specimens).
- Sample ZA.462: 3 specimens (3 ♀♀ on slides).
- Sample ZA.464: 8 specimens (7 ♀♀, 1 juvenile on slides).
- Sample ZA.466: 16 specimens (10 ♀♀ and 2 juveniles on slides, and 4 specimens used for DNA extraction, including 3 hologenophores).
- Sample ZA.467: 1 specimen (1 ♀ on a slide).
- Sample ZA.468: 3 specimens (3 ♀♀ on slides).
- Sample ZA.474: 1 specimen (1 juvenile on a slide).
- Sample ZA.478: 1 specimen (1 ♀ on a slide).
- Sample ZA.479: 3 specimens (3 ♂♂ on slides); found with *Echiniscus attenboroughi* **sp. nov.** and *E. scabrocirrosus* **sp. nov.**
- Sample ZA.491: 6 specimens (6 ♀♀ on slides).
- Sample ZA.496: 9 specimens (7 ♀♀, 1 ♂♂ and 1 specimen of unknown sex on slides).
- Sample ZA.497: 6 specimens (4 ♀♀, 1 ♂♂ and 1 specimen of unknown sex on slides).
- Sample ZA.507: 1 specimen (1 ♀ on a slide); found with *Echiniscus dentatus* **sp. nov.** and *E. setaceus* **sp. nov.**
- Sample ZA.511: 3 specimens (2 ♀♀ and 1 juvenile on a slide); found with *Echiniscus gracilis* **sp. nov.**
- Sample ZA.542: 6 specimens (6 ♀♀ on slides); found with *Echiniscus latruncularis* **sp. nov.** and *E. setaceus* **sp. nov.**
- Sample ZA.543: 6 specimens (6 ♀♀ on slides); found with *Echiniscus latruncularis* **sp. nov.**
- Sample ZA.546: 22 specimens (20 ♀♀, 1 ♂ and 1 juvenile on slides).
- Sample ZA.555: 1 specimen (1 ♀ on a slide); found with *Echiniscus dentatus* **sp. nov.**, *E. gracilis* **sp. nov.**, and *E. irroratus* **sp. nov.**

Literature:

- Original description: Murray (1907).
- Later records: Binda (1984), Pilato *et al*. (1991).

Description. Mature females (*i.e*. from the third instar onwards; measurements and statistics in Table 31). Medium-sized *Echiniscus* with dark yellow to intensively orange body and large red eyes; body colour and eyes disappeared soon after mounting in Hoyer's medium. The species is rather slender for an *Echiniscus* (Fig. 57A–B, 58–59). Dactyloid (Fig. 57A, 58A, 61B) or ovoid (Fig. 57B, 59, 61A) cephalic papillae (secondary clavae) and (primary) clavae; cirri growing out from bulbous cirrophores. Cirri *A* short. Body appendage configuration *A-(B)-(B^d)-C-C^d-D-D^d*, with all trunk appendages flexible, in the form of short cirri/long spines. Single asymmetries are rare, but the appendages *B* and B^d are often symmetrically lacking (Fig. 57A, 59B).

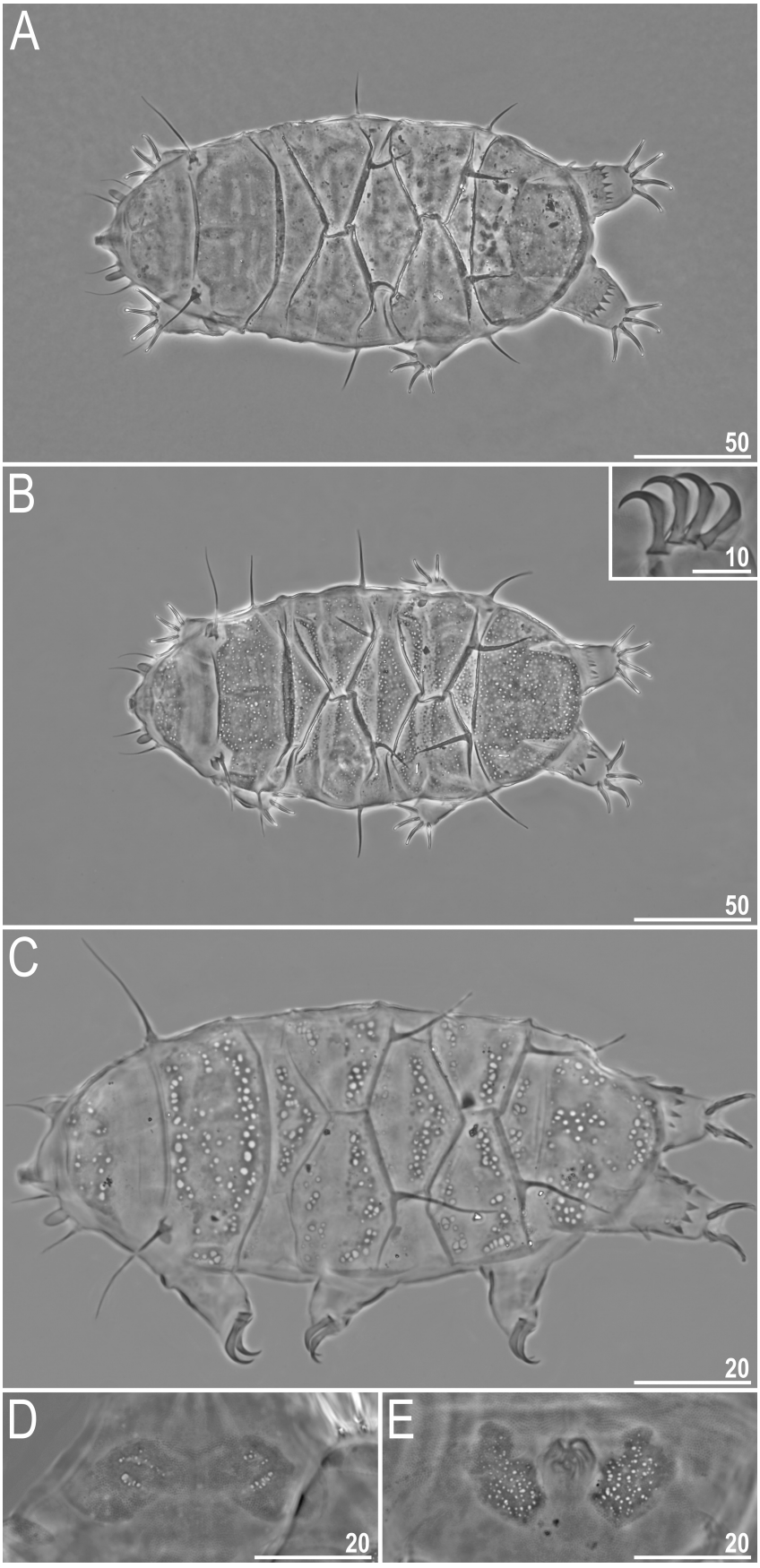

FIGURE 57. Habitus and intraspecific variability of *Echiniscus longispinosus* Murray, 1907 (PCM): A—neotype, female in dorsal view (pores rare), B—female in dorsal view (pores numerous; insert shows claws II), C—larva in dorsal view, D—subcephalic plates, E—genital plates. Scale bars in µm.

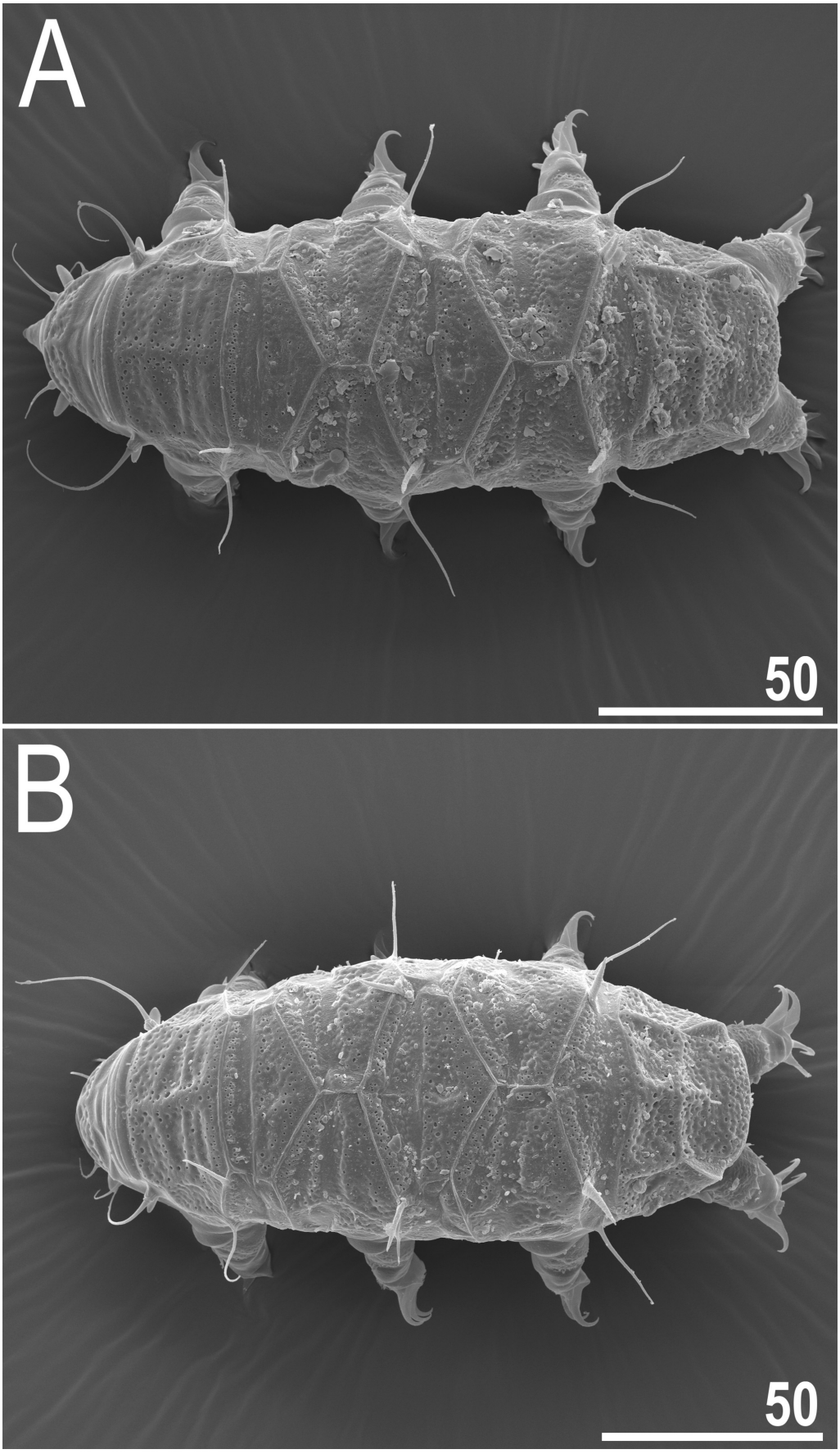

FIGURE 58. Habitus of *Echiniscus longispinosus* (SEM, females in dorsal view). Scale bars = 50 μm.

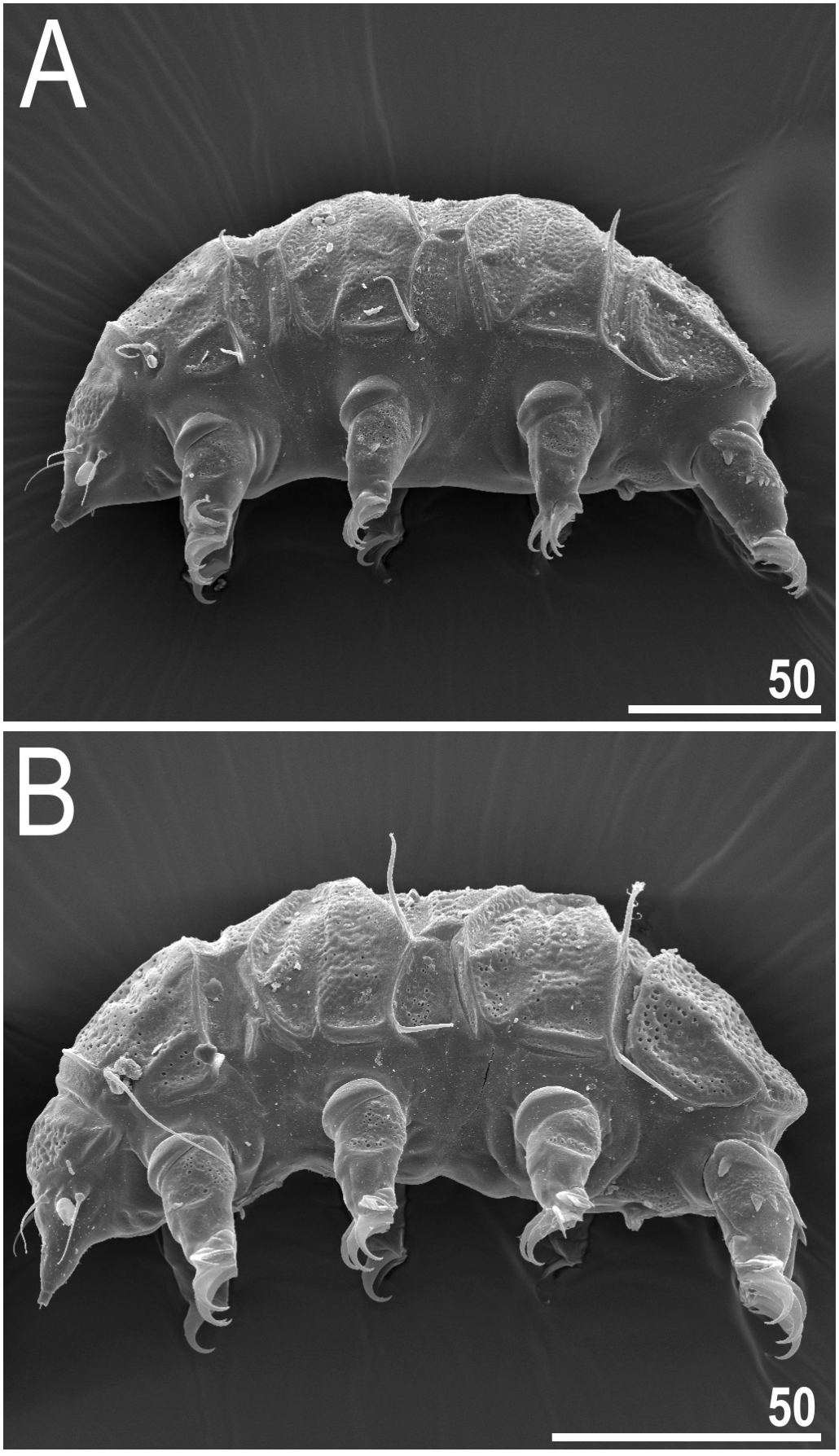

FIGURE 59. Habitus of *Echiniscus longispinosus* (SEM, females in lateral view). Scale bars = 50 µm.

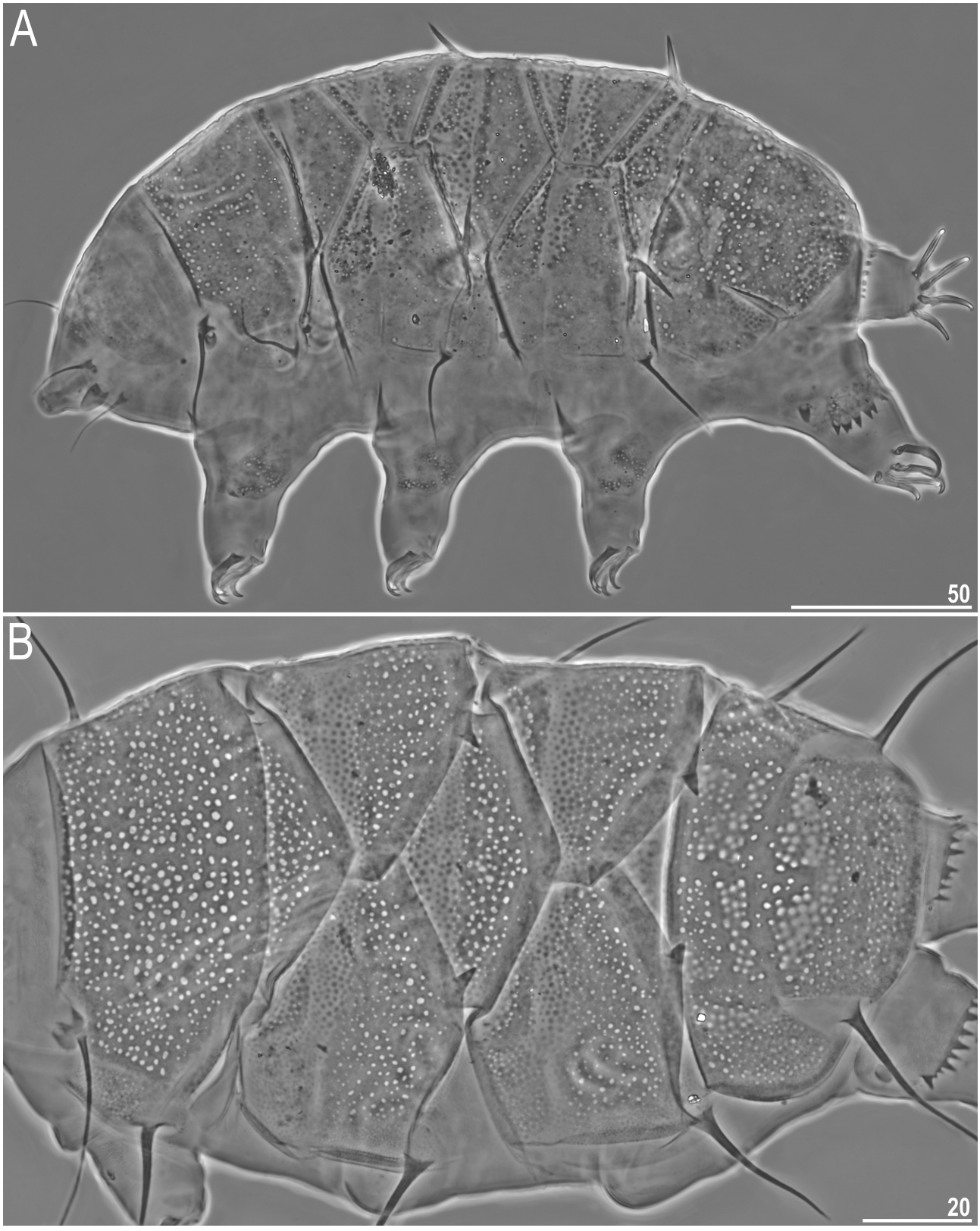

FIGURE 60. The comparison of the dorsal sculpturing of *Echiniscus longispinosus* (A) and *Echiniscus merokensis* Richters, 1904 (B) (PCM, females). Scale bars in μm.

Dorsal plates with the sculpturing very similar to the *E. merokensis* type (compare Fig. 60A–B). Pores irregularly distributed, from very sparse (Fig. 57A) to numerous (Fig. 57B, 58, 60A). Poorly marked faceting on the scapular and caudal (terminal) plates formed by weakly outlined ridges/sutures (Fig. 58). The cephalic plate with

an anterior incision (Fig. 57A–B). The cervical (neck) plate poorly developed as a darkish rectangle anterior to the scapular plate. The scapular plate with poorly marked trapezoid lateral portions (Fig. 59, 60A). Transverse belts on the paired segmental plates I–II fuzzy, often partially covered with epicuticular granules (Fig. 60A). The caudal (terminal) plate with two unsclerotised, poorly developed incisions (Fig. 57A–B, 58–60A). Ventral cuticle with minute endocuticular pillars distributed throughout the whole venter. Ventral plates present: a pair of roughly oval subcephalic plates (Fig. 57D, 61B) and a pair of polygonal/oval genital plates (Fig. 57E, 61C). All ventral plates porous (Fig. 57D–E and 61B–C). Sexpartite gonopore placed between the genital plates, and a trilobed anus between legs IV (Fig. 61C).

Pedal plates I–III present (Fig. 59, 60A), uniquely sculptured, with pores distributed along their distal and posterocaudal margins, with unsculptured centres; pedal plate IV usually weakly sculptured, without pores, but with the dentate collar (Fig. 61F). Pulvini present (Fig. 59 and 60A). A spine on leg I at the distal edge of the pedal plate I (Fig. 59, 60A, 61A); a papilla on leg IV (Fig. 59, 60A, 61E–F). Dentate collar IV with long, acute teeth separated at their bases (Fig. 57A–B, 61F). Claws I–IV of similar heights, or claws IV slightly higher. All external claws spurless. All internal claws with spurs positioned at *ca.* 25% of the branch (Fig. 57B, insert, 61D–F).

Mature males and sexually dimorphic traits (*i.e.* from the second or third instar onwards, see below; measurements and statistics in Table 32). Smaller and with shorter claws than females (see Tables 31–32). Qualitatively like females, excluding the circular gonopore.

Juveniles (*i.e.* from the second instar onwards; measurements and statistics in Table 33). Smaller than females, but equal in size to males. Phenotypically indistinguishable from adults if the smooth ventral cuticle in the gonoporal area is not visible.

Larvae (*i.e.* the first instar; measurements and statistics in Table 34). Gonopore and anus absent. Smaller than juveniles. Body appendage configuration *A*-*C*^{d}-*D*^{d} (in one larva, an asymmetrically developed appendage C was present). The dorsal sculpturing is different from the subsequent life stages, as the pores have an identical diameter as in adults, but they tend to merge into groups along the plate margins (Fig. 57C).

Eggs. Up to three yellow eggs per exuvia were found.

DNA markers and phylogenetic position. The sister species of the subclade (*E. capensis* **sp. nov.** (*E. gracilis* **sp. nov.** + *E. irroratus* **sp. nov.**)) in the South-African endemic clade (Fig. 117). The species closest in ITS-1 is *E. gracilis* **sp. nov.** (p-distance = 8.3%), and in ITS-2—*E. dentatus* **sp. nov.**, *E. gracilis* **sp. nov.**, *E. intricatus* **sp. nov.** and *E. irroratus* **sp. nov.** (5.9–6.2%).

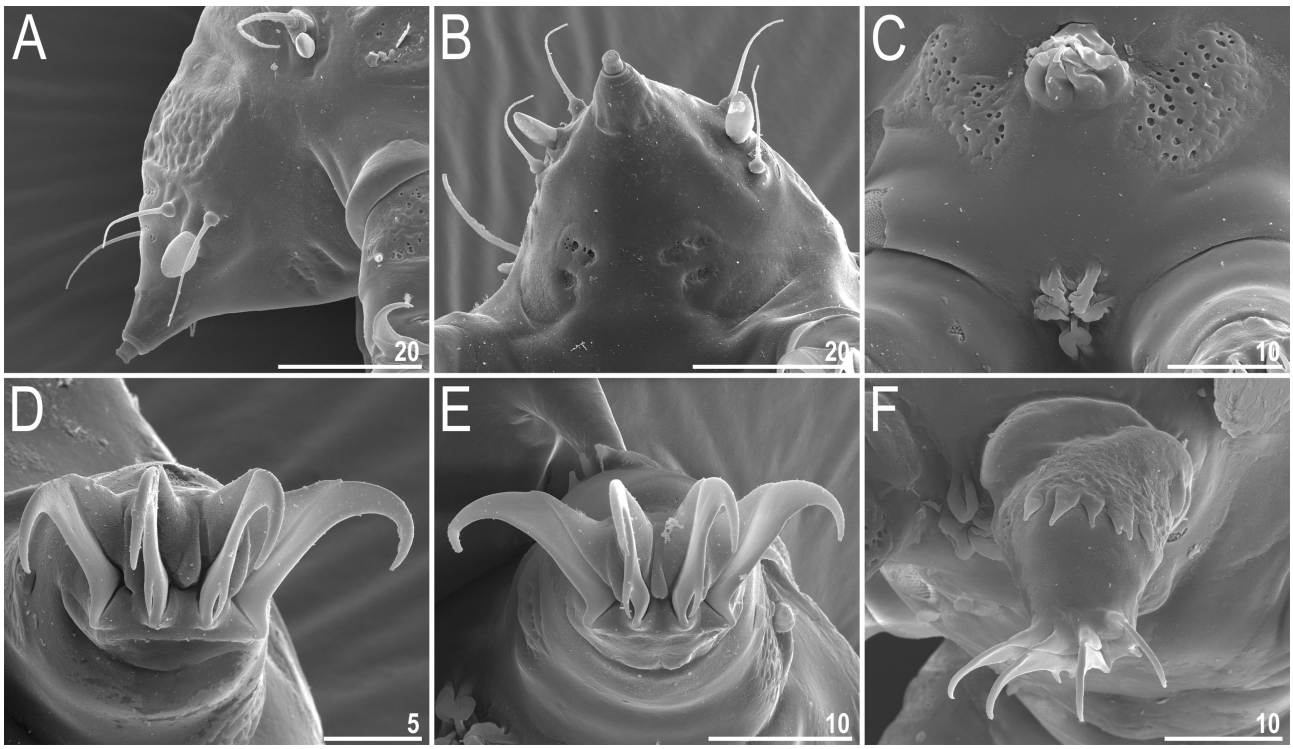

FIGURE 61. Detailed morphology of *Echiniscus longispinosus* (SEM, females): A—cephalic appendages in lateral view, B—cephalic appendages and subcephalic plates, C—genital plates, D—claws I, E—claws IV, F—dentate collar IV. Scale bars in μm.

TABLE 31. Measurements [in µm] of selected morphological structures of the adult females of *Echiniscus longispinosus* mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Neotype	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	20	187	–	251	*533*	–	*710*	219	*624*	19	*47*	213	*638*
Scapular plate length	20	28.5	–	41.5		–		35.2	–	3.5	–	33.4	–
Head appendages lengths													
Cirrus *internus*	17	10.5	–	19.5	*27.9*	–	*56.7*	14.4	*40.9*	2.7	*8.1*	15.5	*46.4*
Cephalic papilla	20	7.0	–	9.5	*18.7*	–	*28.3*	8.0	*23.0*	0.6	*2.1*	8.2	*24.6*
Cirrus *externus*	19	16.1	–	22.9	*44.7*	–	*72.6*	19.4	*55.1*	2.1	*7.5*	21.4	64.1
Clava	20	3.0	–	7.4	*9.3*	–	*20.8*	5.9	*16.8*	1.1	*2.9*	5.6	*16.8*
Cirrus *A*	19	30.7	–	51.1	*86.7*	–	*142.3*	40.6	*115.6*	5.8	*14.4*	35.1	*105.1*
Cirrus *A*/Body length ratio	19	14%	–	23%		–		19%	–	3%	–	16%	–
Body appendages lengths													
Cirrus *B*	10	14.4	–	24.8	*40.7*	–	*77.5*	19.8	*58.2*	3.4	*10.4*	?	*?*
Cirrus B^d	2	12.4	–	16.4	*33.5*	–	*39.5*	14.4	*36.5*	2.8	*4.2*	?	*?*
Cirrus *C*	20	15.2	–	25.3	*42.4*	–	*80.0*	20.1	*57.5*	3.0	*11.0*	20.3	60.8
Cirrus C^d	19	10.8	–	21.0	*30.5*	–	*70.5*	17.6	*50.8*	2.4	*10.2*	17.9	*53.6*
Cirrus *D*	19	14.3	–	27.5	*35.6*	–	*78.3*	20.7	*59.5*	3.1	*11.0*	19.4	*58.1*
Cirrus D^d	20	11.2	–	34.8	*27.0*	–	*122.1*	20.8	*60.6*	5.2	*20.6*	21.4	*64.1*
Spine on leg I length	19	1.9	–	3.8	*5.8*	–	*10.7*	2.8	*8.0*	0.5	*1.4*	31.0	92.8
Papilla on leg IV length	20	2.8	–	5.3	*8.0*	–	*17.0*	4.3	*12.2*	0.6	*2.0*	4.1	*12.3*
Number of teeth on the collar	20	6	–	8		–		6.9	–	0.8	–	8	–
Claw I heights													
Branch	20	11.9	–	15.1	*31.6*	–	*49.0*	13.2	*37.8*	0.9	*4.3*	14.7	*44.0*
Spur	15	1.9	–	3.2	*4.8*	–	*9.0*	2.5	*6.9*	0.4	*1.2*	?	*?*
Spur/branch height ratio	15	14%	–	25%		–		19%	–	3%	–	?	–
Claw II heights													
Branch	20	10.9	–	14.5	*32.5*	–	*45.3*	12.7	*36.2*	1.0	*3.1*	13.2	*39.5*
Spur	18	2.0	–	3.1	*5.1*	–	*9.5*	2.5	*7.0*	0.4	*1.2*	2.7	*8.1*
Spur/branch height ratio	18	15%	–	27%		–		19%	–	3%	–	20%	–
Claw III heights													
Branch	20	11.5	–	14.7	*32.5*	–	*48.0*	13.0	*37.1*	0.8	*3.9*	13.6	*40.7*
Spur	16	1.6	–	3.0	*4.9*	–	*9.8*	2.4	*6.6*	0.4	*1.3*	?	?
Spur/branch height ratio	16	13%	–	23%		–		18%	–	3%	–	?	–
Claw IV heights													
Branch	20	12.3	–	18.6	*37.6*	–	*60.7*	16.1	*46.0*	1.5	*5.5*	17.9	53.6
Spur	10	2.3	–	3.8	*6.3*	–	*11.8*	2.9	*7.7*	0.5	*1.7*	?	*?*
Spur/branch height ratio	10	13%	–	25%		–		18%	–	3%	–	?	–

TABLE 32. Measurements [in µm] of selected morphological structures of the adult males of *Echiniscus longispinosus* mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD	
		µm			*sp*			µm	*sp*	µm	*sp*
Body length	2	153	–	181	*563*	–	*603*	167	*583*	20	*29*
Scapular plate length	2	27.2	–	30.0		–		28.6	–	2.0	–
Head appendages lengths											
Cirrus *internus*	2	12.4	–	12.7	*41.3*	–	*46.7*	12.6	*44.0*	0.2	*3.8*
Cephalic papilla	2	5.7	–	6.4	*21.0*	–	*21.3*	6.1	*21.1*	0.5	*0.3*
Cirrus *externus*	2	13.4	–	16.0	*49.3*	–	*53.3*	14.7	*51.3*	1.8	*2.9*
Clava	2	4.0	–	4.2	*13.3*	–	*15.4*	4.1	*14.4*	0.1	*1.5*
Cirrus *A*	2	29.4	–	39.7	*98.0*	–	*146.0*	34.6	*122.0*	7.3	*33.9*
Cirrus *A*/Body length ratio	2	16%	–	26%		–		21%	–	7%	–
Body appendages lengths											
Cirrus *C*	1	14.8	–	14.8	*49.3*	–	*49.3*	14.8	*49.3*	?	*?*
Cirrus C^d	2	16.4	–	24.1	*54.7*	–	*88.6*	20.3	*71.6*	5.4	*24.0*
Cirrus *D*	2	17.6	–	18.7	*58.7*	–	*68.8*	18.2	*63.7*	0.8	*7.1*
Cirrus D^d	2	18.7	–	29.1	*62.3*	–	*107.0*	23.9	*84.7*	7.4	*31.6*
Spine on leg I length	2	2.4	–	2.5	*8.0*	–	*9.2*	2.5	*8.6*	0.1	*0.8*
Papilla on leg IV length	1	4.3	–	4.3	*14.3*	–	*14.3*	4.3	*14.3*	?	*?*
Number of teeth on the collar	2	5	–	6		–		5.5	–	0.7	–
Claw I heights											
Branch	2	10.7	–	11.0	*35.7*	–	*40.4*	10.9	*38.1*	0.2	*3.4*
Spur	2	1.8	–	2.4	*6.0*	–	*8.8*	2.1	*7.4*	0.4	*2.0*
Spur/branch height ratio	2	17%	–	22%		–		19%	–	4%	–
Claw II heights											
Branch	2	10.0	–	10.2	*34.0*	–	*36.8*	10.1	*35.4*	0.1	*2.0*
Spur	2	2.1	–	2.3	*7.0*	–	*8.5*	2.2	*7.7*	0.1	*1.0*
Spur/branch height ratio	2	21%	–	23%		–		22%	–	2%	–
Claw III heights											
Branch	2	9.6	–	10.0	*33.3*	–	*35.3*	9.8	*34.3*	0.3	*1.4*
Spur	0		?			?		?	*?*	?	?
Spur/branch height ratio	0		?			–		?	–	?	–
Claw IV heights											
Branch	2	10.4	–	12.0	*34.7*	–	*44.1*	11.2	*39.4*	1.1	*6.7*
Spur	1	2.9	–	2.9	*9.7*	–	*9.7*	2.9	*9.7*	?	*?*
Spur/branch height ratio	1	28%	–	28%		–		28%	–	?	–

TABLE 33. Measurements [in µm] of selected morphological structures of the juveniles of *Echiniscus longispinosus* mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD	
		µm			*sp*			µm	*sp*	µm	*sp*
Body length	5	150	–	187	*592*	–	*675*	169	*643*	13	*31*
Scapular plate length	5	23.1	–	31.6		–		26.4	–	3.2	–
Head appendages lengths											
Cirrus *internus*	5	7.5	–	12.9	*28.8*	–	*51.8*	10.0	*38.1*	2.2	*8.7*
Cephalic papilla	5	5.2	–	7.8	*21.6*	–	*24.7*	6.1	*22.9*	1.0	*1.2*
Cirrus *externus*	5	9.8	–	16.0	*37.7*	–	*58.6*	13.2	*50.2*	2.4	7.6
Clava	5	3.8	–	5.9	*15.0*	–	*20.8*	4.8	*18.0*	0.9	*2.3*
Cirrus *A*	5	19.1	–	33.0	*82.7*	–	*126.1*	27.9	*105.4*	5.4	*15.4*
Cirrus *A*/Body length ratio	5	13%	–	19%		–		16%	–	2%	–
Body appendages lengths											
Cirrus *B*	3	15.0	–	16.4	*48.4*	–	*62.1*	15.6	*56.9*	0.7	*7.4*
Cirrus *C*	5	14.8	–	19.4	*59.2*	–	*73.9*	17.5	*66.5*	1.9	*6.8*
Cirrus C^d	5	21.6	–	22.9	*70.3*	–	*98.3*	22.3	*85.5*	0.5	10.5
Cirrus *D*	3	20.7	–	22.1	*66.1*	–	*83.7*	21.2	*77.7*	0.8	*10.0*
Cirrus D^d	5	22.7	–	30.4	*90.9*	–	*109.2*	25.6	*97.2*	3.2	*7.5*
Spine on leg I length	4	2.3	–	2.9	*7.3*	–	*11.0*	2.5	*9.3*	0.3	*1.5*
Papilla on leg IV length	5	3.0	–	3.9	*11.1*	–	*14.8*	3.3	*12.5*	0.4	*1.5*
Number of teeth on the collar	5	4	–	6		–		5.0	–	0.7	–
Claw I heights											
Branch	5	8.5	–	11.2	*35.4*	–	*40.6*	9.9	*37.7*	1.0	2.4
Spur	4	2.2	–	2.4	*7.3*	–	*10.4*	2.3	*8.8*	0.1	*1.3*
Spur/branch height ratio	4	21%	–	28%		–		23%	–	3%	–
Claw II heights											
Branch	5	7.8	–	9.9	*27.5*	–	*38.2*	9.0	*34.3*	0.8	*4.2*
Spur	4	1.7	–	2.2	*6.8*	–	*8.7*	2.0	*7.8*	0.2	*0.9*
Spur/branch height ratio	4	18%	–	26%		–		22%	–	4%	–
Claw III heights											
Branch	5	7.9	–	10.9	*32.6*	–	*41.9*	9.6	*36.5*	1.2	*4.4*
Spur	3	1.5	–	1.9	*5.1*	–	*7.6*	1.7	*6.4*	0.2	1.3
Spur/branch height ratio	3	16%	–	19%		–		18%	–	2%	–
Claw IV heights											
Branch	5	9.4	–	12.8	*32.6*	–	*51.4*	11.6	*44.5*	1.6	*7.8*
Spur	4	1.5	–	2.8	*5.1*	–	*10.6*	1.9	*7.3*	0.6	*2.4*
Spur/branch height ratio	4	14%	–	22%		–		17%	–	3%	–

TABLE 34. Measurements [in µm] of selected morphological structures of the larvae of *Echiniscus longispinosus* mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD	
		µm			*sp*			µm	*sp*	µm	*sp*
Body length	3	110	–	133	*570*	–	*711*	123	*652*	12	*74*
Scapular plate length	3	16.3	–	22.3		–		19.1	–	3.0	–
Head appendages lengths											
Cirrus *internus*	3	7.0	–	8.1	*36.3*	–	*42.9*	7.4	*38.9*	0.6	*3.5*
Cephalic papilla	3	4.0	–	4.9	*22.0*	–	*24.5*	4.4	*23.2*	0.5	*1.3*
Cirrus *externus*	3	8.7	–	10.4	*43.5*	–	*63.8*	9.6	*51.3*	0.9	*11.0*
Clava	3	3.0	–	3.9	*13.5*	–	*22.1*	3.5	*18.8*	0.5	*4.7*
Cirrus *A*	3	20.8	–	25.6	*96.9*	–	*136.9*	22.7	*120.5*	2.6	*21.0*
Cirrus *A*/Body length ratio	3	17%	–	19%		–		18%	–	1%	–
Body appendages lengths											
Cirrus *C*	1	10.3	–	10.3	*55.1*	–	*55.1*	10.3	*55.1*	?	*?*
Cirrus C^d	3	12.1	–	18.4	*63.2*	–	*112.9*	14.9	*80.3*	3.2	*28.3*
Cirrus D^d	3	14.7	–	15.7	*65.9*	–	*96.3*	15.2	*81.0*	0.5	*15.2*
Spine on leg I length	3	1.4	–	1.8	*7.5*	–	*8.6*	1.5	*8.0*	0.2	*0.6*
Papilla on leg IV length	3	2.4	–	2.7	*12.1*	–	*14.7*	2.5	*13.2*	0.2	*1.4*
Number of teeth on the collar	3	4	–	5		–		4.3	–	0.6	–
Claw I heights											
Branch	3	6.7	–	8.3	*30.0*	–	*45.4*	7.5	*39.9*	0.8	*8.6*
Spur	2	1.8	–	1.9	*9.6*	–	*11.7*	1.9	*10.6*	0.1	*1.4*
Spur/branch height ratio	2	22%	–	26%		–		24%	–	3%	–
Claw II heights											
Branch	3	7.0	–	7.7	*31.4*	–	*46.0*	7.4	*39.5*	0.4	*7.4*
Spur	3	1.3	–	1.7	*7.6*	–	*8.0*	1.5	*7.9*	0.2	*0.2*
Spur/branch height ratio	3	17%	–	24%		–		20%	–	4%	–
Claw III heights											
Branch	3	7.0	–	7.9	*31.4*	–	*42.9*	7.3	*38.9*	0.5	*6.5*
Spur	3	1.4	–	1.9	*6.3*	–	*11.7*	1.6	*8.8*	0.3	*2.7*
Spur/branch height ratio	3	20%	–	27%		–		22%	–	4%	–
Claw IV heights											
Branch	3	8.9	–	9.9	*39.9*	–	*60.7*	9.5	*51.0*	0.6	*10.5*
Spur	2	1.6	–	2.0	*8.6*	–	*9.0*	1.8	*8.8*	0.3	*0.3*
Spur/branch height ratio	2	16%	–	22%		–		19%	–	4%	–

Neotype material. 81 ♀♀, 11 juveniles, 1 larva and 2 specimens of unknown sex on slides ZA.274.01–13, 15–18; neotype: mature ♀ on slide ZA.274.02. Mounted together with 5 ♀♀ of *E. regularis* **sp. nov.** About 50 specimens on a SEM stub 18.11.

Neotype locality. 33°58'58.44"S, 20°42'17.88"E, 295 m asl: Republic of South Africa, Western Cape, Tradouw Pass; fynbos, lichen from rock (sample ZA.274).

Etymology. From Latin *longus* = long + *spinosus* = spiny, referring to the morphology of trunk appendages. An adjective in the nominative singular.

Geographic distribution. Likely an Afrotropical endemic. One of the most common South African echiniscids (Fig. 120J).

Remarks. Due to the overlapping size ranges of males and juveniles, it is probable that males develop directly from larvae. *E. longispinosus* has a tendency towards forming large (tens to hundreds of individuals), monospecific populations (see also Binda 1984 and Pilato *et al*. 1991 for the description of a population from Tsitsikamma), but, when found accompanied by other echiniscids, it is always represented by few individuals.

Differential diagnosis. The dentate collar IV composed of acute teeth not joined at their bases, pores in the ventral plates and the body appendage formula *A-(B)-(B^d)-C-C^d-D-D^d* constitute the trait combination unseen in other known *Echiniscus* spp.

Raw measurements. Supplementary Materials (SM.03) and Tardigrada Register (www.tardigrada.net/register/0091.htm).

17. Echiniscus marginatus Binda & Pilato, 1994

Data source:
A total of 3 specimens (3 ♀♀):
- Sample ZA.093: 1 specimen (1 ♀ on a slide); found with *Echiniscus lichenorum*.
- Sample ZA.098: 2 specimens (2 ♀♀ on a slide); found with *Echiniscus draconis* **sp. nov.**, *E. lichenorum*, and *E. scabrospinosus*.

Literature:
- Original description: Binda & Pilato (1994).

DNA markers and phylogenetic position. Given that the only three individuals found in this study were mounted on permanent slides, no DNA analysis was conducted. Consequently, the phylogenetic position of the species remains unknown.

Geographic distribution. The first record outside *locus typicus* in the Hawaiian Islands. Given the lack of DNA sequences for both the type population and the South African records (Fig. 120L), it is not possible to distinguish between a wide tropical-subtropical range/disjunct distribution, or species crypsis.

Remarks. An extremely rare species accompanying other members of the *E. spinulosus* group.

18. Echiniscus merokensis Richters, 1904
Figure 62

Data source:
A total of 13 specimens (7 ♀♀ and 6 juveniles):
- Sample ZA.529: 13 specimens (7 ♀♀, 6 juveniles); found with *Echiniscus scabrospinosus*, *E. setaceus* **sp. nov.**, and *Pseudechiniscus (Pseudechiniscus)* cf. *ehrenbergi*.

Literature:
- Original description: Richters (1904).
- Later trustworthy records: likely most of the Holarctic records from McInnes (1994), including the African Mediterranean (Binda & Pilato 1987).

Shortened description. Body appendage formula *A-C-C^d-D-D^d-E*. All lateral appendages in the form of short cirri. Dorsal sculpturing with well-developed *striae* between multangular elements of endocuticle; the caudal plate faceted (Fig. 62). Pedal plates absent and pulvini I–III barely demarcated. External claws spurless, internal ones with spurs positioned at *ca.* 25% of the claw height and strongly bent downwards.

DNA markers and phylogenetic position. *Echiniscus merokensis* is the sister species of *E. pellucidus*, placed within the poorly sampled *merokensis* clade (Fig. 117). The species closest in ITS-1 and ITS-2 is *E. pellucidus* (2.0–2.6% and 1.8%, respectively).

Geographic distribution. This cosmopolitan species, with molecularly confirmed records from Antarctica,

Arctic, Asia, Europe and South America (Roszkowska *et al*. 2018), exhibits clear stenothermic preferences for cold mountainous habitats in the tropical and subtropical zone (McInnes 1994). Rare (Fig. 120K) and probable anthropogenic introduction to South Africa.

Remarks. None.

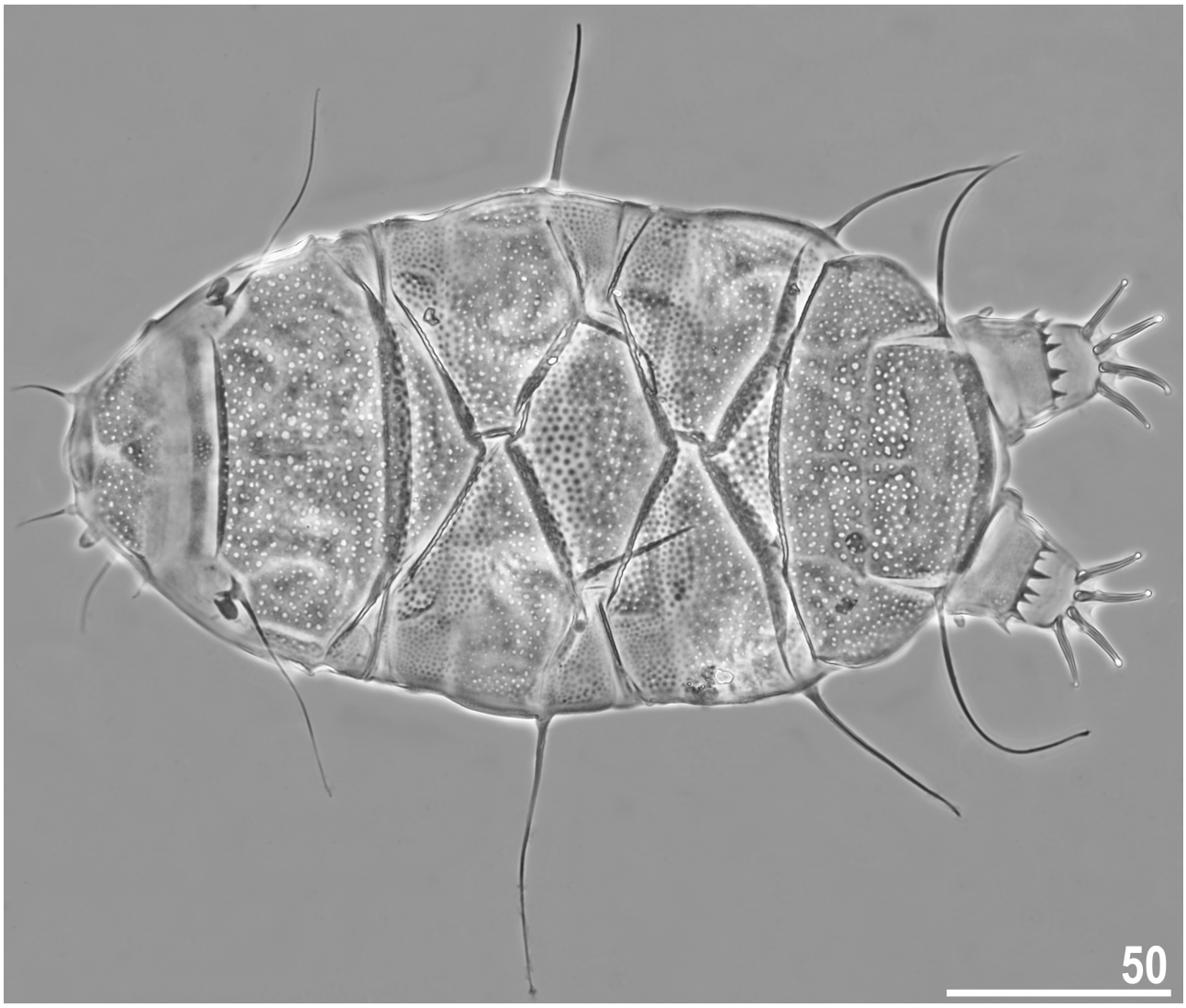

FIGURE 62. Habitus of *Echiniscus merokensis* (PCM, dorsal view). Scale bar = 50 µm.

19. Echiniscus oreas sp. nov. Gąsiorek, Morek & Michalczyk

urn:lsid:zoobank.org:act:31EC7D36-D67F-49FE-98E4-BAEB5CB42FAD

Figures 63–65, Tables 35–37

Data source:

A total of 317 specimens (176 ♀♀, 6 ♂♂, 74 juveniles, 4 larvae, and 57 specimens of unknown instar/sex):

- Sample ZA.152: 11 specimens (11 ♀♀ on slides); found with *Echiniscus longispinosus* and *E. virginicus*.
- Sample ZA.183: 20 specimens (9 ♀♀, 4 juveniles and 1 larva on slides, and 6 specimens used for DNA extraction); found with *Doryphoribius maasaimarensis* Fontoura *et al*., 2013, *Echiniscus regularis* **sp. nov.**, *E. scabrospinosus*, *Pseudechiniscus (Pseudechiniscus)* cf. *ehrenbergi*, *P. (Meridioniscus) wallacei* **sp. nov.**, and *Ramazzottius szeptycki*.
- Sample ZA.185: 2 specimens (2 ♀♀ on slides); found with *Echiniscus regularis* **sp. nov.**, *E. scabrospinosus*, and *Echiniscus virginicus*.
- Sample ZA.190: 45 specimens (14 ♀♀, 1 juvenile on slides, and 30 specimens on SEM stub 18.19); found with

Echiniscus scabrospinosus, *Pseudechiniscus (Pseudechiniscus)* cf. *ehrenbergi*, and *Ramazzottius szeptycki.*

- Sample ZA.201: 17 specimens (2 ♀♀ on a slide, and 15 specimens on SEM stub 19.01); found with *Echiniscus intricatus* **sp. nov.**, *E. tetraspinosus* **sp. nov.**, and *E. tristis*.
- Sample ZA.204: 21 specimens (12 ♀♀ and 6 juveniles on slides, and 3 specimens used for DNA extraction, including 1 retrieved hologenophore); found with *Echiniscus pellucidus*.
- Sample ZA.206: 26 specimens (19 ♀♀ and 4 juveniles on slides, and 3 specimens used for DNA extraction); found with *Echiniscus regularis* **sp. nov.**, *E. scabrospinosus*, and *E. virginicus*.
- Sample ZA.219: 14 specimens (5 ♀♀, 2 ♂♂, 6 juveniles and 1 larva on slides); found with *Echiniscus intricatus* **sp. nov.**
- Sample ZA.224: 54 specimens (47 ♀♀ and 7 juveniles on slides); found with *Echiniscus imitans* **sp. nov.**, *E. regularis* **sp. nov.**, and *E. scabrospinosus*.
- Sample ZA.230: 84 specimens (41 ♀♀, 42 juveniles and 1 larva on slides); found with *Echiniscus blumi*, *E. regularis* **sp. nov.**, and *E. scabrospinosus*.
- Sample ZA.232: 1 specimen (1 ♀ on a slide); found with *Echiniscus regularis* **sp. nov.**
- Sample ZA.247: 3 specimens (2 ♀♀ and 1 ♂ on slides); found with *Echiniscus imitans* **sp. nov.** and *E. regularis* **sp. nov.**
- Sample ZA.249: 13 specimens (6 ♀♀, 3 ♂♂ and 3 juveniles, 1 larva on slides); found with *E. regularis* **sp. nov.** and *Pseudechiniscus (Pseudechiniscus)* cf. *ehrenbergi*.
- Sample ZA.257: 1 specimen (1 ♀ on a slide); found with *Echiniscus blumi*, *E. longispinosus*, and *Pseudechiniscus (Pseudechiniscus)* cf. *ehrenbergi*.
- Sample ZA.258: 1 specimen (1 ♀ on a slide); found with *Echiniscus blumi* and *E. longispinosus*.
- Sample ZA.260: 4 specimens (3 ♀♀ and 1 juvenile on slides); found with *Doryphoribius bindae*, *Echiniscus baius*, *E. longispinosus*, *E. pellucidus*, *E. scabrospinosus*, and *E. virginicus*.

Description. Mature females (*i.e.* from the third instar onwards; measurements and statistics in Table 35). Medium-sized *Echiniscus* with yellow body and large red eyes; body colour and eyes disappeared soon after mounting in Hoyer's medium. Dactyloid (Fig. 63A, 65A) cephalic papillae (secondary clavae) and (primary) clavae; cirri growing out from bulbous cirrophores. Cirri *A* short. Body appendage configuration: *A-(B)-C-C^{d}-D-D^{d}-E*, with all trunk appendages formed as long spines of similar length (Fig. 63–64). Single asymmetries frequent (Fig. 63B).

Dorsal plates with the sculpturing of the *E. spinulosus* type (Fig. 63–64). Pores mostly minute, regularly distributed. Larger pores present on transverse stripes (ridges) in the anterior portions of the segmental plates I–II. Under PCM, pore rims are darker than the surrounding cuticle, which is a distinctive feature of the species (Fig. 63C, 65D–E). Endocuticular dark rings present only in the largest pores located in the anterior portions of paired segmental plates I–II. Anterior portions of paired segmental plates and the median plate 3 reduced to thin belts of much thicker (darker under PCM) cuticle with more densely arranged pores (Fig. 63C, 64A). The cephalic plate with an anterior incision (Fig. 63A); the cervical (neck) plate poorly developed as a dim greyish belt before the scapular plate. The scapular plate large and uniform, without median or lateral sutures (Fig. 63–64). Transverse belts on the paired segmental plates wide and unsculptured (Fig. 63–64). Anterior and posterior margins of the paired segmental plates with irregular, thickened belts (Fig. 63C). The caudal (terminal) plate with two unsclerotised incisions, without signs of faceting (Fig. 63–64). Ventral cuticle with minute endocuticular pillars distributed throughout the whole venter; only subcephalic plates present, small and roundish (Fig. 65A). Sexpartite gonopore placed anteriorly to legs IV (Fig. 65B), and a trilobed anus between legs IV.

Pedal plates absent, even the dentate collar IV embedded on an unsculptured central portion of leg (Fig. 63A, 65C). Pulvini present (Fig. 64). Spine on leg I and a papilla on leg IV present (Fig. 63A, 64). Claws IV slightly longer than claws I–III. All external claws spurless. All internal claws with large, acute spurs positioned at *ca.* 30% of the claw and strongly divergent from the branch (Fig. 65B–C).

Mature males and sexually dimorphic traits (*i.e.* from the third instar onwards; measurements and statistics in Table 36). Qualitatively like females (Fig. 63B), excluding the circular gonopore. Body size differences: mean body length ±SD: 231 ±20 μm *vs* 195 ±5 μm (one-tailed Welch's *t*-test with N♀♀=20 and N♂♂=6: t_{24}=1.71; p<0.001); scapular plate length: ♀♀ 42.1–51.8 μm *vs* ♂♂ 35.9–39.1 μm; relative length of cephalic papillae: ♀♀ *12.2–18.7 vs* ♂♂ *18.1–21.1* (one-tailed Welch's *t*-test with N♀♀=20 and N♂♂=6: t_{11}=1.80; p<0.001). Body appendage configuration *A-C-C^{d}-D-D^{d}-E*.

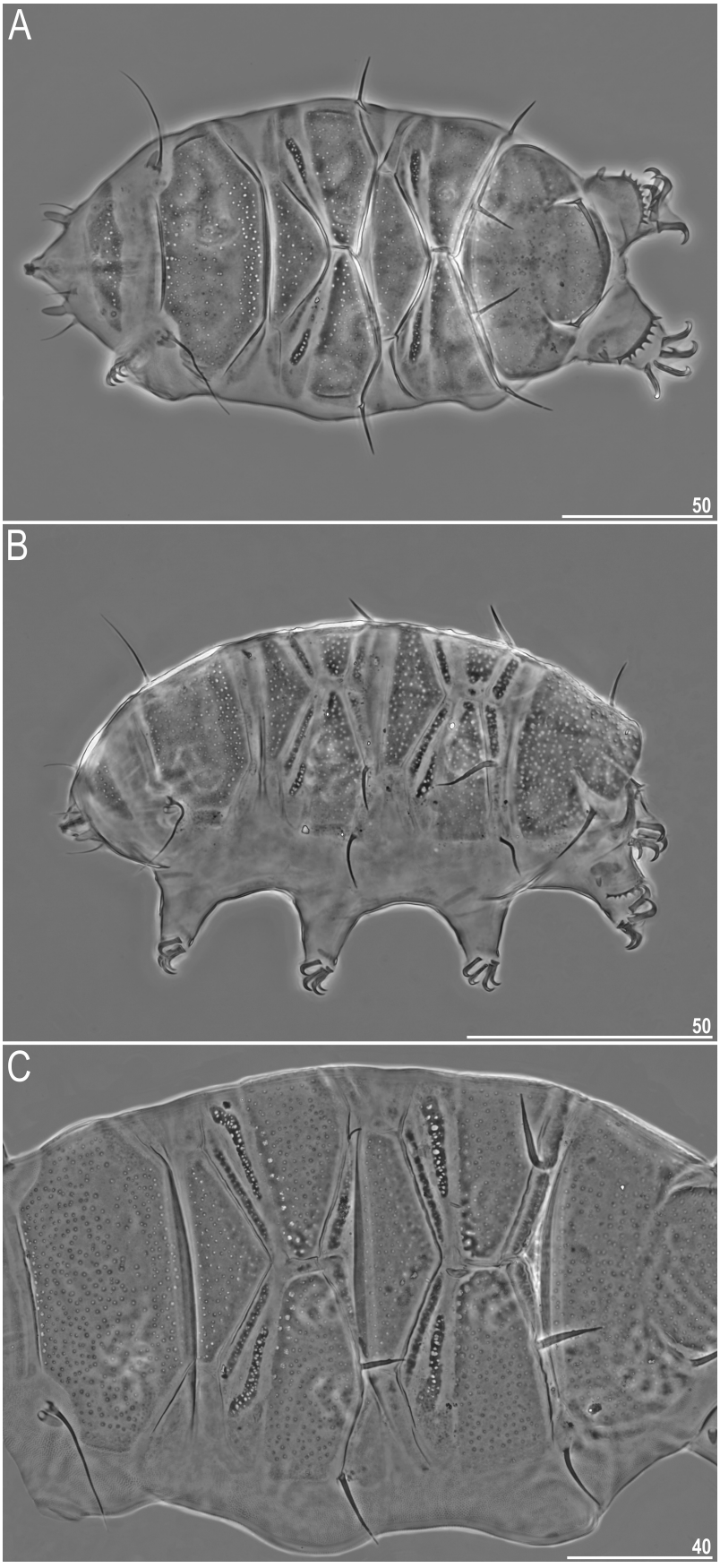

FIGURE 63. *Echiniscus oreas* **sp. nov.** (PCM): A—female habitus (holotype), B—male habitus (paratype), C—dorsal sculpturing (paratype). Scale bars in μm.

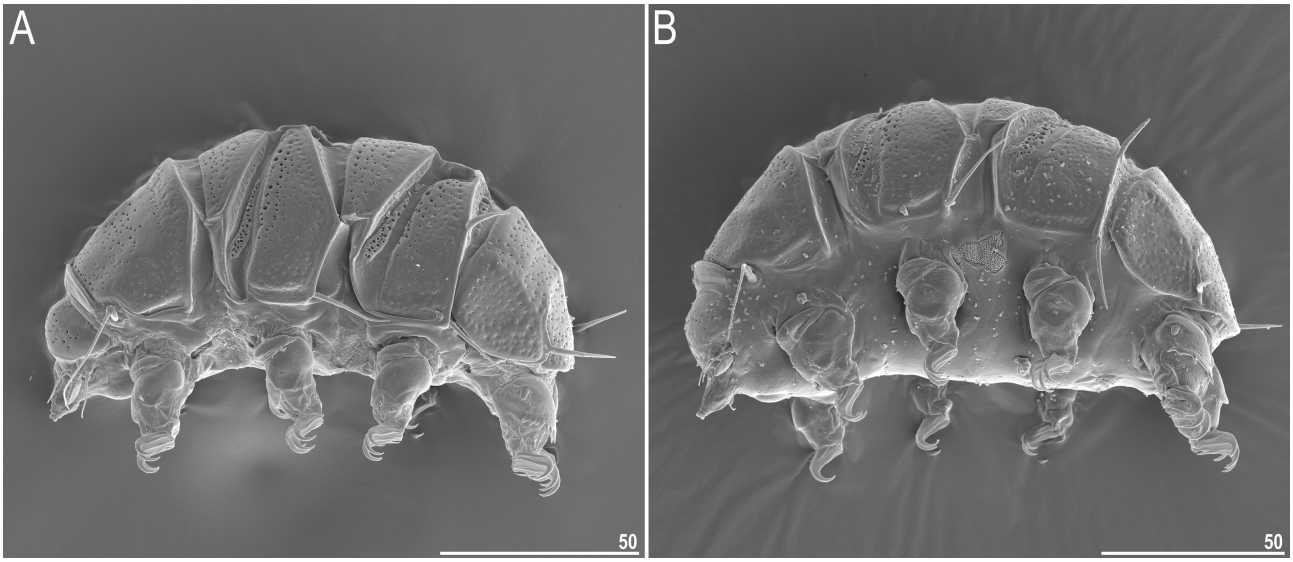

FIGURE 64. Habitus of *Echiniscus oreas* **sp. nov.** (SEM, females in lateral view). Scale bars = 50 µm.

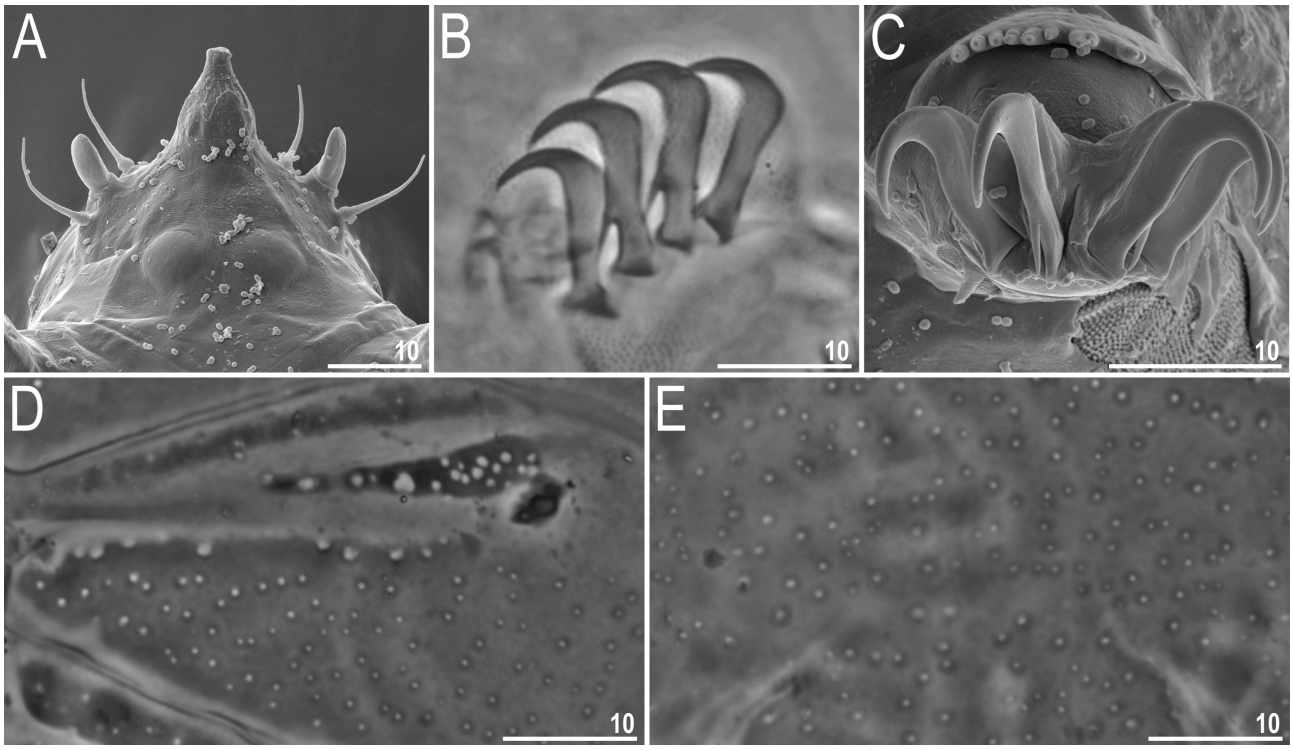

FIGURE 65. Detailed morphology of *Echiniscus oreas* **sp. nov.** (females): A—cephalic appendages and subcephalic plates (SEM), B—claws IV (PCM), C—claws IV (SEM), D—paired segmental plate II, E—caudal (terminal) plate). Scale bars = 10 µm.

Juveniles (*i.e*. from the second instar onwards; measurements and statistics in Table 37). No gonopore. Qualitatively and quantitatively (overlapping morphometric ranges, compare Tables 35, 37) like females.

Larvae (*i.e*. the first instar; measurements and statistics in Table 37). Gonopore and anus absent. Smaller than juveniles (morphometric gap present). Body appendage configuration *A-D*^{d}*-E*. The dorsal sculpturing developed as in adults, with the exception that dark rings surrounding pores are absent.

Eggs. Up to four yellow eggs per exuvia were found.

DNA markers and phylogenetic position. *Echiniscus oreas* **sp. nov.** is the sister species of *E. scabrospinosus* within the *E. spinulosus* complex (Fig. 117). The species closest in COI is *E. similaris* **sp. nov.** (p-distance = 15.8–16.2%), in ITS-1—*E. manuelae*, *E. regularis* **sp. nov.** *E. scabrospinosus*, and *E. tristis* (0.3–1.4%), and in ITS-2—*E. regularis* **sp. nov.** and *E. scabrospinosus* (0.3–0.6%).

TABLE 35. Measurements [in µm] of selected morphological structures of the adult females of *Echiniscus oreas* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Holotype	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	20	186	–	269	*439*	–	*538*	231	*492*	20	*28*	211	*493*
Scapular plate length	20	42.1	–	51.8		–		47.0	–	3.0	–	42.8	–
Head appendages lengths													
Cirrus *internus*	17	8.7	–	14.4	*18.6*	–	*31.6*	11.4	*24.4*	2.0	*3.2*	9.9	*23.1*
Cephalic papilla	20	5.9	–	9.7	*12.2*	–	*18.7*	7.8	*16.5*	0.9	*1.7*	6.9	*16.1*
Cirrus *externus*	18	11.5	–	18.4	*25.2*	–	*35.5*	14.9	*31.5*	2.2	*3.3*	12.2	28.5
Clava	20	4.4	–	7.5	*10.4*	–	*15.6*	6.4	*13.6*	0.8	*1.4*	6.5	*15.2*
Cirrus *A*	20	35.1	–	44.8	*80.6*	–	*94.7*	40.2	*85.6*	2.9	*3.7*	35.1	*82.0*
Cirrus *A*/Body length ratio	20	16%	–	20%		–		17%	–	1%	–	17%	–
Body appendages lengths													
Spine *B*	8	4.3	–	14.2	*9.5*	–	*29.3*	10.6	*22.7*	3.7	*8.0*	?	*?*
Spine *C*	20	16.7	–	26.0	*35.7*	–	*53.9*	22.1	*47.1*	2.4	*4.5*	19.6	*45.8*
Spine C^d	19	5.0	–	16.9	*10.3*	–	*39.9*	11.5	*24.7*	3.7	*8.0*	9.2	21.5
Spine *D*	20	5.2	–	21.3	*10.3*	–	*44.0*	17.4	*37.2*	3.6	*7.5*	15.8	*36.9*
Spine D^d	20	12.4	–	20.0	*26.5*	–	*42.3*	16.5	*35.3*	2.3	*4.5*	16.2	*37.9*
Spine *E*	20	11.4	–	23.0	*23.8*	–	*46.8*	18.9	*40.3*	3.1	*5.9*	16.0	*37.4*
Spine on leg I length	20	2.2	–	5.3	*4.5*	–	*10.5*	3.1	*6.5*	0.8	*1.5*	2.7	6.3
Papilla on leg IV length	18	3.3	–	4.6	*7.1*	–	*9.4*	3.8	*8.1*	0.3	*0.6*	3.4	*7.9*
Number of teeth on the collar	20	8	–	16		–		11.9	–	2.0	–	11	–
Claw I heights													
Branch	20	10.4	–	13.4	*24.0*	–	*26.6*	11.9	*25.3*	0.8	*0.9*	10.4	*24.3*
Spur	20	2.7	–	3.7	*5.6*	–	*7.5*	3.2	*6.7*	0.3	*0.6*	2.8	*6.5*
Spur/branch height ratio	20	22%	–	31%		–		27%	–	2%	–	27%	–
Claw II heights													
Branch	20	9.6	–	13.3	*22.4*	–	*28.0*	11.5	*24.5*	1.0	*1.4*	9.6	*22.4*
Spur	20	2.2	–	3.5	*5.1*	–	*7.3*	3.0	*6.4*	0.3	*0.6*	2.2	*5.1*
Spur/branch height ratio	20	23%	–	32%		–		26%	–	2%	–	23%	–
Claw III heights													
Branch	20	9.5	–	13.2	*22.2*	–	*27.0*	11.8	*25.1*	0.9	*1.1*	9.5	*22.2*
Spur	17	2.5	–	3.7	*5.4*	–	*7.8*	3.1	*6.5*	0.3	*0.7*	2.5	5.8
Spur/branch height ratio	17	21%	–	30%		–		26%	–	2%	–	26%	–
Claw IV heights													
Branch	20	11.7	–	15.8	*26.5*	–	*32.3*	13.7	*29.2*	1.1	*1.5*	11.9	27.8
Spur	20	3.1	–	4.6	*7.0*	–	*9.7*	3.8	*8.1*	0.5	*0.9*	3.4	*7.9*
Spur/branch height ratio	20	22%	–	35%		–		28%	–	4%	–	29%	–

TABLE 36. Measurements [in µm] of selected morphological structures of the adult males of *Echiniscus oreas* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Allotype	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	6	189	–	203	*510*	–	*548*	195	*530*	5	*14*	195	*537*
Scapular plate length	6	35.9	–	39.1		–		36.9	–	1.2	–	36.3	–
Head appendages lengths													
Cirrus *internus*	6	8.7	–	13.4	*23.8*	–	*34.3*	10.5	*28.5*	1.9	*4.4*	12.1	33.3
Cephalic papilla	6	6.5	–	8.1	*18.1*	–	*21.1*	7.2	*19.5*	0.7	*1.3*	6.6	*18.2*
Cirrus *externus*	6	11.4	–	17.9	*31.3*	–	*45.8*	14.6	*39.5*	2.1	*4.7*	14.7	*40.5*
Clava	6	4.0	–	5.9	*11.1*	–	*15.9*	5.2	*14.0*	0.7	*1.7*	5.5	*15.2*
Cirrus *A*	6	27.2	–	40.4	*74.7*	–	*107.5*	34.0	*92.1*	4.8	*11.9*	32.5	*89.5*
Cirrus *A*/Body length ratio	6	14%	–	20%		–		17%	–	2%	–	17%	–
Body appendages lengths													
Spine *C*	6	15.5	–	22.2	*41.9*	–	*61.0*	19.9	*53.9*	2.5	*6.9*	19.5	*53.7*
Spine C^d	6	8.7	–	15.2	*23.5*	–	*41.9*	11.6	*31.6*	2.7	*7.8*	15.2	*41.9*
Spine *D*	5	14.8	–	18.2	*40.5*	–	*48.2*	16.6	*44.9*	1.3	*2.9*	17.5	*48.2*
Spine D^d	6	15.2	–	23.4	*41.1*	–	*64.3*	21.3	*57.7*	3.0	*8.6*	23.0	*63.4*
Spine *E*	6	17.4	–	21.7	*47.0*	–	*60.4*	20.1	*54.7*	1.6	*4.7*	20.9	*57.6*
Spine on leg I length	6	1.9	–	2.9	*5.2*	–	*8.1*	2.4	*6.4*	0.4	*1.1*	2.1	*5.8*
Papilla on leg IV length	6	2.8	–	4.0	*7.7*	–	*11.1*	3.6	*9.7*	0.4	*1.2*	2.8	*7.7*
Number of teeth on the collar	4	12	–	14		–		12.8	–	1.0	–	?	–
Claw I heights													
Branch	6	8.9	–	11.1	*24.1*	–	*30.9*	10.1	*27.5*	0.8	*2.2*	9.9	*27.3*
Spur	6	2.0	–	2.7	*5.5*	–	*7.4*	2.3	*6.3*	0.2	*0.7*	2.4	*6.6*
Spur/branch height ratio	6	20%	–	27%		–		23%	–	3%	–	24%	–
Claw II heights													
Branch	5	9.3	–	10.0	*25.1*	–	*27.9*	9.7	*26.2*	0.4	*1.1*	9.3	*25.6*
Spur	5	2.0	–	2.7	*5.1*	–	*7.4*	2.5	*6.7*	0.3	*0.9*	2.5	*6.9*
Spur/branch height ratio	5	20%	–	28%		–		26%	–	3%	–	27%	–
Claw III heights													
Branch	6	9.3	–	10.3	*25.6*	–	*28.7*	9.9	*26.8*	0.5	*1.1*	9.3	*25.6*
Spur	6	2.0	–	2.7	*5.5*	–	*7.5*	2.4	*6.4*	0.3	*0.7*	2.1	*5.8*
Spur/branch height ratio	6	21%	–	26%		–		24%	–	2%	–	23%	–
Claw IV heights													
Branch	6	10.7	–	12.5	*29.4*	–	*34.8*	11.6	*31.3*	0.7	*2.0*	11.0	*30.3*
Spur	6	2.4	–	3.9	*6.6*	–	*10.0*	3.1	*8.4*	0.5	*1.1*	3.0	*8.3*
Spur/branch height ratio	6	22%	–	32%		–		27%	–	3%	–	27%	–

TABLE 37. Measurements [in µm] of selected morphological structures of the juveniles and a larva of *Echiniscus oreas* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Larva	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	5	149	–	210	*463*	–	*507*	185	*488*	24	*21*	129	*608*
Scapular plate length	5	29.4	–	45.4		–		38.1	–	5.8	–	21.2	–
Head appendages lengths													
Cirrus *internus*	5	6.9	–	12.1	*23.5*	–	*31.8*	10.2	*26.7*	2.0	*3.4*	5.3	*25.0*
Cephalic papilla	5	4.5	–	7.6	*15.3*	–	*20.0*	6.7	*17.4*	1.3	*1.8*	3.6	*17.0*
Cirrus *externus*	5	8.7	–	15.6	*28.0*	–	*38.8*	12.1	*31.7*	2.5	*4.4*	7.0	*33.0*
Clava	5	4.0	–	5.8	*11.5*	–	*15.3*	5.0	*13.2*	0.7	*1.6*	3.7	*17.5*
Cirrus *A*	5	26.0	–	38.9	*85.7*	–	*102.7*	35.7	*93.9*	5.5	*7.1*	24.8	*117.0*
Cirrus *A*/Body length ratio	5	17%	–	21%		–		19%	–	2%	–	19%	–
Body appendages lengths													
Spine *C*	5	14.6	–	23.3	*45.0*	–	*51.3*	18.3	*48.1*	3.2	*2.5*	lacking	
Spine C^d	3	3.2	–	13.6	*8.5*	–	*33.7*	9.9	*24.1*	5.8	*13.6*	lacking	
Spine *D*	3	15.0	–	16.8	*35.2*	–	*44.2*	15.9	*39.8*	0.9	*4.5*	lacking	
Spine D^d	5	11.8	–	19.4	*39.6*	–	*51.1*	17.3	*45.4*	3.1	*5.2*	7.6	*35.8*
Spine *E*	5	12.4	–	19.9	*42.2*	–	*46.5*	16.9	*44.4*	2.9	*1.6*	9.3	*43.9*
Spine on leg I length	3	1.8	–	2.9	*4.8*	–	*6.4*	2.2	*5.8*	0.6	*0.9*	1.0	*4.7*
Papilla on leg IV length	5	2.5	–	3.9	*7.7*	–	*10.3*	3.4	*9.0*	0.5	*1.0*	1.9	*9.0*
Number of teeth on the collar	4	9	–	11		–		9.8	–	1.0	–	6.0	–
Claw I heights													
Branch	5	7.4	–	10.7	*22.5*	–	*27.4*	9.7	*25.5*	1.3	*1.9*	6.4	*30.2*
Spur	5	1.8	–	3.2	*6.1*	–	*8.4*	2.7	*7.0*	0.6	*0.9*	2.2	*10.4*
Spur/branch height ratio	5	24%	–	31%		–		28%	–	3%	–	34%	–
Claw II heights													
Branch	5	6.6	–	10.3	*22.4*	–	*26.3*	9.2	*24.1*	1.5	*1.8*	6.0	*28.3*
Spur	5	1.9	–	3.4	*5.7*	–	*8.9*	2.5	*6.6*	0.6	*1.3*	1.9	*9.0*
Spur/branch height ratio	5	24%	–	34%		–		27%	–	4%	–	32%	–
Claw III heights													
Branch	4	7.2	–	10.6	*23.3*	–	*26.4*	9.3	*24.5*	1.5	*1.3*	6.1	*28.8*
Spur	2	2.4	–	2.9	*6.0*	–	*6.4*	2.7	*6.2*	0.4	*0.3*	2.0	*9.4*
Spur/branch height ratio	2	25%	–	27%		–		26%	–	2%	–	33%	–
Claw IV heights													
Branch	5	7.9	–	12.7	*26.9*	–	*29.9*	10.8	*28.3*	1.8	*1.1*	7.1	*33.5*
Spur	5	2.4	–	3.5	*7.7*	–	*8.3*	3.0	*8.0*	0.4	*0.3*	2.4	*11.3*
Spur/branch height ratio	5	26%	–	30%		–		28%	–	2%	–	34%	–

Type material. 31 ♀♀ and 10 juveniles on slides ZA.204.01–3, ZA.206.01–3, 5–10; holotype: mature ♀ on slide ZA.204.02. Mounted together with 14 ♀♀ of *E. virginicus*, 3 ♀♀ of *E. regularis* **sp. nov.** and 4 ♀♀ of *E. scabrospinosus*. 6 specimens used for DNA extraction, 1 secured as hologenophore.

Type locality. 29°03'33.8''S, 29°22'52.7''E, 1850 m asl: Republic of South Africa, KwaZulu-Natal, Drakensberg, Giants Castle Game Reserve; montane grassland, lichens from rocks and stunted trees (samples ZA.204, 206).

Etymology. From Latin *oreas* = mountain nymph (ὀρειαὶς in Ancient Greek). The name has a twofold sense as

females dominate populations of the species (nymphs were young, beautiful feminine spirits in the Greek mythology) and it occurs exclusively in the mountains. A noun in apposition.

Geographic distribution. Only recorded from South Africa, common in the mountains, especially in their highest parts (Fig. 120G).

Remarks. The new species forms large populations intermingled with other echiniscids.

Differential diagnosis. The species is a classic representative of the *E. spinulosus* group, and can be distinguished from:

- *E. angolensis*, probably widely distributed in Africa (da Cunha & do Nascimento Ribeiro 1964; McInnes *et al*. 2017; the species is inadequately described, thus there is a high risk of misidentification with similar species), by a larger body size (adult females 186–269 μm long in *E. oreas* **sp. nov.** *vs* adult females 132–183 μm long in *E. angolensis*), and by the morphology of spines D^d and *E* (smooth in *E. oreas* **sp. nov.** *vs* rough and slightly serrated in *E. angolensis*);
- *E. crassispinosus*, by the morphology of spine D^d (as thin as the remaining appendages in *E. oreas* **sp. nov.** *vs* massive and much thicker than the remaining appendages in *E. crassispinosus*), and by the type of sculpture (minute pores with dark circumporal rings visible under PCM in *E. oreas* **sp. nov.** *vs* large pores without dark circumporal rings in *E. crassispinosus*);
- *E. dreyfusi*, insufficiently described based on animals from Brazil (de Barros 1942), by the body appendage configuration (*A-(B)-C-*C^d*-D-*D^d*-E* in *E. oreas* **sp. nov.** *vs A-B-C-D-*D^d*-E* in *E. dreyfusi*), and by spurs on internal claws (present in *E. oreas* **sp. nov.** *vs* absent in *E. dreyfusi*);
- *E. marcusi*, a likely Australian endemic (Pilato *et al*. 1989), by the morphology of trunk lateral appendages (long spines in *E. oreas* **sp. nov.** *vs* minute triangular spicules in *E. marcusi*), and by the dorsal sculpturing (*striae* absent in *E. oreas* **sp. nov.** *vs striae* present in the anterior portion of the median plate 2 and in the area adjacent to the transverse belts in paired segmental plates I–II in *E. marcusi*);
- *E. marginatus*, with a disjunctive distribution embracing Hawaiian Islands (Binda & Pilato 1994) and South Africa (present study), by the body appendage configuration (*A-(B)-C-*C^d*-D-*D^d*-E* in *E. oreas* **sp. nov.** *vs A-C-D-*D^d*-E* in *E. marginatus*), and by the dorsal sculpturing (posterior portions of the median and paired segmental plates with pores in *E. oreas* **sp. nov.** *vs* posterior portions of the median and paired segmental plates without pores in *E. marginatus*, see Pilato *et al*. 2008);
- *E. ornamentatus*, currently considered a Tanzanian endemic (Gąsiorek & Kristensen 2018), by the body appendage configuration (*A-(B)-C-*C^d*-D-*D^d*-E* in *E. oreas* **sp. nov.** *vs A-(B)-C-D-*D^d*-E* in *E. ornamentatus*), and by faceting of the scapular and caudal plates (absent in *E. oreas* **sp. nov.** *vs* present in *E. ornamentatus*);
- *E. scabrospinosus*, characterised by a wide geographic distribution covering the Iberian Peninsula and many African locales (Fontoura 1982; Pilato *et al*. 2008; McInnes *et al*. 2017), by the body appendage configuration (*A-(B)-C-*C^d*-D-*D^d*-E* in *E. oreas* **sp. nov.** *vs A-C-D-*D^d*-E* in *E. scabrospinosus*), the presence of endocuticular rings (generally absent in *E. oreas* **sp. nov.** *vs* present and evident in all pores in *E. scabrospinosus*), and by lateral non-porous plate portions (absent in *E. oreas* **sp. nov.** *vs* present in *E. scabrospinosus*);
- *E. tristis*, a likely Afrotropical species (Gąsiorek & Kristensen 2018; Bartylak *et al*. 2019; present study), by the type of sculpture (pores with dark circumporal rings visible under PCM in *E. oreas* **sp. nov.** *vs* pores without dark circumporal rings in *E. tristis*);
- *E. tropicalis*, a species widely distributed in the Indian Ocean basin (Binda & Pilato 1995b; Kiosya *et al*. 2021), by the morphology of trunk appendages (long spines in *E. oreas* **sp. nov.** *vs* minute triangular spicules in *E. tropicalis*), and by the heteromorphy of spurs on internal claws (spurs I–IV homomorphic in *E. oreas* **sp. nov.** *vs* spurs IV different in size and shape from spurs I–III in *E. tropicalis*).

African *E. ornamentatus* and *E. tristis* are morphologically closest to *E. oreas* **sp. nov.**, but the presented phylogenetic analysis (Fig. 117) negatively verified their close relationship within the *E. spinulosus* group.

Raw measurements. Supplementary Materials (SM.03) and Tardigrada Register (www.tardigrada.net/register/0092.htm).

20. Echiniscus pellucidus Gąsiorek, Bochnak, Vončina & Michalczyk, 2021

Figures 66–67

Data source:

A total of 7 specimens (4 ♀♀, 2 juveniles and 1 specimen of unknown instar/sex):

- Sample ZA.204: 1 specimen (1 specimen observed *in vivo* under microscope and used for DNA extraction); found with *Echiniscus oreas* **sp. nov.**
- Sample ZA.228: 1 specimen (1 ♀ on a slide); found with *Cornechiniscus madagascariensis*.
- Sample ZA.259: 1 specimen (1 ♀ on a slide); found with *Echiniscus scabrospinosus* and *Pseudechiniscus (Pseudechiniscus)* cf. *ehrenbergi*.
- Sample ZA.260: 4 specimens (2 ♀♀ and 2 juveniles on slides); found with *Echiniscus baius*, *E. longispinosus*, *E. oreas* **sp. nov.**, *E. scabrospinosus*, and *E. virginicus*.

Shortened description. Body appendage formula *A-C-C^{d}-D-E*. All appendages in the form of cirri. Dorsal sculpturing of the *E. merokensis* type, with well-developed *striae* between multangular elements of endocuticle (Fig. 66A, 67). Oval and densely granulated genital plates (Fig. 66C). Pedal plates marked as grey zones in central leg portions; pulvini I–III marked as swollen dark grey belts at proximal leg portions (Fig. 66A). External claws spurless, internal ones with heteromorphic spurs positioned at *ca.* 20% (I–III) or 30–35% (IV) of the claw height (Fig. 66B, D–E).

DNA markers and phylogenetic position. *Echiniscus pellucidus* is the sister species of *E. merokensis* (Fig. 117). The closest species in COI is *E. siticulosus* Gąsiorek & Michalczyk, 2020 (p-distance = 15.2–16.0%), and *E. merokensis* in ITS (ITS-1: 2.0–2.6%, ITS-2: 1.8%).

Geographic distribution. This possibly parthenogenetic species has a documented disjunct distribution embracing Neotropical Patagonia (Gąsiorek *et al*. 2021c) and southern Afrotropics. This could be interpreted in two ways: either as a sign of Gondwanan ancestry or a secondary dispersal event. In South Africa, rare and restricted to Drakensberg (Fig. 120I).

Remarks. In contrast to the Neotropical examples (Gąsiorek *et al*. 2021c), the Afrotropical individuals may have less regular sculpturing (Fig. 67B), and spines *D^{d}* are always absent.

21. Echiniscus perarmatus Murray, 1907

Figures 68–72, Table 38

Data source:

A total of 15 specimens (14 ♀♀ and 1 juvenile):

- Sample ZA.214: 10 specimens (9 ♀♀ on slides and 1 juvenile used for DNA extraction and secured as a hologenophore); found with *Echiniscus africanus*, *E. baius*, *E. virginicus*, *E. oreas* **sp. nov.**, *Pseudechiniscus (P.)* cf. *ehrenbergi*, *Doryphoribius bindae*, and *Ramazzottius szeptycki*.
- Sample ZA.362: 4 specimens (4 ♀♀ on slides); found with *Ramazzottius szeptycki*.
- Sample ZA.364: 1 specimen (1 ♀ on a slide); found with *Pseudechiniscus (P.)* cf. *ehrenbergi*, *P. (P.) linnaei* **sp. nov.**, and *P. (Meridioniscus) wallacei* **sp. nov.**
- New Asian records: Sample ID.518: 1°51’20”S, 120°19’30”E, 1 311 m asl: Malay Archipelago, Celebes, Sulawesi Tengah, Lore Lindu, Bada Lembah; moss+lichen from tree bark in a mountain tropical forest (12 specimens: 2 ♀♀ and 2 juveniles on slides, 5 ♀♀ on a SEM stub 15.20, and 3 specimens used for DNA extraction); coll. 25.08.2017, Artur Oczkowski & Piotr Gąsiorek; Sample ID.850: 3°10’37’’S, 129°03’04’’E, 331 m asl: Malay Archipelago, Moluccas, Seram Tengah, pass between Triana and Jerili/Sawai; moss+lichen from a palm tree in mountain tropical forest (3 specimens: 1 ♀ and 1 juvenile on slides, and 1 specimen used for DNA extraction); coll. 01.07.2018, Łukasz Krzywański & Piotr Gąsiorek; Sample MM.010: 20°38’28”N, 97°04’14”E, 1 333 m asl: Indochinese Peninsula, Burma, Szan, Kakku Pagodas, Taunggyi; moss+lichen from a tree in rural environment (5 specimens: 1 ♀ on slides and 4 specimens used for DNA extraction); coll. 21.02.2019, Katarzyna Vončina.

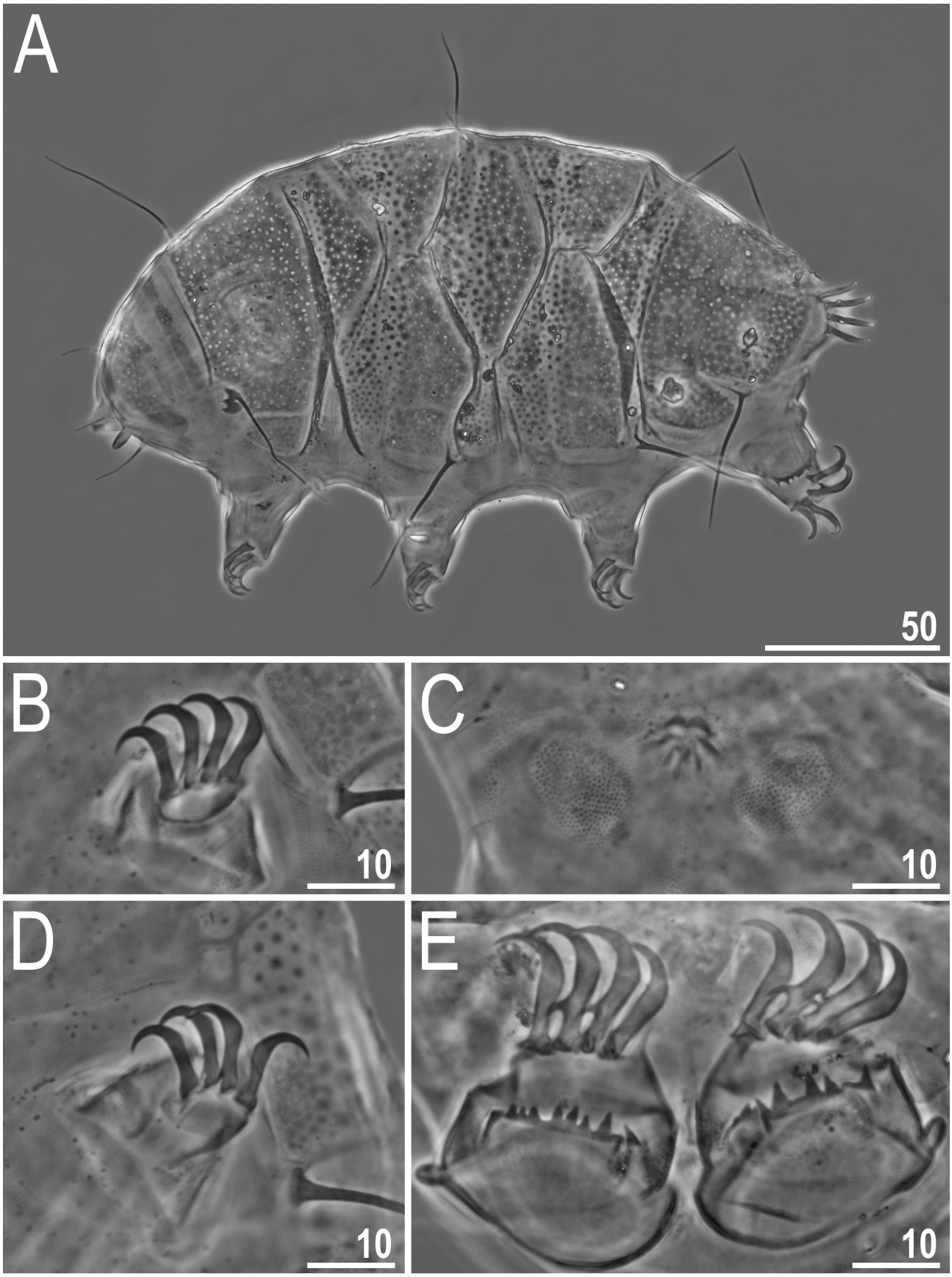

FIGURE 66. Detailed morphology of *Echiniscus pellucidus* Gąsiorek *et al*., 2021 (PCM, females): A—habitus, dorsolateral view, B—claws II, C—genital plates and gonopore, D—claws III, E—claws IV. Scale bars in µm.

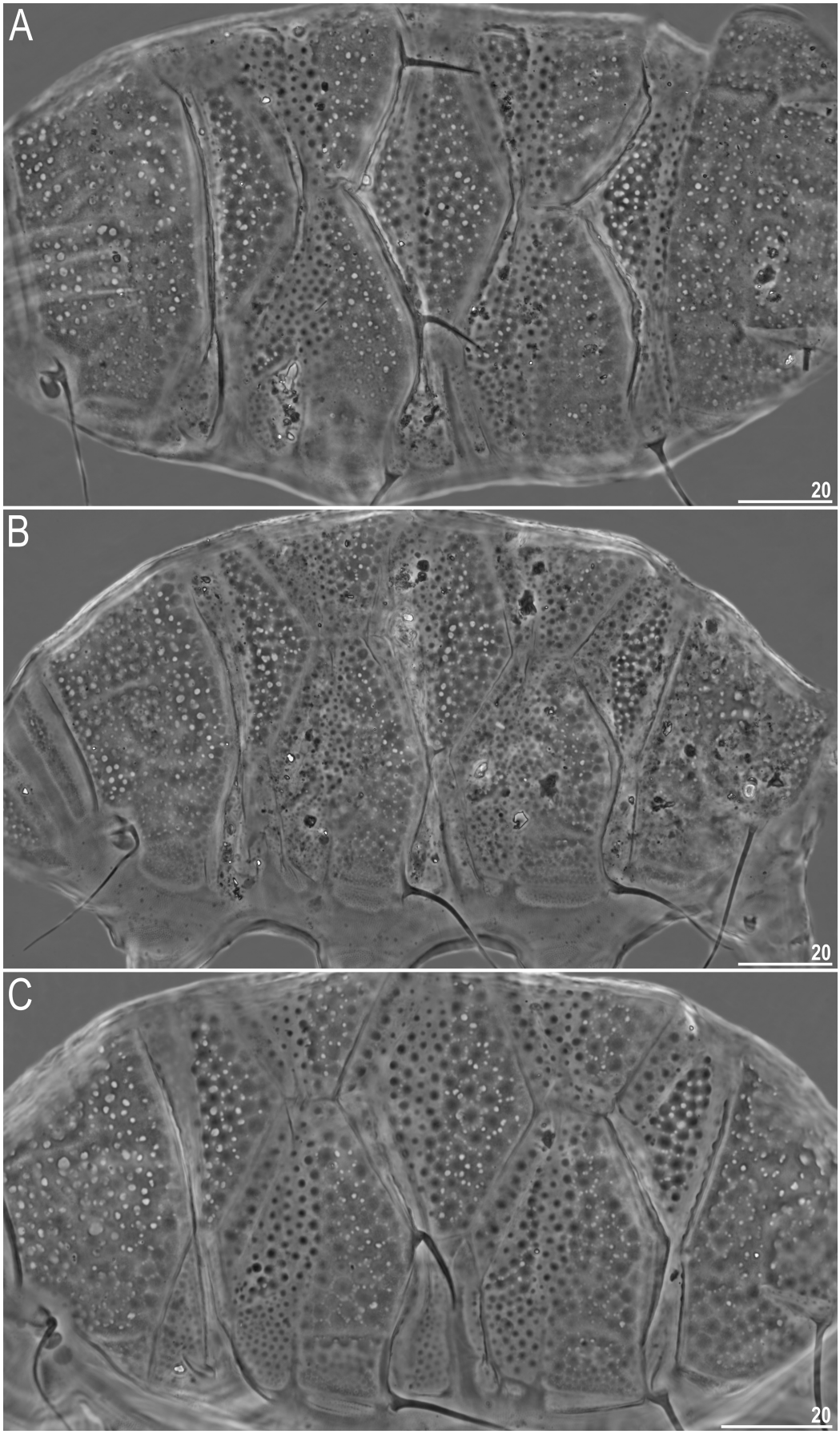

FIGURE 67. Dorsal plate sculpturing of *Echiniscus pellucidus* (PCM): A, B—females, C—juvenile. Scale bars in μm.

Literature:

- Original description: Murray (1907a).
- Later records: Marcus (1936), Grigarick *et al*. (1983), Séméria (1985), Pilato & Binda (1990), Binda *et al*. (2001), Kaczmarek & Michalczyk (2010), Meyer *et al*. (2013), Lisi *et al*. (2017), McInnes *et al*. (2017), Kiosya *et al*. (2021).

Description. Mature females (*i.e*. from the third instar onwards; measurements and statistics in Table 38). Medium-sized *Echiniscus* with dark orange, plump body (Fig. 68A, 69A, 70) and large red eyes; body colour and eyes disappeared soon after mounting in Hoyer's medium. Dactyloid cephalic papillae (secondary clavae) and (primary); cirri growing out from bulbous cirrophores. Cirri *A* short. Body appendage configuration *A-C-D-(D^d)-E*; appendages *C* and *D* are minuscule spicules, whereas appendage *E* is a cirrus, usually slightly longer than cirrus *A*. Single asymmetries frequent.

Dorsal plates with densely arranged endocuticular pillars and regularly, but more sparsely distributed pores; Fig. 68C–D, 71A–B). Anterior portions of paired segmental plates I–II smooth (Fig. 68A, C, 69A, 70). The cephalic plate semicircular; the cervical (neck) plate poorly developed as a dim, thin belt before the scapular plate. The scapular plate large and uniform, without median or lateral sutures. Median plates 1–2 unipartite, m3 absent. The caudal (terminal) plate with two unsclerotised incisions, without signs of faceting (Fig. 68A, D), but with a continuous row of minuscule teeth at its posteriormost margin (Fig. 71B), as originally reported by Claxton (2004). Ventral cuticle with a delicate, dense wrinkling; a pair of subcephalic, trapezoid plates that may merge into single large plate (Fig. 72A), and a pair of genital plates (Fig. 72B). Sexpartite gonopore placed between genital plates, and a trilobed anus between legs IV.

Pedal plates present as accumulations of endocuticular pillars in the centre of legs (Fig. 68B). Pulvini weakly outlined. Spines on legs I–III (Fig. 68A–B, 69A) and a papilla on leg IV present (Fig. 68A, 69A, 70B). Claws I–IV of similar heights. All external claws spurless. All internal claws with large, acute spurs positioned at *ca.* 25–35% of the claw height (Fig. 68B, 71C, 72C–D).

Juveniles (*i.e*. from the second instar onwards). Qualitatively and quantitatively like females (Fig. 69B), except for the lack of the gonopore.

Larvae. Two-clawed individuals with the dorsal sculpturing and appendages developed as in adults (Fig. 69C). No gonopore and anus.

Eggs. Unknown.

DNA markers and phylogenetic position. All analyses indicated the affinity of *E. perarmatus* within the *E. virginicus* complex at the base of the *Echiniscus* phyletic tree (Fig. 117). The species closest in COI are the representatives of the *blumi-canadensis* complex, *E. lineatus*, and *E. quadrispinosus* (p-distance = 13.9–15.2%), in ITS-1—*E. lineatus* and *E. virginicus* (6.0–7.1%), and in ITS-2—*E. hoonsooi* Moon & Kim, 1990 (4.4–4.7%). The ranges of intraspecific variability are narrow in all three fast evolving markers: COI—0.6–1.2%, ITS-1—0.3–1.1%, and ITS-2 (gene fragment did not amplify for the Mauritian material)—0.3–0.9%.

Neotype material. 7 ♀♀ on slides ZA.214.01–6, 12; neotype: mature ♀ on slide ZA.214.06. 2 ♀♀ and 1 juvenile used for DNA extraction and secured as hologenophore.

Neotype locality. 29°03'3.4''S, 29°24'7.4''E, 1520 m asl: Republic of South Africa, KwaZulu-Natal, Drakensberg, Giants Castle Game Reserve; secondary forest, lichens from a tree trunk (sample ZA.214).

Etymology. From Latin *perarmo* = to arm/equip well. The name refers to numerous leg and trunk appendages in the form of spines in *E. perarmatus*. An adjective in the nominative singular.

Geographic distribution. The species is very rare in South Africa (Fig. 120G). A widely distributed pantropical-subtropical taxon (Marcus 1936; Pilato & Binda 1990; McInnes *et al*. 2017). With the genetically verified localities embracing South Africa, Mauritius, and several Asian sampling sites, the conspecificity of Australian, Neotropical and southern Nearctic populations seems probable (Grigarick *et al*. 1983; Séméria 1985; Claxton 2004; Kaczmarek & Michalczyk 2010; Meyer *et al*. 2013; Lisi *et al*. 2017).

Remarks. According to the original description, the species is equipped with spicules *B* and spines *D^d*, but these were absent in the Afrotropical populations. This was also the most frequent morphotype present in the Malay Archipelago and Indochina, although the morphotype depicted by Murray was occasionally also found in Asia (Fig. 69A–B).

Differential diagnosis. Leg spines I–III and the morphology of trunk appendages make *E. perarmatus* a unique taxon among all *Echiniscus* spp. Nevertheless, the phylogenetic analysis clearly shows that the species belongs to *Echiniscus*.

Raw measurements. Supplementary Materials (SM.03) and Tardigrada Register (www.tardigrada.net/register/0093.htm).

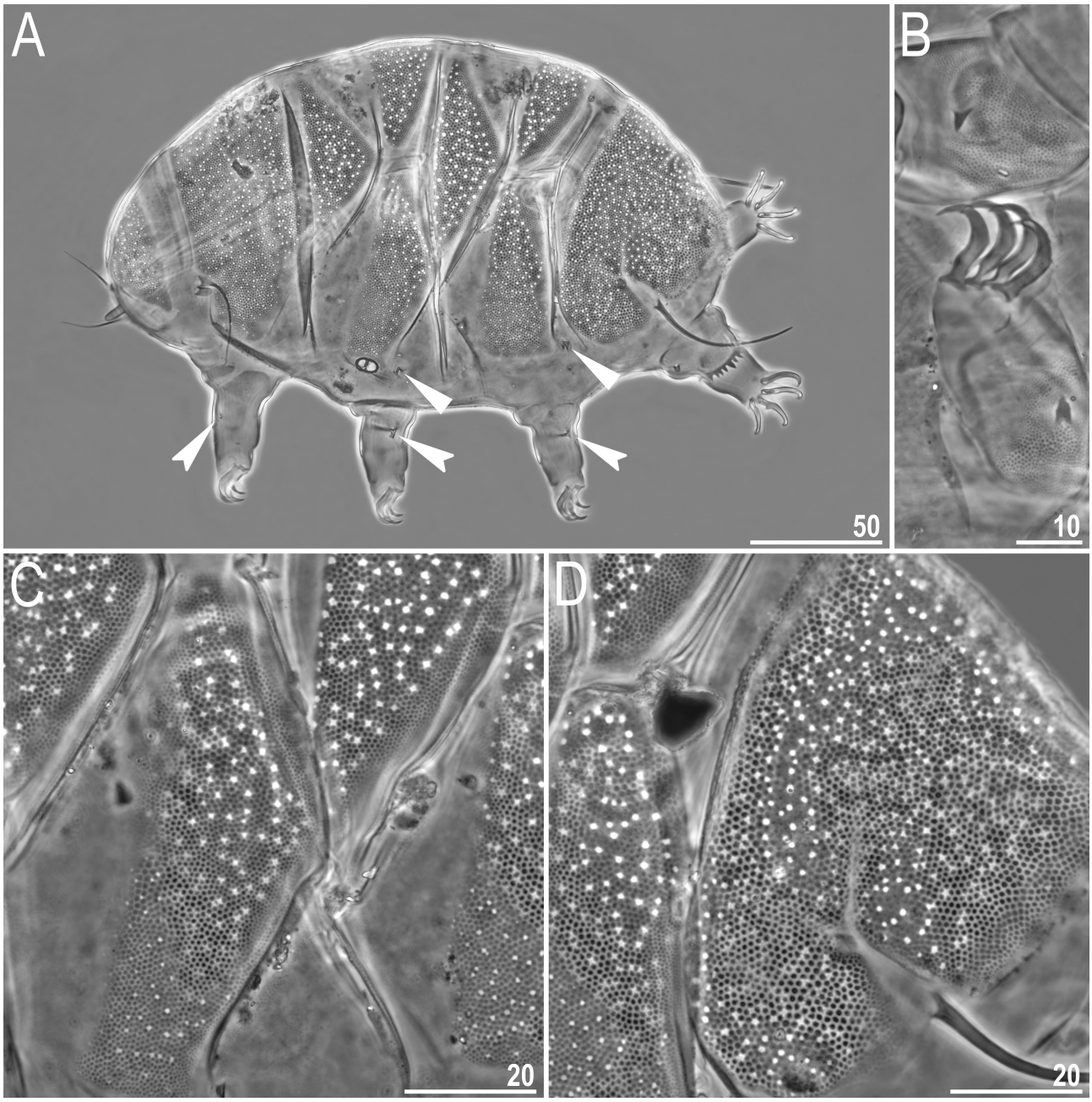

FIGURE 68. Detailed morphology of *Echiniscus perarmatus* Murray, 1907 (PCM, neotype from South Africa): A—habitus (arrowheads indicate minute lateral spicules, and incised arrowheads point out spines I–III, B—claws II (spines II–III visible), C—dorsal sculpturing of paired segmental and median plates, D—dorsal sculpturing of the caudal (terminal) plate. Scale bars in μm.

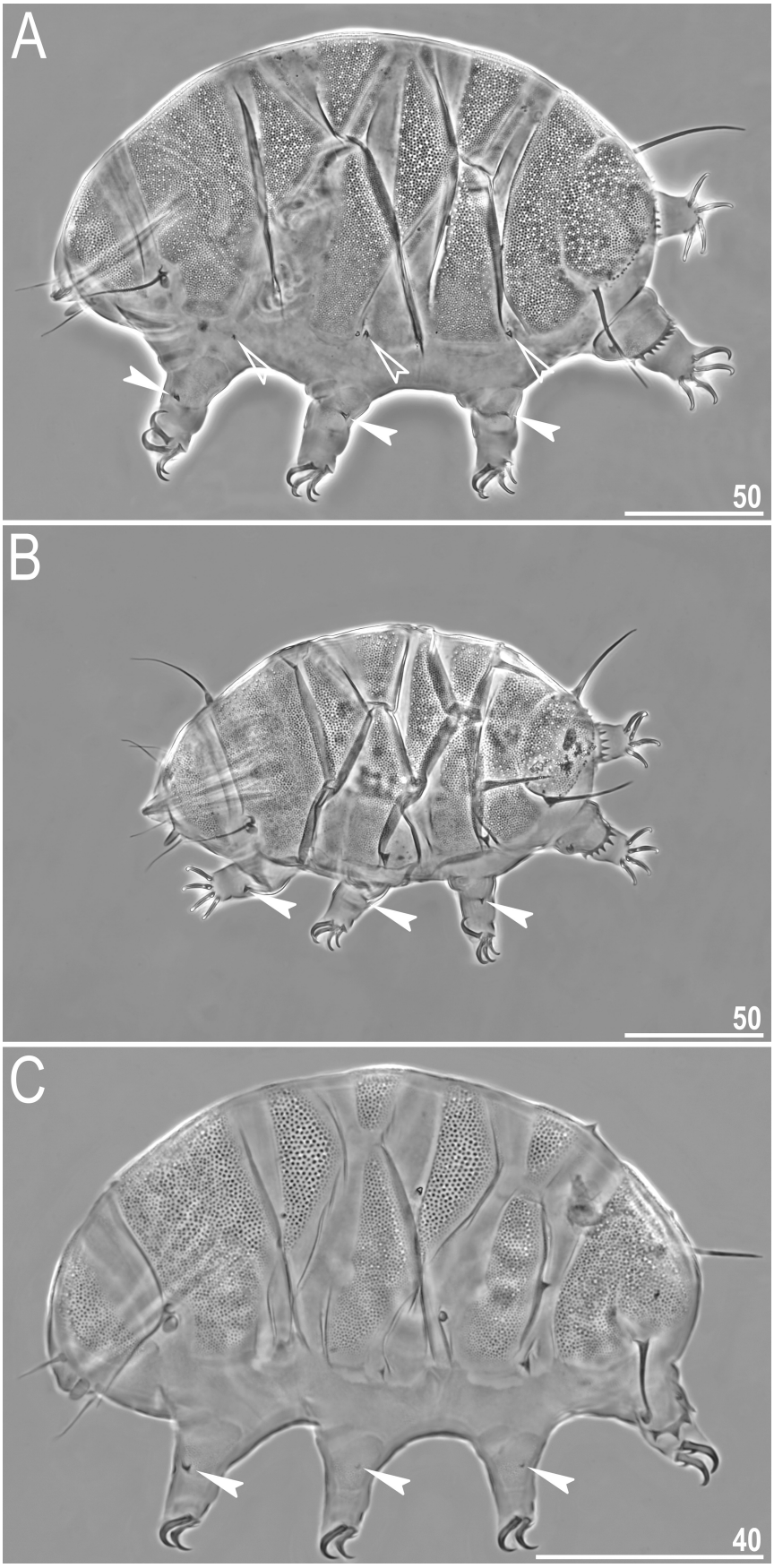

FIGURE 69. Habitus and intraspecific variability of *Echiniscus perarmatus* (PCM, Asian examples): A—female in dorsolateral view, B—juvenile in dorsolateral view, C—larva in dorsolateral view. Incised arrowheads point out spines I–III, and empty incised arrowheads indicate lateral spicules. Scale bars in µm.

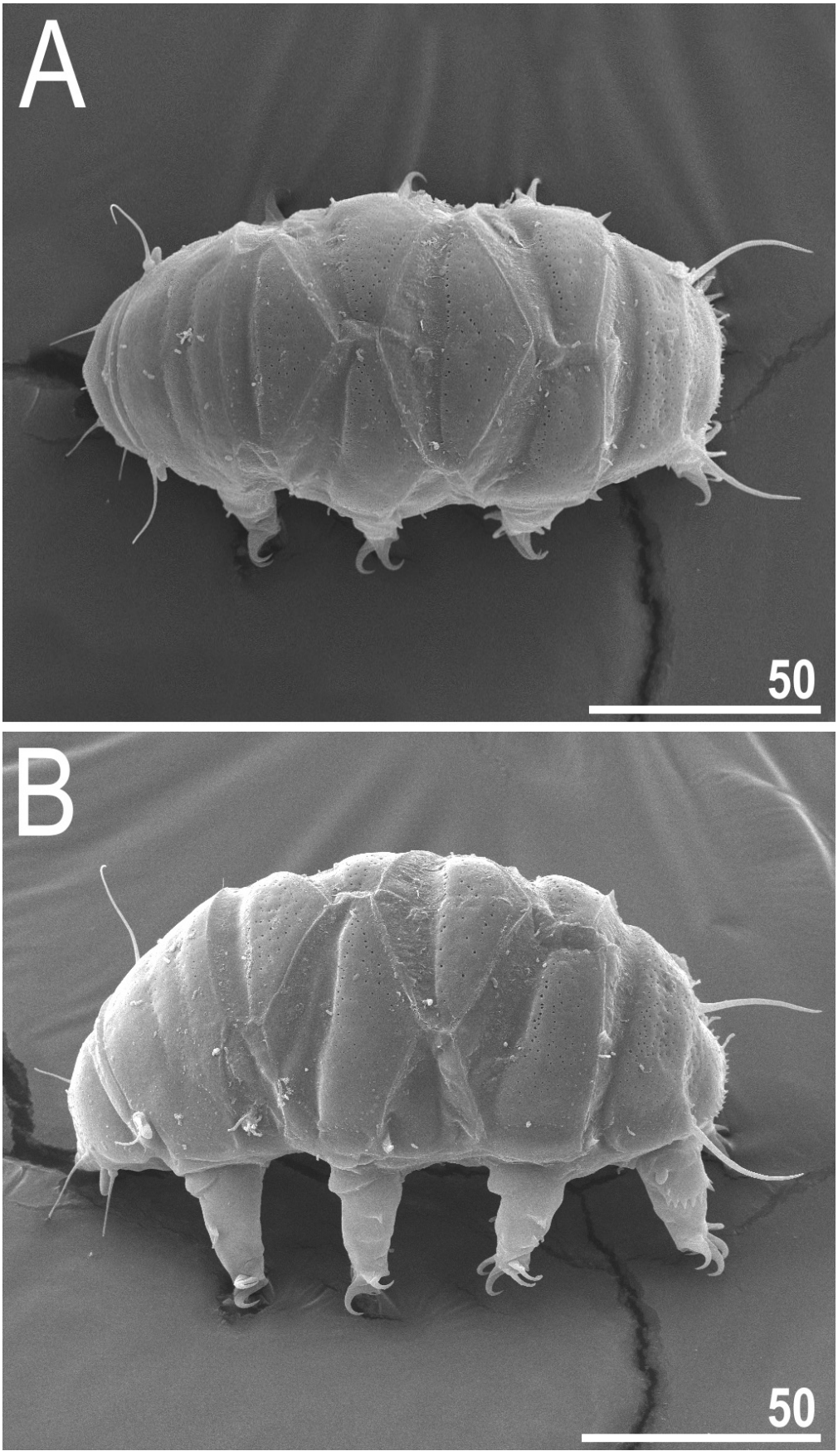

FIGURE 70. Habitus of *Echiniscus perarmatus* (SEM, Asian examples): A—female in dorsal view, B—female in lateral view. Scale bars = 50 μm.

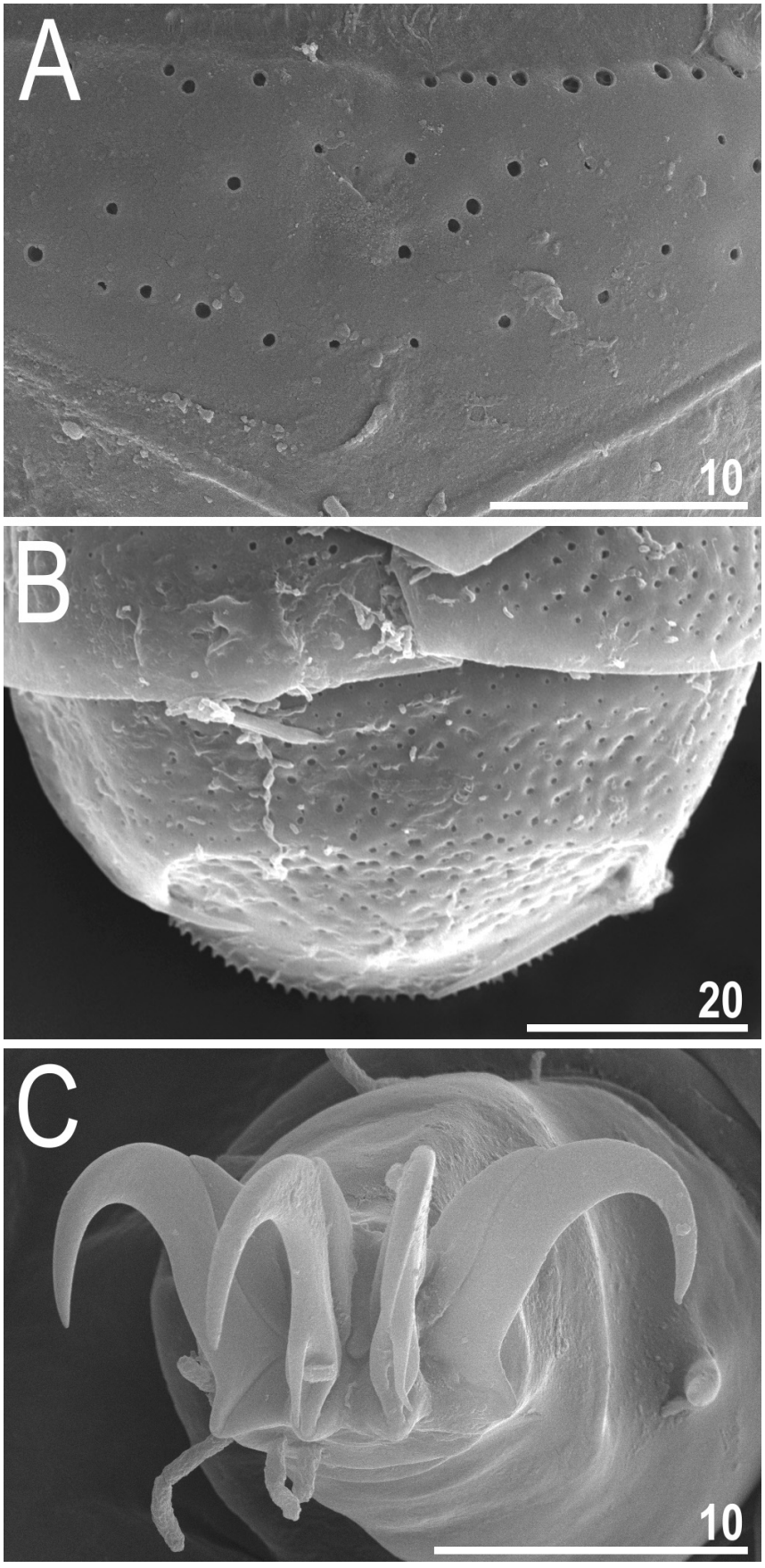

FIGURE 71. Morphological details of *Echiniscus perarmatus* (SEM, Asian examples): A—pores in the median plate 2, B—caudal plate with a line of posteriormost teeth, C—claws II. Scale bars in μm.

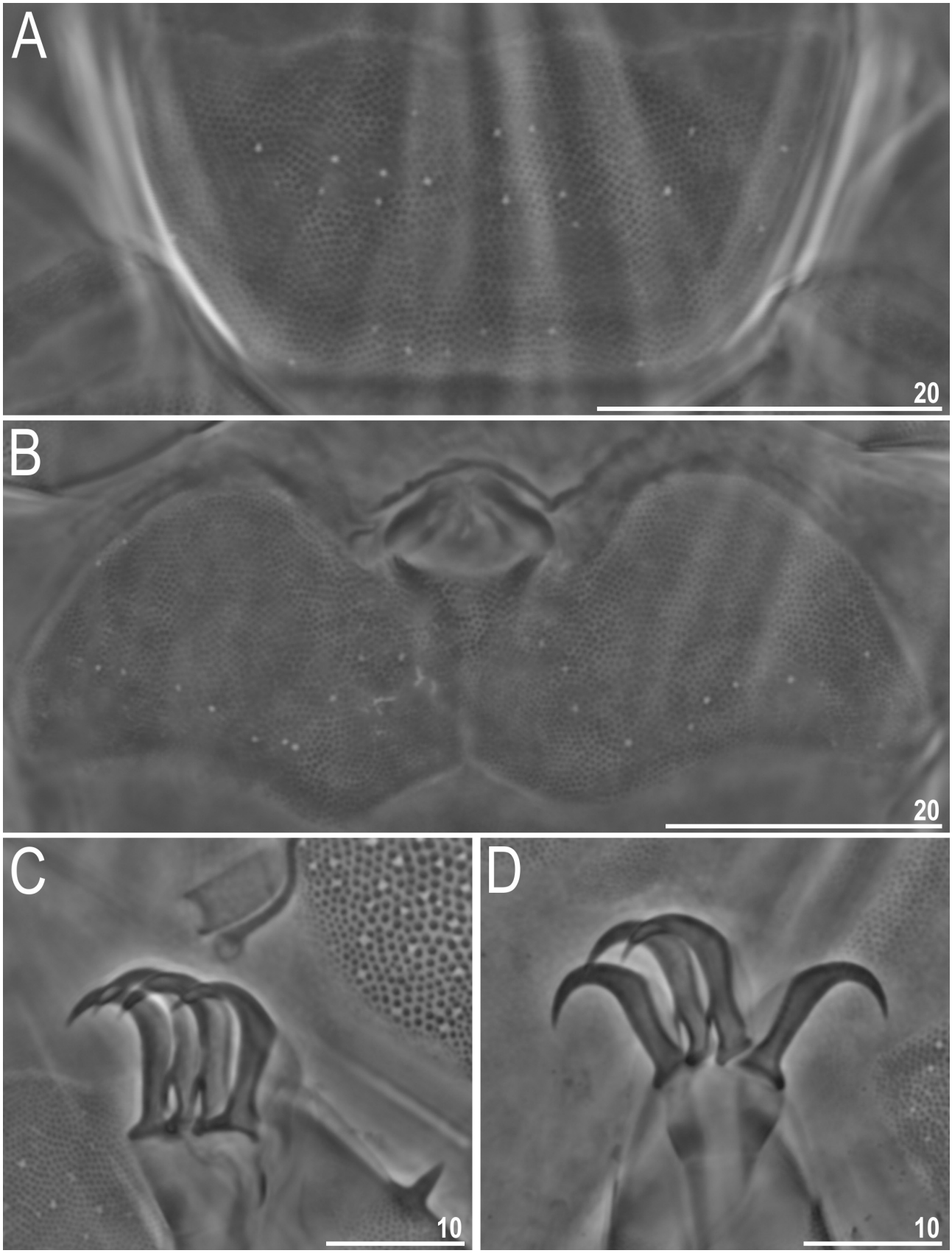

FIGURE 72. Morphological details of *Echiniscus perarmatus* (PCM, Asian examples): A—subcephalic plate, B—genital plates and gonopore, C—claws I, D—claws III. Scale bars in μm.

TABLE 38. Measurements [in µm] of selected morphological structures of the adult females of *Echiniscus perarmatus* mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Neotype	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	10	191	–	251	*398*	–	*479*	221	*442*	23	*25*	236	*462*
Scapular plate length	11	42.7	–	60.4		–		50.3	–	5.3	–	51.1	–
Head appendages lengths													
Cirrus *internus*	9	18.1	–	24.1	*34.3*	–	*47.2*	21.2	*41.7*	1.9	*3.4*	24.1	*47.2*
Cephalic papilla	11	6.4	–	8.9	*12.4*	–	*18.8*	8.0	*16.1*	0.8	*2.1*	8.0	*15.7*
Cirrus *externus*	11	19.9	–	25.1	*40.6*	–	*52.7*	22.7	*45.4*	1.7	*3.4*	25.0	*48.9*
Clava	9	5.4	–	7.1	*9.4*	–	*14.8*	6.3	*12.7*	0.5	*1.8*	7.1	*13.9*
Cirrus *A*	9	34.4	–	46.9	*76.2*	–	*96.8*	41.7	*83.8*	4.2	*5.9*	42.6	*83.4*
Cirrus *A*/Body length ratio	9	17%	–	22%		–		19%	–	1%	–	18%	–
Body appendages lengths													
Cirrus *E*	11	26.5	–	59.6	*50.8*	–	*116.6*	43.5	*87.4*	11.0	*24.5*	59.6	*116.6*
Spine on leg I length	11	2.3	–	3.7	*4.4*	–	*6.9*	2.9	*5.8*	0.5	*0.8*	2.4	*4.7*
Spine on leg II length	11	2.3	–	4.4	*4.8*	–	*8.4*	3.2	*6.3*	0.7	*1.2*	3.9	7.6
Spine on leg III length	10	2.4	–	4.0	*4.6*	–	*7.1*	3.0	*5.9*	0.5	*0.7*	3.0	*5.9*
Papilla on leg IV length	11	3.4	–	4.5	*6.5*	–	*8.6*	3.7	*7.5*	0.4	*0.7*	3.5	*6.8*
Number of teeth on the collar	11	10	–	17		–		13.7	–	2.3	–	15	–
Claw I heights													
Branch	11	11.1	–	15.8	*23.3*	–	*32.1*	13.4	*26.8*	1.4	*2.9*	15.8	*30.9*
Spur	8	2.4	–	3.6	*5.2*	–	*8.0*	3.2	*6.4*	0.4	*0.9*	3.6	*7.0*
Spur/branch height ratio	8	22%	–	26%		–		24%	–	2%	–	23%	–
Claw II heights													
Branch	11	10.4	–	14.1	*21.0*	–	*27.1*	12.2	*24.2*	1.2	*1.6*	13.0	*25.4*
Spur	6	2.6	–	3.0	*5.2*	–	*6.6*	2.8	*5.8*	0.2	*0.4*	?	*?*
Spur/branch height ratio	6	21%	–	27%		–		24%	–	2%	–	?	–
Claw III heights													
Branch	11	9.9	–	13.2	*21.7*	–	*26.2*	12.1	*24.1*	1.0	*1.7*	13.2	*25.8*
Spur	6	2.6	–	3.5	*4.9*	–	*6.3*	2.9	*5.6*	0.3	*0.5*	?	*?*
Spur/branch height ratio	6	21%	–	27%		–		24%	–	2%	–	?	–
Claw IV heights													
Branch	10	12.3	–	16.1	*24.3*	–	*33.3*	14.5	*28.5*	1.4	*2.6*	16.1	*31.5*
Spur	7	3.0	–	4.1	*5.6*	–	*7.8*	3.5	*6.7*	0.4	*0.9*	?	*?*
Spur/branch height ratio	7	21%	–	28%		–		24%	–	2%	–	?	–

22. Echiniscus pusae Marcus, 1928

Literature:

- Original description: Murray (1907a) in Marcus (1928).
- Later records: Pilato *et al*. (2003), Gąsiorek & Kristensen (2018).

Geographic distribution. A very rare species, recorded in South Africa only once as an undescribed species (Murray 1907a), later elevated to the species rank (Marcus 1928). Possibly with a pantropical-subtropical distribu-

tion (Marcus 1928; Pilato *et al*. 2003; Claxton 2004; McInnes *et al*. 2017; Gąsiorek & Kristensen 2018; Bochnak *et al*. 2020), although no DNA markers are available. All records outside the type locality must be verified genetically to exclude species crypsis and confidently delineate the geographic range of the species.

DNA markers and phylogenetic position. Unknown.

Remarks. The presence of the mixed type of sculpturing on the dorsum, *i.e*. pores of the *E. blumi-canadensis* type in the scapular and caudal (terminal) plates and the dominant endocuticular pillars with epicuticular ornamentation of the *E. virginicus* type in the median and paired segmental plates, suggests affinity to the *E. africanus* complex of species.

23. Echiniscus regularis sp. nov. Gąsiorek, Morek & Michalczyk

urn:lsid:zoobank.org:act:24CF4728-4690-41CA-A963-5FE8795BD3D1

Figures 73–76, Tables 39–41

Data source:

A total of 637 specimens (353 ♀♀, 9 ♂♂, 186 juveniles, 19 larvae, and 70 specimens of unknown instar/sex):

- Sample ZA.183: 3 specimens (3 ♀♀ on slides); found with *Doryphoribius maasaimarensis*, *Echiniscus oreas* **sp. nov.**, *E. scabrospinosus*, *Pseudechiniscus (P.)* cf. *ehrenbergi*, *P. (Meridioniscus) wallacei* **sp. nov.**, and *Ramazzottius szeptycki*.
- Sample ZA.185: 4 specimens (4 ♀♀ on slides); found with *Echiniscus oreas* **sp. nov.**, *E. scabrospinosus*, and *E. virginicus*.
- Sample ZA.206: 3 specimens (3 ♀♀ on slides); found with *Echiniscus oreas* **sp. nov.**, *E. scabrospinosus*, and *E. virginicus*.
- Sample ZA.219: 31 specimens (21 ♀♀, 5 juveniles and 5 larvae on slides); found with *Echiniscus intricatus* **sp. nov.** and *E. oreas* **sp. nov.**
- Sample ZA.224: 16 specimens (12 ♀♀, 4 juveniles on slides); found with *Echiniscus imitans* **sp. nov.**, *E. oreas* **sp. nov.**, and *E. scabrospinosus*.
- Sample ZA.225: 104 specimens (49 ♀♀, 33 juveniles and 2 larvae on slides, 10 specimens on SEM stub 19.02, and 10 specimens used for DNA extraction); found with *Echiniscus blumi* and *E. intricatus* **sp. nov.**
- Sample ZA.227: 315 specimens (140 ♀♀, 114 juveniles and 11 larvae on slides, and 50 specimens on SEM stub 18.18); found with *Echiniscus imitans* **sp. nov.**
- Sample ZA.230: 7 specimens (3 ♀♀ and 4 juveniles on slides); found with *Echiniscus blumi*, *E. oreas* **sp. nov.**, and *E. scabrospinosus*.
- Sample ZA.232: 55 specimens (47 ♀♀, 1 ♂ and 7 juveniles on slides); found with *E. oreas* **sp. nov.**
- Sample ZA.235: 4 specimens (4 ♀♀ on slides); found with *Echiniscis longispinosus*.
- Sample ZA.238: 11 specimens (9 ♀♀ and 2 juveniles on slides); found with *Echiniscus intricatus* **sp. nov.**
- Sample ZA.247: 10 specimens (9 ♀♀ and 1 juvenile on slides); found with *Echiniscus imitans* **sp. nov.** and *E. oreas* **sp. nov.**
- Sample ZA.249: 33 specimens (20 ♀♀, 1 ♂ and 12 juveniles on slides); found with *Echiniscus oreas* **sp. nov.** and *Pseudechiniscus (P.)* cf. *ehrenbergi.*
- Sample ZA.252: 25 specimens (15 ♀♀, 7 ♂♂ and 3 juveniles on slides).
- Sample ZA.255: 2 specimens (2 ♀♀ on a slide); found with *Echiniscus blumi* and *E. imitans* **sp. nov.**
- Sample ZA.263: 1 specimen (1 ♀ on a slide); found with *Echiniscus longispinosus*, *Pseudechiniscus (P.)* cf. *ehrenbergi,* and *P. (Meridioniscus) wallacei* **sp. nov.**
- Sample ZA.265: 8 specimens (6 ♀♀, 1 juvenile and 1 larva on slides); found with *Echiniscus scabrospinosus* and *Pseudechiniscus (P.)* cf. *ehrenbergi*.
- Sample ZA.274: 5 specimens (5 ♀♀ on slides); found with *Echiniscus crassispinosus* and *E. longispinosus*.

Description. Mature females (*i.e*. from the third instar onwards; measurements and statistics in Table 39). Medium-sized *Echiniscus* with light yellow body and small red eyes; body colour and eyes disappeared soon after mounting in Hoyer's medium. Dactyloid/ovoid cephalic papillae (secondary clavae) and (primary) clavae (Fig. 73A–B, 74C);

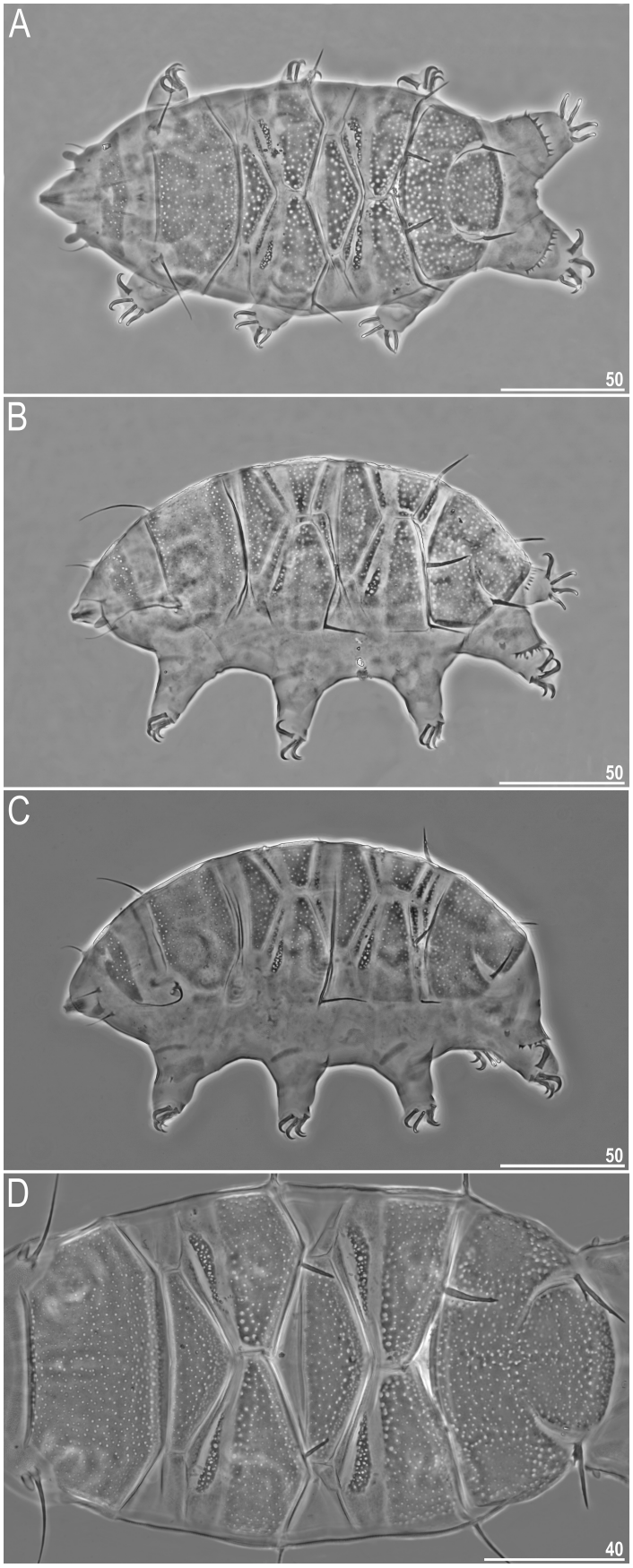

FIGURE 73. Habitus of *Echiniscus regularis* **sp. nov.** (PCM): A—holotype, female in dorsal view, B—paratype, female in dorsolateral view, C—paratype, male in dorsolateral view, D—close-up on dorsal sculpturing. Scale bars in μm.

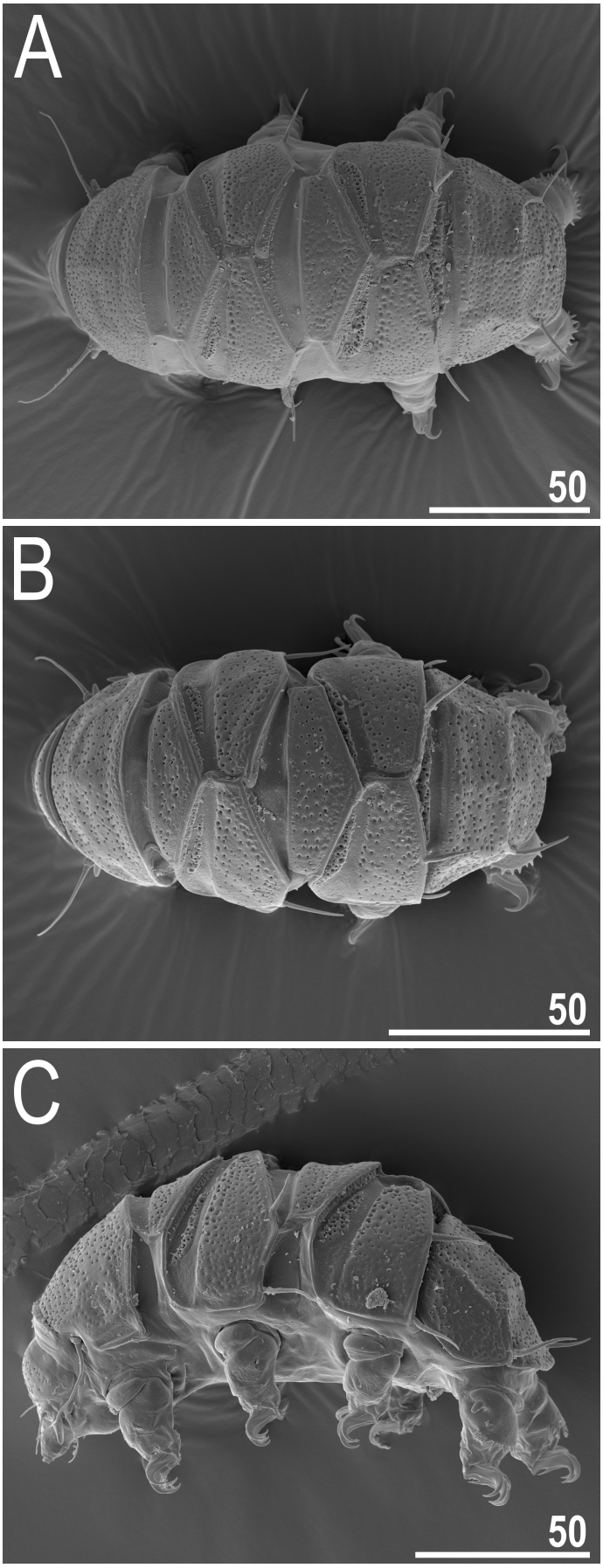

FIGURE 74. Habitus of *Echiniscus regularis* **sp. nov.** (SEM, females): A, B—dorsal view, C—lateral view. Scale bars = 50 µm.

cirri growing out from bulbous cirrophores. Cirri *A* short. Body appendage configuration *A-C-(C^d)-D-D^d-E*, with all trunk appendages formed as long spines of similar lengths, usually smooth (Fig. 73–74). Only rarely are spines *E* gently serrated or bifurcating at their bases (Fig. 73D). Single asymmetries frequent.

Dorsal plates with the sculpturing of the *E. spinulosus* type; pores of similar size, regularly distributed in the plates, and without dark endocuticular rings (Fig. 73–75). Anterior portions of paired segmental plates and the median plate 3 reduced to thin belts of much thicker (darker under PCM) cuticle with more densely arranged pores (Fig. 73, 74A–B, 75B–C). The cephalic plate with a very pronounced, chalice-shaped anterior incision (Fig. 73A); the cervical (neck) plate absent. The scapular plate large and uniform, without the median suture/groove under PCM (Fig. 73A), but under SEM a weakly developed faceting is visible (Fig. 74, 75A). Poorly developed lateral sutures are positioned below the clavae and delimit small lateral rectangular portions devoid of pores (Fig. 73B, 74C). Transverse belts on the paired segmental plates wide and unsculptured (Fig. 73D, 75B). Median plate 1 slightly smaller than the posterior portion of m2; the anterior portion of m2 smooth (Fig. 73D, 75B). The caudal (terminal) plate with two unsclerotised incisions, without faceting under PCM (Fig. 73), but under SEM the faceting is weakly marked (Fig. 74, 75C). Ventral cuticle with minute endocuticular pillars distributed throughout the whole venter; ventral plates absent. Sexpartite gonopore placed anteriorly to legs IV, and a trilobed anus between legs IV.

Pedal plates are absent, even the dentate collar on legs IV is placed on an unsculptured central portion of leg (Fig. 73B, 74C, 76C). Pulvini present, but weakly marked (Fig. 73B, 74C). Spine on leg I and a papilla on leg IV present (Fig. 74C). Claws I–IV of similar heights. All external claws spurless. All internal claws with rather delicate, thin spurs positioned at *ca.* 25%–30% of the branch (Fig. 76).

Mature males and sexually dimorphic traits (*i.e.* from the third instar onwards; measurements and statistics in Table 40). Qualitatively like females (Fig. 73C), excluding the circular gonopore. Smaller than females: no gap in body length ranges, but statistically different in mean body length ±SD: 219 ±12 μm *vs* 186 ±10 μm (one-tailed Welch's *t*-test with N♀♀=20 and N♂♂=9: t_{18}=1.73; p<0.001); scapular plate length: ♀♀ 40.0–49.2 μm *vs* ♂♂ 31.3–35.4 μm.

Juveniles (*i.e.* from the second instar onwards; measurements and statistics in Table 41). No gonopore. Qualitatively similar to females. There is a clear morphometric gap between juveniles and adult females in body and scapular plate lengths, and in the lengths of cephalic appendages (see Tables 38–39).

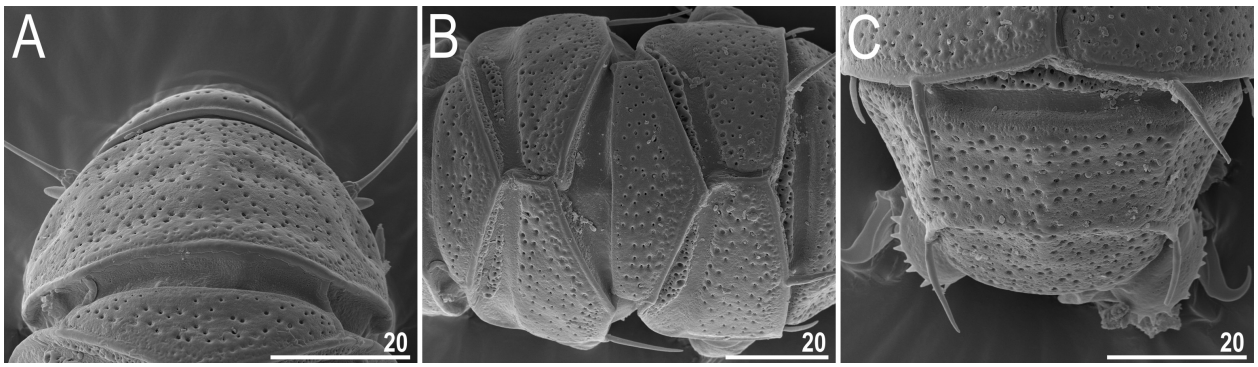

FIGURE 75. Dorsal sculpturing of *Echiniscus regularis* **sp. nov.** (SEM, females): A—scapular plate, B—paired segmental and median plates, C—caudal (terminal) plate. Scale bars in μm.

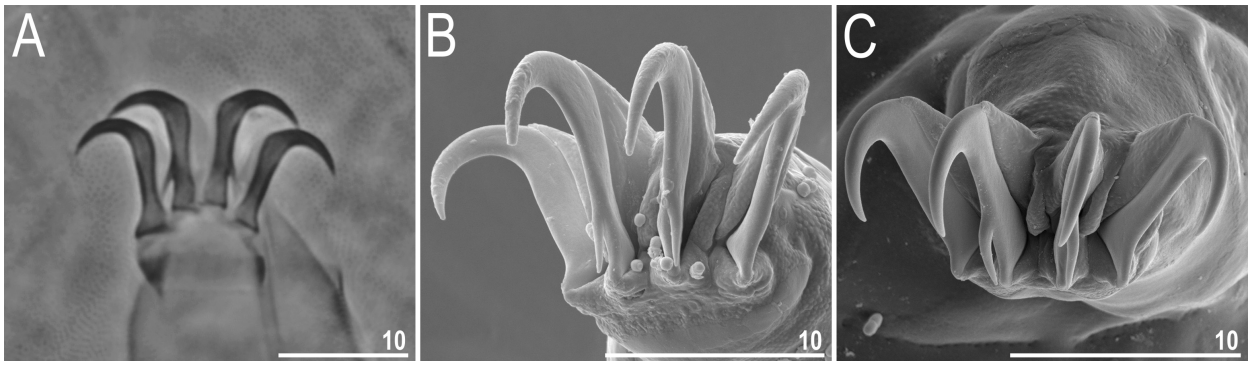

FIGURE 76. Claws of *Echiniscus regularis* **sp. nov.** (females): A—claws I (PCM), B—claws I (SEM), C—claws III (SEM). Scale bars = 10 μm.

TABLE 39. Measurements [in µm] of selected morphological structures of the adult females of *Echiniscus regularis* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Holotype	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	20	198	–	242	*456*	–	*575*	219	*506*	12	*33*	211	*520*
Scapular plate length	20	40.0	–	49.2		–		43.3	–	2.9	–	40.6	–
Head appendages lengths													
Cirrus *internus*	20	10.2	–	15.1	*24.4*	–	*36.8*	12.3	*28.4*	1.4	*3.1*	13.0	*32.0*
Cephalic papilla	20	6.5	–	7.8	*13.3*	–	*18.5*	7.2	*16.6*	0.3	*1.3*	7.3	*18.0*
Cirrus *externus*	20	12.1	–	16.5	*25.5*	–	*39.0*	14.4	*33.3*	1.2	*3.4*	15.5	*38.2*
Clava	19	4.8	–	5.9	*10.3*	–	*14.3*	5.4	*12.7*	0.4	*1.3*	5.8	*14.3*
Cirrus *A*	20	31.4	–	38.9	*65.4*	–	*94.3*	34.8	*80.7*	2.3	*7.7*	33.6	*82.8*
Cirrus *A*/Body length ratio	20	14%	–	18%		–		16%	–	1%	–	16%	–
Body appendages lengths													
Spine *C*	20	12.1	–	22.7	*27.4*	–	*56.6*	18.6	*43.3*	2.7	*7.2*	18.4	*45.3*
Spine C^d	11	5.9	–	15.9	*13.3*	–	*32.3*	10.7	*25.1*	2.8	*5.9*	10.8	*26.6*
Spine *D*	20	5.0	–	20.0	*10.5*	–	*43.6*	14.7	*34.2*	3.7	*8.9*	16.5	*40.6*
Spine D^d	20	7.6	–	23.2	*16.0*	–	*54.0*	16.8	*39.1*	3.6	*8.9*	17.1	*42.1*
Spine *E*	19	13.2	–	24.8	*27.8*	–	*60.2*	19.1	*44.5*	3.0	*8.4*	19.8	*48.8*
Spine on leg I length	19	1.7	–	2.5	*3.5*	–	*6.2*	2.0	*4.7*	0.3	*0.7*	?	*?*
Papilla on leg IV length	20	3.0	–	3.9	*6.9*	–	*9.0*	3.5	*8.0*	0.2	*0.6*	3.3	*8.1*
Number of teeth on the collar	19	9	–	19		–		12.6	–	2.4	–	12	–
Claw I heights													
Branch	20	10.6	–	13.4	*24.2*	–	*32.5*	11.6	*26.9*	0.9	*2.1*	10.7	*26.4*
Spur	17	2.4	–	3.5	*6.0*	–	*7.9*	3.0	*6.9*	0.3	*0.5*	3.2	*7.9*
Spur/branch height ratio	17	22%	–	30%		–		26%	–	3%	–	30%	–
Claw II heights													
Branch	20	9.4	–	12.9	*22.4*	–	*27.5*	10.8	*25.0*	0.9	*1.6*	10.5	*25.9*
Spur	17	2.3	–	3.2	*5.5*	–	*7.8*	2.7	*6.3*	0.3	*0.5*	2.7	*6.7*
Spur/branch height ratio	17	22%	–	29%		–		25%	–	2%	–	26%	–
Claw III heights													
Branch	20	9.6	–	12.4	*22.6*	–	*28.4*	10.8	*25.0*	0.7	*1.7*	10.0	*24.6*
Spur	18	2.4	–	3.4	*5.3*	–	*8.5*	2.8	*6.5*	0.3	*0.8*	3.0	*7.4*
Spur/branch height ratio	18	22%	–	31%		–		26%	–	3%	–	30%	–
Claw IV heights													
Branch	20	11.3	–	13.6	*26.7*	–	*33.0*	12.8	*29.6*	0.6	*1.8*	12.9	*31.8*
Spur	12	3.0	–	4.2	*6.7*	–	*9.5*	3.5	*8.0*	0.3	*1.0*	?	*?*
Spur/branch height ratio	12	23%	–	32%		–		28%	–	3%	–	?	–

TABLE 40. Measurements [in µm] of selected morphological structures of the adult males of *Echiniscus regularis* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Allotype	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	9	164	–	199	*487*	–	*612*	186	*554*	10	*35*	186	*560*
Scapular plate length	9	31.3	–	35.4		–		33.6	–	1.2	–	33.2	–
Head appendages lengths													
Cirrus *internus*	8	7.1	–	10.7	*21.3*	–	*32.8*	9.2	*27.6*	1.1	*3.7*	8.5	*25.6*
Cephalic papilla	9	4.5	–	6.7	*13.3*	–	*20.4*	5.6	*16.8*	0.9	*2.9*	5.9	*17.8*
Cirrus *externus*	8	10.4	–	12.8	*30.7*	–	*39.3*	11.6	*34.7*	1.1	*3.3*	10.5	*31.6*
Clava	9	3.9	–	6.1	*11.5*	–	*18.0*	5.2	*15.4*	0.9	*2.3*	5.8	17.5
Cirrus *A*	9	22.4	–	34.5	*71.6*	–	*97.5*	29.2	*86.5*	3.5	*8.1*	31.2	*94.0*
Cirrus *A*/Body length ratio	9	12%	–	18%		–		16%	–	2%	–	17%	–
Body appendages lengths													
Spine *C*	9	14.2	–	18.2	*44.5*	–	*54.8*	16.1	*47.9*	1.3	*3.0*	18.2	*54.8*
Spine C^d	3	2.4	–	4.4	*7.7*	–	*13.0*	3.3	*9.9*	1.0	*2.7*	?	*?*
Spine *D*	9	8.5	–	14.2	*24.5*	–	*40.1*	10.4	*31.0*	2.1	*5.7*	8.5	*25.6*
Spine D^d	9	10.3	–	17.0	*32.7*	–	*50.1*	13.0	*38.7*	2.1	*5.7*	13.6	*41.0*
Spine *E*	9	13.1	–	17.6	*41.9*	–	*52.1*	15.8	*47.0*	1.3	*3.0*	15.8	*47.6*
Spine on leg I length	6	1.4	–	2.2	*4.2*	–	*6.3*	1.8	*5.4*	0.3	*0.9*	1.5	*4.5*
Papilla on leg IV length	8	2.8	–	3.8	*8.1*	–	*12.1*	3.1	*9.2*	0.4	*1.5*	?	*?*
Number of teeth on the collar	8	9	–	11		–		10.0	–	0.5	–	10	–
Claw I heights													
Branch	9	9.0	–	10.9	*25.9*	–	*32.4*	10.1	*30.2*	0.6	*1.9*	9.8	*29.5*
Spur	9	2.3	–	3.0	*6.9*	–	*8.9*	2.7	*8.0*	0.2	*0.7*	2.5	*7.5*
Spur/branch height ratio	9	22%	–	29%		–		27%	–	2%	–	26%	–
Claw II heights													
Branch	8	8.1	–	10.1	*24.4*	–	*30.2*	9.3	*27.8*	0.6	*1.9*	8.1	*24.4*
Spur	8	1.8	–	2.5	*5.7*	–	*7.5*	2.2	*6.6*	0.3	*0.7*	1.9	*5.7*
Spur/branch height ratio	8	20%	–	27%		–		24%	–	2%	–	23%	–
Claw III heights													
Branch	8	9.0	–	10.3	*26.2*	–	*30.8*	9.6	*28.2*	0.5	*1.4*	9.0	*27.1*
Spur	8	2.0	–	3.0	*5.8*	–	*8.8*	2.3	*6.9*	0.3	*1.0*	2.4	*7.2*
Spur/branch height ratio	8	21%	–	32%		–		24%	–	4%	–	27%	–
Claw IV heights													
Branch	8	10.8	–	12.1	*32.4*	–	*34.9*	11.4	*33.5*	0.4	*0.9*	11.0	*33.1*
Spur	8	2.1	–	3.1	*6.3*	–	*9.1*	2.6	*7.7*	0.4	*1.0*	2.1	*6.3*
Spur/branch height ratio	8	19%	–	27%		–		23%	–	3%	–	19%	–

TABLE 41. Measurements [in µm] of selected morphological structures of the juveniles and a larva of *Echiniscus regularis* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Larva	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	5	164	–	189	*490*	–	*562*	178	*516*	10	*27*	128	*582*
Scapular plate length	5	31.7	–	38.6		–		34.6	–	3.0	–	22.0	–
Head appendages lengths													
Cirrus *internus*	5	7.8	–	10.3	*24.1*	–	*30.0*	9.2	*26.6*	0.9	*2.2*	5.8	*26.4*
Cephalic papilla	5	5.5	–	6.4	*15.2*	–	*19.6*	5.9	*17.3*	0.4	*1.6*	3.5	*15.9*
Cirrus *externus*	5	9.0	–	11.8	*27.8*	–	*37.2*	10.7	*31.0*	1.3	*3.7*	5.8	*26.4*
Clava	5	4.5	–	4.8	*11.7*	–	*15.1*	4.7	*13.6*	0.1	*1.3*	?	*?*
Cirrus *A*	5	23.2	–	32.8	*71.6*	–	*88.9*	28.3	*81.7*	4.1	*6.5*	19.9	*90.5*
Cirrus *A*/Body length ratio	5	14%	–	18%		–		16%	–	1%	–	16%	–
Body appendages lengths													
Spine *C*	5	13.7	–	21.6	*35.5*	–	*64.9*	18.1	*52.9*	3.7	*12.5*	lacking	
Spine C^d	1	5.7	–	5.7	*18.0*	–	*18.0*	5.7	*18.0*	?	*?*	lacking	
Spine *D*	5	6.8	–	12.9	*18.9*	–	*39.8*	9.8	*28.8*	2.9	*9.7*	lacking	
Spine D^d	5	10.1	–	16.7	*30.3*	–	*50.2*	13.7	*39.9*	2.7	*9.5*	5.0	*22.7*
Spine *E*	5	11.9	–	18.6	*30.8*	–	*57.1*	15.9	*46.7*	2.7	*11.1*	8.5	*38.6*
Spine on leg I length	5	1.3	–	1.9	*4.0*	–	*5.1*	1.6	*4.7*	0.2	*0.4*	1.2	*5.5*
Papilla on leg IV length	4	3.0	–	3.2	*7.8*	–	*9.5*	3.1	*8.8*	0.1	*0.8*	2.2	*10.0*
Number of teeth on the collar	5	9	–	14		–		10.0	–	2.2	–	7.0	–
Claw I heights													
Branch	5	8.8	–	10.9	*26.7*	–	*30.9*	9.9	*28.6*	0.8	*1.6*	6.5	*29.5*
Spur	4	2.0	–	2.8	*6.0*	–	*7.6*	2.4	*6.8*	0.3	*0.7*	1.8	*8.2*
Spur/branch height ratio	4	22%	–	27%		–		24%	–	3%	–	28%	–
Claw II heights													
Branch	5	7.7	–	10.4	*24.3*	–	*28.2*	9.1	*26.4*	1.0	*1.9*	5.7	*25.9*
Spur	3	2.0	–	2.5	*6.3*	–	*6.6*	2.2	*6.5*	0.3	*0.1*	1.8	*8.2*
Spur/branch height ratio	3	24%	–	27%		–		26%	–	1%	–	32%	–
Claw III heights													
Branch	5	7.6	–	10.0	*24.0*	–	*29.0*	9.2	*26.6*	0.9	*2.0*	5.3	*24.1*
Spur	4	1.9	–	2.4	*6.0*	–	*6.6*	2.2	*6.3*	0.2	*0.3*	1.6	*7.3*
Spur/branch height ratio	4	23%	–	25%		–		24%	–	1%	–	30%	–
Claw IV heights													
Branch	5	9.2	–	12.6	*29.0*	–	*34.1*	10.8	*31.3*	1.3	*2.1*	6.6	*30.0*
Spur	3	2.1	–	2.8	*6.6*	–	*8.6*	2.5	*7.6*	0.4	*1.0*	2.1	*9.5*
Spur/branch height ratio	3	23%	–	26%		–		25%	–	2%	–	32%	–

Larvae (*i.e.* the first instar; measurements and statistics in Table 41). Gonopore and anus absent. Smaller than juveniles (a morphometric gap present). Body appendage configuration *A*-D^d-*E*. The dorsal sculpturing of the same type as in adults, but not so strongly developed.

Eggs. Up to four yellow eggs per exuvia were found.

DNA markers and phylogenetic position. *Echiniscus regularis* **sp. nov.** is the sister species of the clade *E. oreas* **sp. nov.** + *E. scabrospinosus* (Fig. 117), both being the closest species in ITS-1 and ITS-2 (p-distance = 0.6–2.3% and 0.6–1.2%, respectively).

Type material. 49 ♀♀, 33 juveniles and 2 larvae on slides ZA.225.01, 3–9; holotype: mature ♀ on slide ZA.225.01. Mounted together with 5 ♀♀, 4 juveniles and 1 larva of *E. blumi*, 16 ♀♀ and 8 juveniles of *E. intricatus* **sp. nov.** 10 specimens on SEM stub 19.02. 10 specimens used for DNA extraction, 6 secured as hologenophores.

Type locality. 29°16'4"S, 29°30'34.3"E, 1800 m asl: Republic of South Africa, KwaZulu-Natal, Drakensberg, Giants Castle Game Reserve; montane grassland, lichen from rock (samples ZA.224 and ZA.225).

Etymology. From Latin *regularis* = regular, underlying the regular distribution of dorsal pores. An adjective in the nominative singular.

Geographic distribution. The new species is common in the mountains (Fig. 120D), occurring almost exclusively at high elevations above 1500 m asl.

Remarks. The new species forms populations of diverse sizes, mixed with other echiniscids, most frequently with *E. oreas* **sp. nov.**

Differential diagnosis. The species is a classic representative of the *E. spinulosus* group. Although it is very similar to *E. oreas* **sp. nov.** and *E. tristis*, our phylogenetic analysis shows that it is a clearly distinct species (Fig. 117). Morphologically, it can be distinguished from:

- *E. angolensis*, by a larger body size (adult females 198–242 µm long in *E. regularis* **sp. nov.** *vs* adult females 132–183 µm long in *E. angolensis*), and by the morphology of spines D^d (smooth in *E. regularis* **sp. nov.** *vs* rough and slightly serrated in *E. angolensis*);
- *E. crassispinosus*, by the morphology of spine D^d (as thin as the remaining appendages in *E. regularis* **sp. nov.** *vs* massive and much thicker than the remaining appendages in *E. crassispinosus*), and the body shape (elongated in *E. regularis* **sp. nov.** *vs* plump in *E. crassispinosus*);
- *E. dreyfusi*, by the body appendage configuration (*A-C-(C^d)-D-D^d-E* in *E. regularis* **sp. nov.** *vs A-B-C-D-D^d-E* in *E. dreyfusi*), and spurs on internal claws (present in *E. regularis* **sp. nov.** *vs* absent in *E. dreyfusi*);
- *E. marcusi*, by the morphology of trunk lateral appendages (long spines in *E. regularis* **sp. nov.** *vs* minute triangular spicules in *E. marcusi*), and by the dorsal sculpturing (*striae* absent in *E. regularis* **sp. nov.** *vs striae* present in the anterior portion of the median plate 2 and in the area adjacent to the transverse belts in paired segmental plates I–II in *E. marcusi*);
- *E. marginatus*, by the body appendage configuration (*A-C-(C^d)-D-D^d-E* in *E. regularis* **sp. nov.** *vs A-C-D-D^d-E* in *E. marginatus*), and by the dorsal sculpturing (posterior portions of the median and paired segmental plates with pores in *E. regularis* **sp. nov.** *vs* posterior portions of the median and paired segmental plates without pores in *E. marginatus*, see Pilato *et al*. 2008);
- *E. oreas* **sp. nov.**, by the presence of dark circumporal rings (absent in *E. regularis* **sp. nov.** *vs* present in *E. oreas* **sp. nov.**), the shape of internal spurs (more delicate and thinner in *E. regularis* **sp. nov.** *vs* more robust and more divergent from the claw branch in *E. oreas* **sp. nov.**), and by sexual dimorphism in relative cephalic papillae length (cephalic papillae of the same length in both sexes in *E. regularis* **sp. nov.** *vs* cephalic papillae on average longer in males relative to the scapular plate length in *E. oreas* **sp. nov.**);
- *E. ornamentatus*, by the body appendage configuration (*A-C-(C^d)-D-D^d-E* in *E. regularis* **sp. nov.** *vs A-(B)-C-D-D^d-E* in *E. ornamentatus*), and by the development of faceting on the scapular and the caudal plate (weak in *E. regularis* **sp. nov.** *vs* strong in *E. ornamentatus*);
- *E. scabrospinosus*, by the body appendage configuration (*A-C-(C^d)-D-D^d-E* in *E. regularis* **sp. nov.** *vs A-C-D-D^d-E* in *E. scabrospinosus*), the presence of endocuticular rings (absent in *E. regularis* **sp. nov.** *vs* present and evident in all pores in *E. scabrospinosus*), and by lateral non-porous portions of the paired segmental plates I–II (absent in *E. regularis* **sp. nov.** *vs* present in *E. scabrospinosus*);
- *E. tristis*, by development of the pedal plate IV (weak in *E. regularis* **sp. nov.** *vs* strong in *E. tristis*), the shape of internal spurs (delicate and thinner in *E. regularis* **sp. nov.** *vs* robust and more divergent from the claw branch in *E. tristis*);
- *E. tropicalis*, by the morphology of trunk appendages (long spines in *E. regularis* **sp. nov.** *vs* minute triangular spicules in *E. tropicalis*), and the heteromorphy of spurs on internal claws (spurs I–IV homomorphic in *E. regularis* **sp. nov.** *vs* spurs IV different in size and shape from spurs I–III in *E. tropicalis*).

Raw measurements. Supplementary Materials (SM.03) and Tardigrada Register (www.tardigrada.net/register/0094.htm).

24. Echiniscus scabrocirrosus sp. nov. Gąsiorek, Vončina, Morek & Michalczyk

urn:lsid:zoobank.org:act:72225C84-30C9-47EF-804A-8548B01D3415

Figures 77–81, Tables 42–45

Data source:

A total of 323 specimens (79 ♀♀, 46 ♂♂, 17 juveniles, 7 larvae, and 174 specimens of unknown instar/sex):

- Sample ZA.431: 259 specimens (50 ♀♀, 28 ♂♂, 14 juveniles and 7 larvae on slides, 50 specimens used for SEM, 10 specimens used for DNA extraction, and 100 frozen specimens); found with *Echiniscus draconis* **sp. nov**., *E. imitans* **sp. nov.**, and *E. lichenorum*.
- Sample ZA.432: 19 specimens (11 ♀♀, 7 ♂♂, 1 juvenile on slides); found with *Echiniscus draconis* **sp. nov.**
- Sample ZA.434: 1 specimen (1 ♂ on a slide); found with *Echiniscus draconis* **sp. nov.**
- Sample ZA.436: 17 specimens (2 ♀♀ and 3 ♂♂ on slides, 2 specimens used for DNA extraction, and 10 specimens on SEM stub 19.09); found with *Echiniscus attenboroughi* **sp. nov.**, *E. draconis* **sp. nov.**, and *E. setaceus* **sp. nov.**
- Sample ZA.445: 2 specimens (2 ♀♀ on a slide).
- Sample ZA.473: 1 specimen (1 ♀ on a slide).
- Sample ZA.479: 3 specimens (2 ♂♂ and 1 juvenile on slides); found with *Echiniscsus attenboroughi* **sp. nov.** and *E. longispinosus*.
- Sample ZA.480: 21 specimens (13 ♀♀, 5 ♂♂, 1 juvenile and 2 specimens of unidentified sex on slides); found with *Echiniscus draconis* **sp. nov.** and *E. imitans* **sp. nov.**

Description. Mature females (*i.e*. from the third instar onwards; measurements and statistics in Table 42). Large *Echiniscus* with light yellow body and small red eyes; body colour and eyes disappeared soon after mounting in Hoyer's medium. Dactyloid cephalic papillae (secondary clavae) and (primary) clavae (Fig. 77A, 80B); cirri growing out from bulbous cirrophores. Cirri *A* short. Body appendage configuration *A*-*C*-*C*^{d}-*D*, with all trunk appendages formed as long, thick cirri with a thick wall and a hollow centre (the capillary structure visible only in LCM; Fig. 77A, 78–79). Cirri with the bases only slightly broader than the *flagellum* (Fig. 77A, 80A) and typically scabrous in their central and distal portions (Fig. 77A, 79). The flagellar part of trunk cirri can be easily broken. The configuration is very stable, single asymmetries uncommon.

Dorsal plates with a simple sculpturing consisting of numerous small pores irregularly distributed in all dorsal plates between the homomorphic endocuticular matrix (Fig. 77A, 78, 80A). Sometimes, pores may be larger in the caudal (terminal) plate than in the other dorsal plates (Fig. 78A). The cephalic plate with a very pronounced, chalice-shaped anterior incision (Fig. 77A); the cervical (neck) plate rudimental (Fig. 77–78). The scapular plate large, with a median groove present (Fig. 77A, 78A) or absent (Fig. 78B); its lateral sutures clearly delimit lateral rhomboid portions (Fig. 77A, 78, 80A). Transverse belts on the paired segmental plates I–II thin and poorly marked (Fig. 78, 80A). Median plate 1 slightly smaller than the posterior portion of m2 or equal in size; the anterior portion of m2 smooth (Fig. 78). Median plate 3 reduced to a thin porous stripe covered under paired segmental plate II and the caudal plate. The caudal (terminal) plate with two unsclerotised incisions, and with clear or barely visible faceting delineated by three longitudinal and three transverse poreless ridges/sutures (Fig. 77A, 78). Ventral cuticle with minute endocuticular pillars distributed throughout the whole venter; ventral plates absent. Sexpartite gonopore placed anteriorly to legs IV, and a trilobed anus between legs IV.

Pedal plates I–IV present and sculptured, with minute pores (Fig. 77A, 80A). Pulvini present and well-marked (Fig. 77A, 80A). A minuscule spine on leg I and a tiny papilla on leg IV (Fig. 77A, 80A). Dentate collar IV with numerous minute teeth (Fig. 77B–C, 80A) or few irregularly distributed teeth or without teeth (Fig. 77A). Compared to the body, claws are very short. Claws IV slightly longer than claws I–III. All external claws spurless. All internal claws with delicate, thin spurs positioned at *ca.* 25% of the branch and tightly adjacent to it (Fig. 80C–D). Spurs are often asymmetrically lacking on one of the internal claws (Fig. 80C).

Mature males and sexually dimorphic traits (*i.e*. from the third instar onwards; measurements and statistics in Table 43). Qualitatively like females, excluding the circular gonopore. On average smaller and slenderer than females (Fig. 77B–C). Body size differences: mean body length ±SD: 274 ±23 µm *vs* 323 ±44 µm (one-tailed Welch's *t*-test with N♀♀=10 and N♂♂=10: t_{13}=3.10; p=0.004); average scapular plate length: 48.8 ±3.4 µm *vs* 61.0 ±9.3 µm (t_{11}=3.90; p=0.001). Differences in the relative size of papillae (*sp* values): cephalic papilla length ±SD: *18.7 ±1.0 vs 13.9 ±2.2* (one-tailed Welch's *t*-test with N♀♀=10 and N♂♂=10: t_{13}=-6.13; p<0.001); papilla IV length: 8.8 ±1.2 *vs* 6.7 ±1.0 (t_{17}=-4.32; p<0.001).

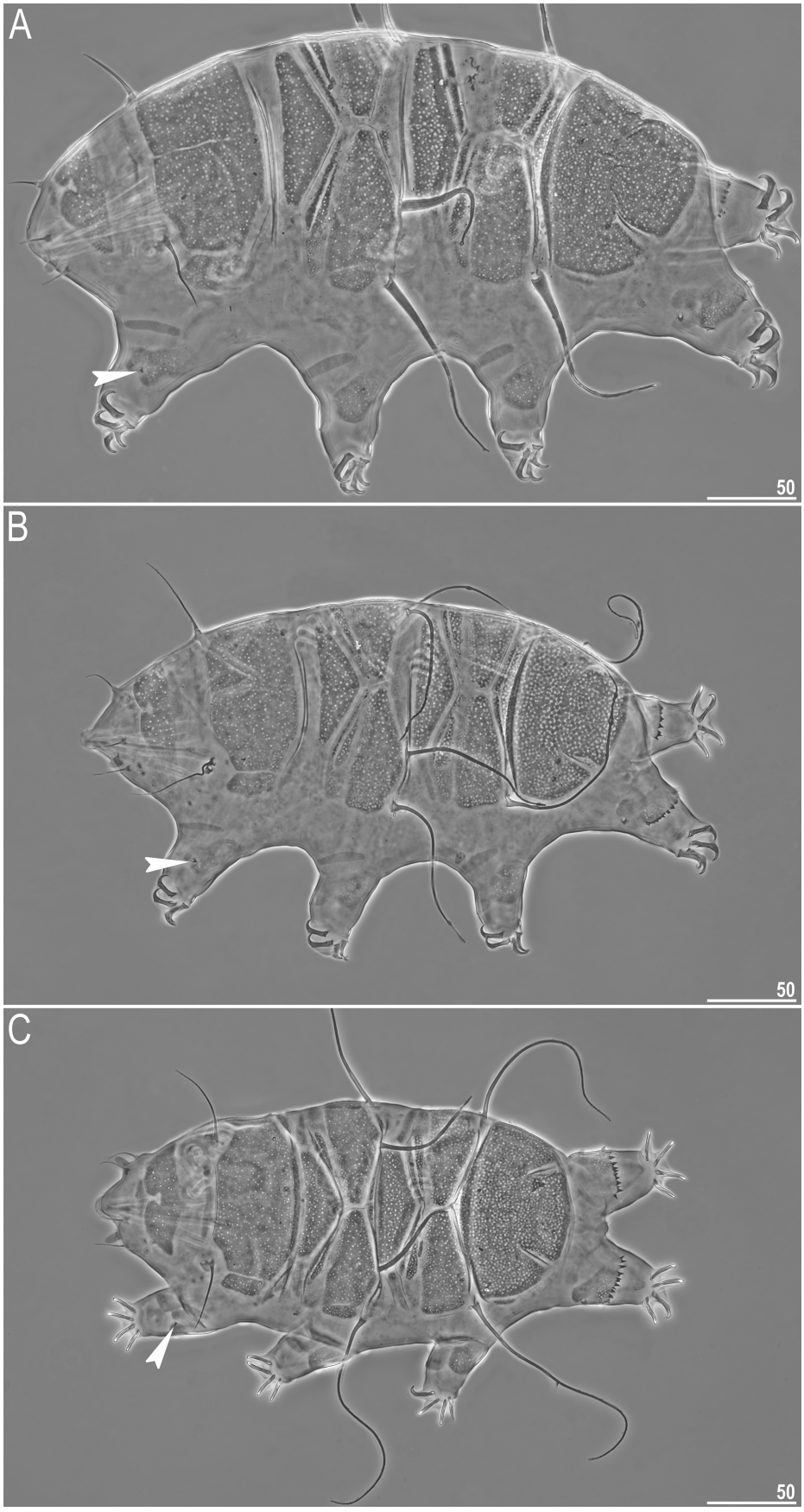

FIGURE 77. Habitus and intraspecific variability of *Echiniscus scabrocirrosus* **sp. nov.** (PCM): A—holotype, female in dorsolateral view, B—allotype, male in dorsolateral view, C—paratype, male in dorsal view. Arrowheads indicate the minuscule spine I. Scale bars = 50 µm.

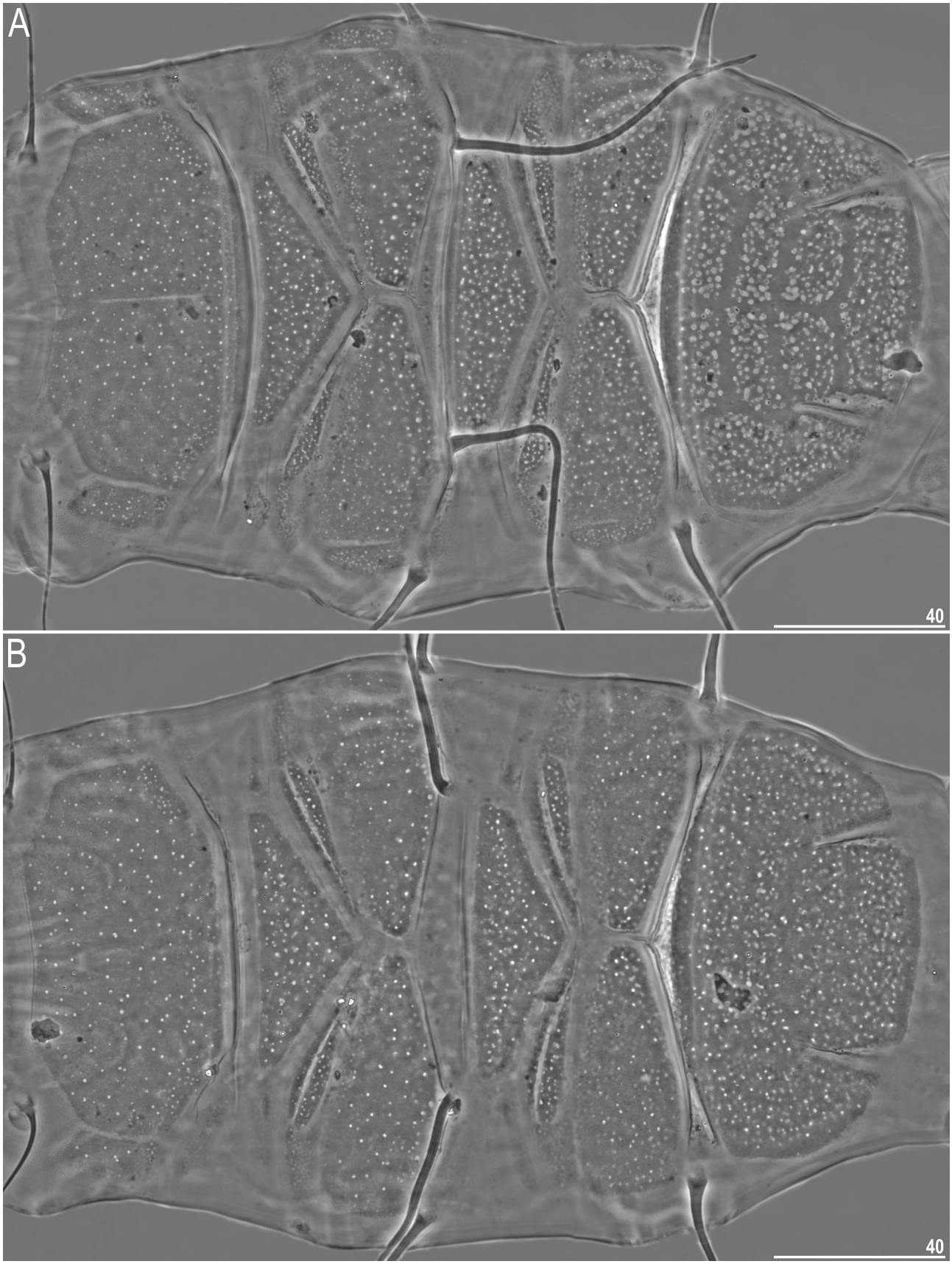

FIGURE 78. Dorsal sculpturing of *Echiniscus scabrocirrosus* **sp. nov.** (PCM, females). Scale bars = 40 μm.

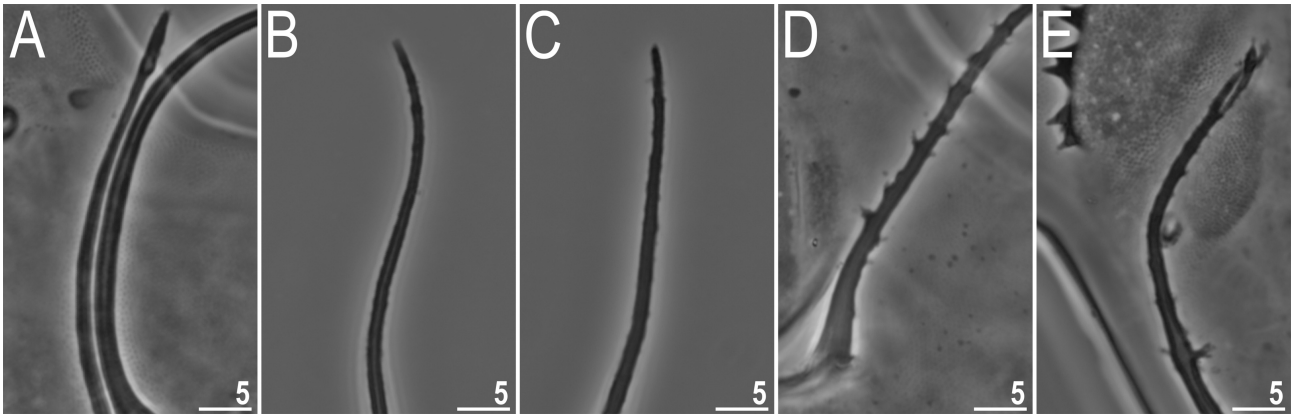

FIGURE 79. Variability in the roughness of cirri of *Echiniscus scabrocirrosus* **sp. nov.** (PCM). Scale bars = 5 μm.

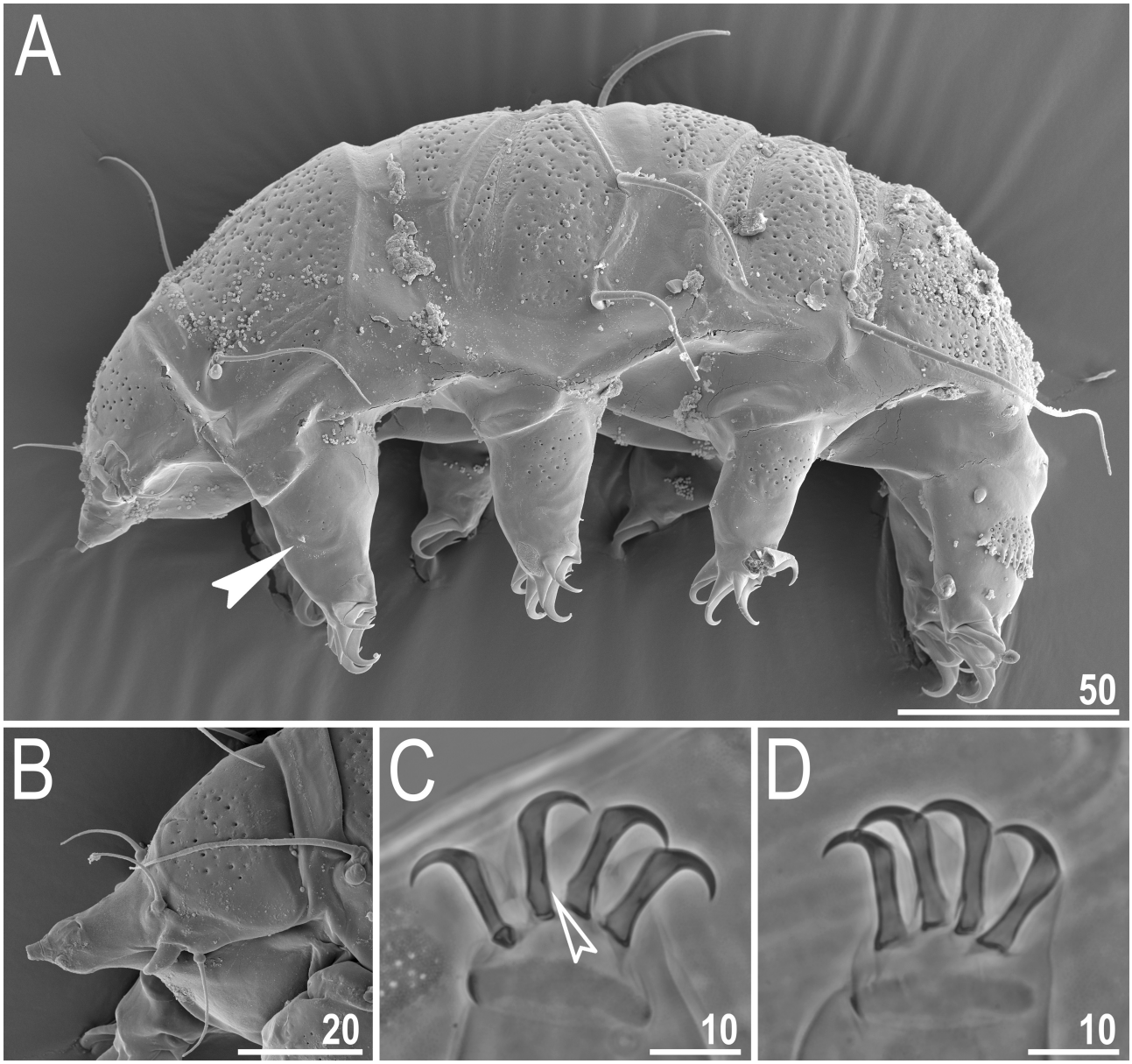

FIGURE 80. Detailed morphology of *Echiniscus scabrocirrosus* **sp. nov.**: A—female in lateral view (SEM, arrowhead indicates the minuscule spine I), B—cephalic appendages (SEM), C—claws II (PCM, empty arrowhead indicates smooth branch), D—claws III (PCM). Scale bars in μm.

Juveniles (*i.e*. from the second instar onwards; measurements and statistics in Table 44). No gonopore. Qualitatively and quantitatively similar to females.

Larvae (*i.e*. the first instar; measurements and statistics in Table 45). Gonopore and anus absent. Smaller than juveniles (a morphometric gap occurs). Body appendage configuration *A-(C)-C^{d}-(D)*. The dorsal sculpturing of the same type as in adults, but fainter (Fig. 81).

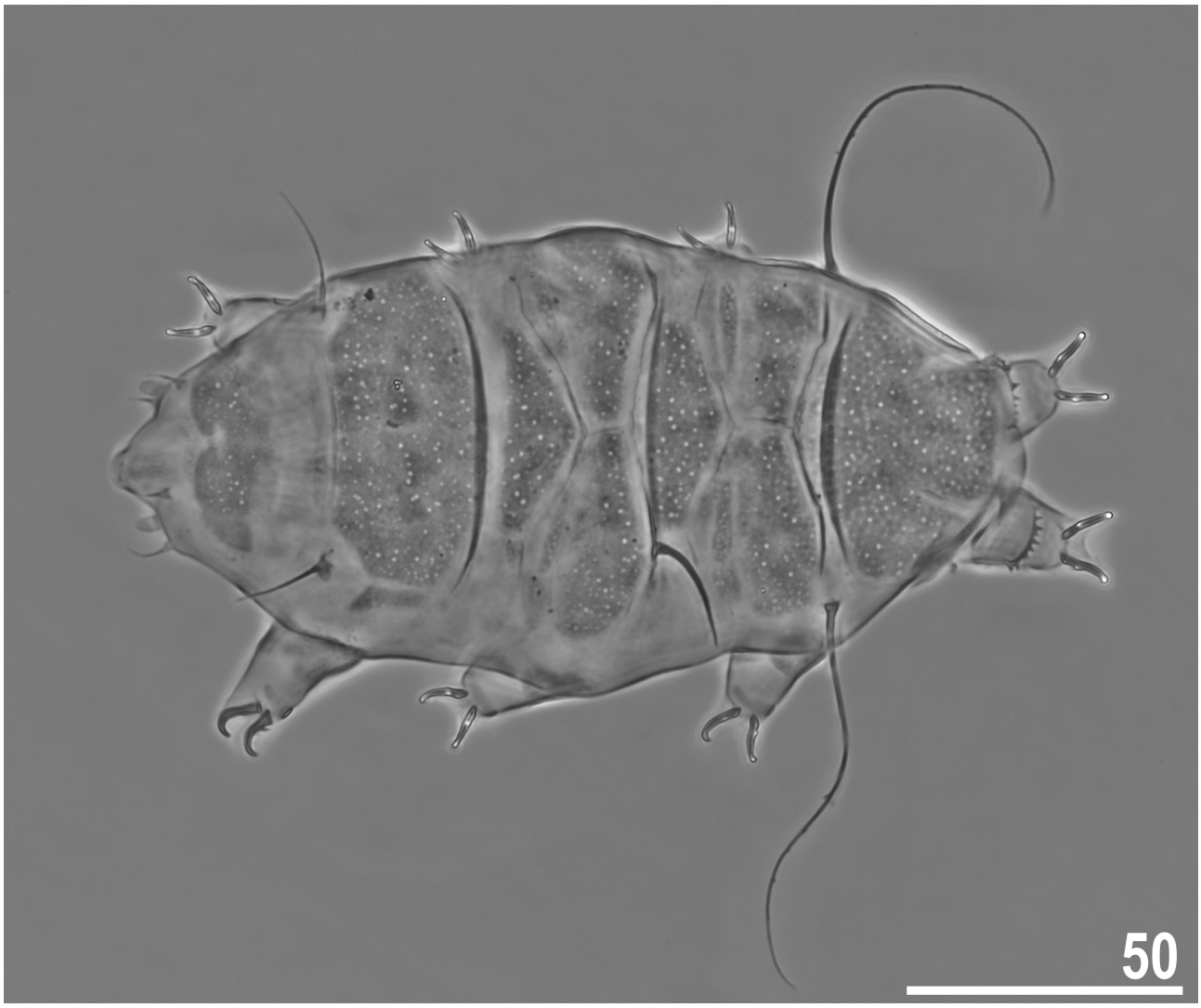

FIGURE 81. Habitus of larval *Echiniscus scabrocirrosus* (PCM). Scale bar = 50 μm.

Eggs. Up to eight yellow eggs per exuvia were found.

DNA markers and phylogenetic position. *Echiniscus scabrocirrosus* **sp. nov.** is the sister species of *E. latruncularis* **sp. nov.** in the mostly South-African endemic clade (Fig. 117). The species closest in COI are *E. draconis* **sp. nov.** and *E. latruncularis* **sp. nov.** (p-distance = 13.5–14.1%), in ITS-1 and ITS-2—*E. latruncularis* **sp. nov.** (1.4–2.3% and 0.9%, respectively).

Type material. 50 ♀♀, 28 ♂♂, 14 juveniles and 7 larvae on slides ZA.431.01–13, 17; holotype: mature ♀ on slide ZA.431.02, allotype: mature ♂ on slide ZA.431.04. Mounted together with 1 ♀, 5 juveniles and 13 larvae of *E. draconis* **sp. nov.**, 1 ♀ of *E. imitans* **sp. nov.**, 3 ♀♀ and 1 juvenile of *E. lichenorum*. 40 specimens on SEM stub 19.10; and 10 specimens used for DNA extraction, including 7 secured as hologenophores.

Type locality. 33°20’27.18”S, 22°1’15.9”E, 1360 m asl: Republic of South Africa, Western Cape, Groot Swartberg Nature Reserve; Afromontane karoo-veld (shrubland; Vorster & Roux 1983), lichen from rock (sample ZA.431).

Etymology. From Latin *scaber* = rough, scabrous + *cirrosus* = cirrous, which underlines an irregular, tufted surface of the trunk cirri. An adjective in the nominative singular.

TABLE 42. Measurements [in µm] of selected morphological structures of the adult females of *Echiniscus scabrocirrosus* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Holotype	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	sp
Body length	10	231	–	387	*456*	–	*645*	323	*534*	44	*62*	387	*568*
Scapular plate length	10	50.4	–	80.0		–		61.0	–	9.3	–	68.2	–
Head appendages lengths													
Cirrus *internus*	9	11.1	–	17.3	*19.6*	–	*29.4*	14.6	*24.5*	2.3	*3.6*	15.9	*23.3*
Cephalic papilla	10	6.8	–	10.8	*8.9*	–	*17.6*	8.3	*13.9*	1.2	*2.2*	9.1	*13.3*
Cirrus *externus*	10	14.5	–	23.6	*28.1*	–	*36.3*	19.4	*31.9*	2.6	*3.0*	20.2	*29.6*
Clava	10	6.0	–	9.8	*10.3*	–	*15.1*	7.4	*12.2*	1.0	*1.4*	7.0	*10.3*
Cirrus *A*	10	38.1	–	53.0	*52.8*	–	*86.2*	45.3	*75.3*	4.7	*10.6*	41.6	*61.0*
Cirrus *A*/Body length ratio	10	11%	–	19%		–		14%	–	3%	–	11%	–
Body appendages lengths													
Cirrus *C*	8	60.3	–	151.1	*89.7*	–	*292.3*	116.4	*190.9*	28.2	*58.2*	143.8	*210.9*
Cirrus C^d	10	38.4	–	77.9	*48.0*	–	*148.1*	67.7	*113.8*	13.1	*27.6*	75.2	*110.3*
Cirrus *D*	7	98.9	–	176.4	*163.6*	–	*341.2*	127.0	*217.9*	24.1	*61.3*	120.3	*176.4*
Spine on leg I length	9	2.1	–	5.7	*3.7*	–	*7.1*	3.2	*5.1*	1.1	*1.2*	2.9	*4.3*
Papilla on leg IV length	10	2.8	–	4.7	*5.0*	–	*7.7*	4.0	*6.7*	0.6	*1.0*	4.7	6.9
Number of teeth on the collar	7	11	–	20		–		14.9	–	3.5	–	12	–
Claw I heights													
Branch	9	15.0	–	19.6	*24.5*	–	*32.7*	16.8	*28.0*	1.8	*2.7*	19.3	*28.3*
Spur	8	2.9	–	4.6	*5.0*	–	*7.2*	3.8	*6.3*	0.6	*0.7*	4.6	*6.7*
Spur/branch height ratio	8	19%	–	25%		–		22%	–	2%	–	24%	–
Claw II heights													
Branch	8	15.6	–	19.6	*24.5*	–	*31.8*	17.1	*28.1*	1.4	*2.6*	?	*?*
Spur	8	3.1	–	4.5	*4.6*	–	*7.3*	3.8	*6.2*	0.4	*0.9*	?	*?*
Spur/branch height ratio	8	19%	–	26%		–		22%	–	2%	–	?	–
Claw III heights													
Branch	7	14.9	–	18.9	*26.4*	–	*33.1*	16.9	*28.7*	1.5	*2.2*	18.9	*27.7*
Spur	7	3.2	–	4.9	*5.4*	–	*7.2*	3.8	*6.4*	0.6	*0.7*	4.9	*7.2*
Spur/branch height ratio	7	19%	–	26%		–		22%	–	2%	–	26%	–
Claw IV heights													
Branch	7	17.0	–	22.7	*28.4*	–	*36.0*	19.2	*31.1*	1.9	*3.1*	19.6	*28.7*
Spur	7	3.2	–	5.3	*4.8*	–	*7.9*	4.1	*6.6*	0.9	*1.1*	5.2	*7.6*
Spur/branch height ratio	7	17%	–	27%		–		21%	–	4%	–	27%	–

TABLE 43. Measurements [in µm] of selected morphological structures of the adult males of *Echiniscus scabrocirrosus* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Allotype	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	10	238	–	315	*520*	–	*594*	274	*562*	23	*24*	315	*576*
Scapular plate length	10	44.6	–	54.7		–		48.8	–	3.4	–	54.7	–
Head appendages lengths													
Cirrus *internus*	9	10.2	–	17.4	*20.4*	–	*31.8*	12.7	*26.0*	2.3	*4.0*	17.4	*31.8*
Cephalic papilla	10	7.8	–	10.8	*17.2*	–	*20.3*	9.1	*18.7*	0.8	*1.0*	10.0	*18.3*
Cirrus *externus*	10	15.7	–	24.0	*32.5*	–	*43.9*	18.3	*37.4*	2.4	*3.3*	24.0	*43.9*
Clava	10	5.7	–	8.6	*11.5*	–	*18.4*	6.8	*13.9*	0.9	*2.1*	6.3	*11.5*
Cirrus *A*	8	34.8	–	52.3	*75.0*	–	*102.9*	42.5	*87.9*	5.7	*9.7*	52.3	*95.6*
Cirrus *A*/Body length ratio	8	13%	–	19%		–		16%	–	2%	–	17%	–
Body appendages lengths													
Cirrus *C*	8	74.3	–	138.0	*150.1*	–	*294.9*	105.3	*219.8*	22.4	*47.8*	132.6	*242.4*
Cirrus C^d	10	49.0	–	90.5	*99.0*	–	*165.4*	66.7	*137.0*	11.9	*22.4*	90.5	*165.4*
Cirrus *D*	8	104.2	–	159.8	*224.5*	–	*297.6*	127.1	*259.3*	19.8	*27.8*	142.9	*261.2*
Spine on leg I length	7	2.7	–	4.1	*5.2*	–	*7.5*	3.1	*6.3*	0.5	*0.8*	4.1	*7.5*
Papilla on leg IV length	10	3.7	–	4.8	*7.5*	–	*12.0*	4.1	*8.8*	0.4	*1.2*	4.6	*12.0*
Number of teeth on the collar	5	14	–	17		–		15.2	–	1.3	–	16	–
Claw I heights													
Branch	8	13.2	–	16.7	*26.8*	–	*32.7*	14.9	*30.1*	1.3	*2.1*	15.7	*28.7*
Spur	7	2.8	–	3.7	*5.6*	–	*7.7*	3.3	*6.7*	0.3	*0.7*	3.4	*6.2*
Spur/branch height ratio	7	18%	–	25%		–		22%	–	2%	–	22%	–
Claw II heights													
Branch	9	11.5	–	15.5	*24.1*	–	*31.9*	14.1	*28.9*	1.2	*2.7*	15.3	*28.0*
Spur	8	2.0	–	3.7	*4.3*	–	*7.4*	3.2	*6.5*	0.6	*1.0*	3.7	*6.8*
Spur/branch height ratio	8	15%	–	25%		–		22%	–	3%	–	24%	–
Claw III heights													
Branch	9	12.4	–	15.5	*25.9*	–	*31.6*	13.8	*28.5*	1.1	*1.9*	15.5	*28.3*
Spur	8	2.6	–	3.6	*5.3*	–	*7.3*	3.2	*6.5*	0.3	*0.6*	3.3	*6.0*
Spur/branch height ratio	8	20%	–	27%		–		23%	–	3%	–	21%	–
Claw IV heights													
Branch	5	14.6	–	17.4	*32.7*	–	*38.8*	16.3	*35.1*	1.0	*2.3*	?	*?*
Spur	5	2.8	–	3.6	*6.0*	–	*7.4*	3.2	*6.9*	0.3	*0.6*	?	*?*
Spur/branch height ratio	5	17%	–	22%		–		20%	–	2%	–	?	–

TABLE 44. Measurements [in µm] of selected morphological structures of the juveniles of *Echiniscus scabrocirrosus* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	**RANGE**						**MEAN**		**SD**	
		µm			***sp***			**µm**	***sp***	**µm**	***sp***
Body length	5	259	–	283	*525*	–	*624*	272	*573*	9	*44*
Scapular plate length	5	43.4	–	53.8		–		47.6	–	4.0	–
Head appendages lengths											
Cirrus *internus*	4	8.3	–	14.7	*18.2*	–	*27.3*	10.9	*22.2*	3.0	*4.6*
Cephalic papilla	5	7.5	–	10.8	*15.7*	–	*20.1*	8.6	*18.0*	1.3	*1.6*
Cirrus *externus*	5	11.1	–	18.7	*24.7*	–	*34.8*	14.5	*30.4*	2.7	*3.7*
Clava	5	5.2	–	6.1	*11.2*	–	*13.1*	5.7	*12.0*	0.4	*0.9*
Cirrus *A*	4	29.0	–	40.1	*64.6*	–	*86.6*	36.1	*78.3*	4.9	*9.7*
Cirrus *A*/Body length ratio	4	11%	–	15%		–		13%	–	2%	–
Body appendages lengths											
Cirrus *C*	3	89.0	–	117.6	*202.3*	–	*218.6*	101.1	*208.7*	14.8	*8.7*
Cirrus C^d	4	49.4	–	83.9	*110.0*	–	*193.3*	64.6	*137.2*	14.6	*37.9*
Cirrus *D*	2	123.8	–	141.9	*275.7*	–	*327.0*	132.9	*301.3*	12.8	*36.2*
Spine on leg I length	5	1.9	–	3.0	*4.0*	–	*6.2*	2.4	*5.1*	0.4	*0.9*
Papilla on leg IV length	4	3.0	–	3.8	*6.3*	–	*8.8*	3.4	*7.5*	0.3	*1.0*
Number of teeth on the collar	3	13	–	14		–		13.3	–	0.6	–
Claw I heights											
Branch	5	13.3	–	14.3	*26.4*	–	*31.8*	13.9	*29.4*	0.4	*2.1*
Spur	5	2.8	–	3.6	*5.9*	–	*6.9*	3.1	*6.5*	0.3	*0.5*
Spur/branch height ratio	5	20%	–	25%		–		22%	–	2%	–
Claw II heights											
Branch	5	13.1	–	14.3	*26.6*	–	*32.3*	13.8	*29.2*	0.4	*2.4*
Spur	5	2.7	–	3.1	*5.4*	–	*6.7*	2.9	*6.2*	0.1	*0.5*
Spur/branch height ratio	5	19%	–	23%		–		21%	–	1%	–
Claw III heights											
Branch	5	13.4	–	15.0	*27.9*	–	*31.6*	14.0	*29.4*	0.6	*1.4*
Spur	5	2.5	–	3.2	*5.2*	–	*6.7*	2.9	*6.1*	0.3	*0.7*
Spur/branch height ratio	5	18%	–	23%		–		21%	–	2%	–
Claw IV heights											
Branch	5	14.8	–	16.4	*30.5*	–	*36.3*	15.8	*33.4*	0.6	*2.8*
Spur	5	3.3	–	3.9	*6.9*	–	*9.0*	3.6	*7.6*	0.2	*0.8*
Spur/branch height ratio	5	20%	–	25%		–		23%	–	2%	–

TABLE 45. Measurements [in μm] of selected morphological structures of the larvae of *Echiniscus scabrocirrosus* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD	
		μm			*sp*			μm	*sp*	μm	*sp*
Body length	2	162	–	178	*600*	–	*602*	170	*601*	11	*2*
Scapular plate length	2	26.9	–	29.7		–		28.3	–	2.0	–
Head appendages lengths											
Cirrus *internus*	1	5.1	–	5.1	*17.2*	–	*17.2*	5.1	*17.2*	?	*?*
Cephalic papilla	2	4.9	–	5.8	*16.5*	–	*21.6*	5.4	*19.0*	0.6	*3.6*
Cirrus *externus*	2	7.2	–	7.6	*24.2*	–	*28.3*	7.4	*26.2*	0.3	*2.8*
Clava	2	4.0	–	4.3	*13.5*	–	*16.0*	4.2	*14.7*	0.2	*1.8*
Cirrus *A*	2	22.3	–	24.0	*75.1*	–	*89.2*	23.2	*82.2*	1.2	*10.0*
Cirrus *A*/Body length ratio	2	13%	–	15%		–		14%	–	2%	–
Body appendages lengths											
Cirrus *C*	1	45.0	–	45.0	*151.5*	–	*151.5*	45.0	*151.5*	?	*?*
Cirrus C^d	2	22.8	–	34.0	*84.8*	–	*114.5*	28.4	*99.6*	7.9	*21.0*
Cirrus *D*	1	47.1	–	47.1	*158.6*	–	*158.6*	47.1	*158.6*	?	*?*
Spine on leg I length	0		?			?		?	*?*	?	*?*
Papilla on leg IV length	2	2.7	–	3.0	*9.1*	–	*11.2*	2.9	*10.1*	0.2	*1.5*
Number of teeth on the collar	2	9	–	12		–		10.5	–	2.1	–
Claw I heights											
Branch	2	9.0	–	9.9	*30.3*	–	*36.8*	9.5	*33.6*	0.6	*4.6*
Spur	2	2.1	–	2.2	*7.4*	–	*7.8*	2.2	*7.6*	0.1	*0.3*
Spur/branch height ratio	2	21%	–	24%		–		23%	–	2%	–
Claw II heights											
Branch	1	9.1	–	9.1	*30.6*	–	*30.6*	9.1	*30.6*	?	*?*
Spur	1	1.8	–	1.8	*6.1*	–	*6.1*	1.8	*6.1*	?	*?*
Spur/branch height ratio	1	20%	–	20%		–		20%	–	?	–
Claw III heights											
Branch	1	8.7	–	8.7	*29.3*	–	*29.3*	8.7	*29.3*	?	*?*
Spur	1	2.3	–	2.3	*7.7*	–	*7.7*	2.3	*7.7*	?	*?*
Spur/branch height ratio	1	26%	–	26%		–		26%	–	?	–
Claw IV heights											
Branch	1	9.0	–	9.0	*30.3*	–	*30.3*	9.0	*30.3*	?	*?*
Spur	1	2.4	–	2.4	*8.1*	–	*8.1*	2.4	*8.1*	?	*?*
Spur/branch height ratio	1	27%	–	27%		–		27%	–	?	–

Geographic distribution. The new species is known only from South Africa, possibly even to the Swartberg range (Fig. 120H).

Remarks. The new species was always accompanied by other echiniscids, most frequently by *E. draconis* **sp. nov.**, as well as by milnesiids and ramazzottiids.

Differential diagnosis. The species is compared to other *Echiniscus* spp. without appendages *B* and *E*, but with very long, filamentous cirri *C* and *D*. Therefore, it can be distinguished from:

- *E. becki*, a likely Nearctic endemic (Schuster & Grigarick 1966a), by the body appendage formula (*A*-*C*-C^d-*D* in *E. scabrocirrosus* **sp. nov.** *vs A*-*C*-*D* in *E. becki*), and by secondary spurs on external claws IV (absent in

E. scabrocirrosus **sp. nov.** *vs* present in *E. becki*);
- *E. knowltoni*, by the body appendage formula (*A-C-C^d-D* in *E. scabrocirrosus* **sp. nov.** *vs A-C-C^d-D-D^d* in *E. knowltoni*), and by secondary spurs on external claws IV (absent in *E. scabrocirrosus* **sp. nov.** *vs* present in *E. knowltoni*);
- *E. punctus*, known from the sub-Antarctic Signy Island (McInnes 1995), by the body appendage formula (*A-C-C^d-D* in *E. scabrocirrosus* **sp. nov.** *vs A-C-C^d-D-D^d* in *E. punctus*), and by the number of teeth in the dentate collar IV (11–20 in adults of *E. scabrocirrosus* **sp. nov.** *vs* 5–8 in adults of *E. punctus*);
- *E. trisetosus*, widely distributed in the Palaearctic realm (Cuénot 1932; McInnes 1994), by the body appendage formula (*A-C-C^d-D* in *E. scabrocirrosus* **sp. nov.** *vs A-C-C^d-D-D^d* in *E. trisetosus*), the secondary spurs on external claws IV (absent in *E. scabrocirrosus* **sp. nov.** *vs* present in *E. trisetosus*), and by the dorsal sculpturing (minute pores densely arranged in the endocuticular matrix in *E. scabrocirrosus* **sp. nov.** *vs* large pores surrounded by polygonal edges [the *blumi-canadensis* type] in *E. trisetosus*).

Raw measurements. Supplementary Materials (SM.03) and Tardigrada Register (www.tardigrada.net/register/0095.htm).

25. Echiniscus scabrospinosus Fontoura, 1982

Figures 82–85

Data source:

A total of 323 specimens (251 ♀♀, 35 juveniles, 4 larvae, and 33 specimens of unknown instar/sex):
- Sample ZA.081: 1 specimen (1 juvenile on a slide).
- Sample ZA.097:4 specimens (4 ♀♀ on slides); found with *Echiniscus lichenorum*.
- Sample ZA.098: 9 specimens (4 ♀♀, 2 juveniles on slides, and 3 specimens used for DNA extraction, including 1 hologenophore); found with *Echiniscus draconis* **sp. nov.**, *E. lichenorum*, and *E. marginatus*.
- Sample ZA.125: 2 specimens (2 ♀♀ on a slide).
- Sample ZA.141: 1 specimen (1 ♀ on a slide).
- Sample ZA.145: 1 specimen (1 ♀ on a slide).
- Sample ZA.157: 20 specimens (20 ♀♀ on slides); found with *Pseudechiniscus (P.)* cf. *ehrenbergi* and *P. (Meridioniscus) wallacei* **sp. nov.**
- Sample ZA.158: 1 specimen (1 ♀ on a slides); found with *Echiniscus virginicus* and *Pseudechiniscus (Meridioniscus) wallacei* **sp. nov.**
- Sample ZA.183: 1 specimen (1 juvenile on a slide); found with *Doryphoribius maasaimarensis*, *Echiniscus oreas* **sp. nov.**, *E. regularis* **sp. nov.**, *Pseudechiniscus (Pseudechiniscus)* cf. *ehrenbergi, P. (Meridioniscus) wallacei* **sp. nov.**, and *Ramazzottius szeptycki*.
- Sample ZA.185: 1 specimen (1 ♀ on a slide); found with *Echiniscus oreas* **sp. nov.**, *E. regularis* **sp. nov.**, and *E. virginicus*.
- Sample ZA.190: 1 specimen (1 ♀ on a slide); found with *Echiniscus oreas* **sp. nov.**, *E. regularis* **sp. nov.**, and *Pseudechiniscus (Pseudechiniscus)* cf. *ehrenbergi*.
- Sample ZA.196: 4 specimens (4 specimens used for DNA extraction).
- Sample ZA.199: 1 specimen (1 juvenile on a slide).
- Sample ZA.200: 11 specimens (4 ♀♀ and 1 juvenile on slides, 4 specimens used for SEM analysis, and 2 specimens used for DNA extraction, including 1 hologenophore).
- Sample ZA.202: 23 specimens (11 ♀♀ on slides, 10 specimens used for SEM analysis, and 2 specimens used for DNA extraction); found with *Pseudechiniscus (P.)* cf. *ehrenbergi*.
- Sample ZA.206: 4 specimens (4 ♀♀ on slides); found with *Echiniscus oreas* **sp. nov.**, *E. regularis* **sp. nov.**, and *E. virginicus*.
- Sample ZA.224: 1 specimen (1 ♀ on a slide); found with *Echiniscus imitans* **sp. nov.**, *E. oreas* **sp. nov.**, and *E. regularis* **sp. nov.**
- Sample ZA.230: 6 specimens (3 ♀♀ and 3 juveniles on slides); found with *Echiniscus blumi*, *E. oreas* **sp. nov.**, and *E. regularis* **sp. nov**.

- Sample ZA.231: 13 specimens (6 ♀♀ and 3 juveniles on slides, and 4 specimens used for DNA extraction, including 3 retrieved hologenophores); found with *Pseudechiniscus (P.)* cf. *ehrenbergi*.
- Sample ZA.259: 2 specimens (2 ♀♀ on a slide); found with *Echiniscus pellucidus* and *Pseudechiniscus (P.)* cf. *ehrenbergi*.
- Sample ZA.260: 2 specimens (2 ♀♀ on a slide); found with *Doryphoribius bindae*, *Echiniscus baius*, *E. longispinosus*, *E. oreas* **sp. nov.**, *E. pellucidus*, and *E. virginicus*.
- Sample ZA.265: 11 specimens (9 ♀♀ and 2 juveniles on slides); found with *Echiniscus regularis* **sp. nov.** and *Pseudechiniscus (P.)* cf. *ehrenbergi*.
- Sample ZA.266: 4 specimens (3 ♀♀ and 1 juvenile on slides); found with *Pseudechiniscus (P.)* cf. *ehrenbergi*.
- Sample ZA.288: 77 specimens (66 ♀♀ and 7 juveniles on slides, and 4 specimens used for DNA extraction, including 2 hologenophores).
- Sample ZA.296: 90 specimens (84 ♀♀, 4 juveniles and 2 larvae on slides).
- Sample ZA.337: 1 specimen (1 ♀ on a slide).
- Sample ZA.360: 1 specimen (1 ♀ on a slide); found with *Echiniscus draconis* **sp. nov.**, *E. lichenorum*, and *E. longispinosus*.
- Sample ZA.366: 1 specimen (1 ♀ on a slide); found with *Echiniscus virginicus*.
- Sample ZA.367: 7 specimens (5 ♀♀ and 2 larvae on slides); found with *Pseudechiniscus (P.) linnaei* **sp. nov.** and *Ramazzottius szeptycki*.
- Sample ZA.404: 1 specimen (1 ♀ on a slide); found with *Echiniscus cavagnaroi*.
- Sample ZA.418: 2 specimens (1 ♀ and 1 juvenile on a slide).
- Sample ZA.490: 1 specimen (1 juvenile on a slide); found with *Echiniscus setaceus* **sp. nov.**
- Sample ZA.513: 2 specimens (2 ♀♀ on a slide); found with *Echiniscus gracilis* **sp. nov.**, *E. latruncularis* **sp. nov.**, and *E. setaceus* **sp. nov.**
- Sample ZA.518: 2 specimens (1 ♀ and 1 juvenile on slides); found with *Echiniscus dentatus* **sp. nov.**, *E. irroratus* **sp. nov.**, *Pseudechiniscus (P.)* cf. *ehrenbergi*, and *P. (Meridioniscus) wallacei* **sp. nov.**
- Sample ZA.519: 1 specimen (1 ♀ on a slide).
- Sample ZA.524: 1 specimen (1 ♀ on a slide); found with *Diphascon zaniewi* Kaczmarek & Michalczyk, 2004, *Echiniscus dentatus* **sp. nov.**, and *Pseudechiniscus (P.)* cf. *ehrenbergi*.
- Sample ZA.525: 1 specimen (1 ♀ on a slide).
- Sample ZA.529: 3 specimens (1 ♀ and 2 juveniles on slides); found with *Echiniscus merokensis*, *E. setaceus* **sp. nov.**, and *Pseudechiniscus (P.)* cf. *ehrenbergi*.
- Sample ZA.532: 5 specimens (2 ♀♀ and 3 juveniles on slides); found with *Echiniscus setaceus* **sp. nov.**
- Sample ZA.534: 1 specimen (1 ♀ on a slide).
- Sample ZA.539: 2 specimens (1 ♀ and 1 juvenile on a slide).
- Comparative Iberian material: Sample PT.002: 38°41’32’’N, 9°25’18’’W, 16 m asl: Portugal, Cascais, Parque do Gandarinha; lichen from tree bark in an urban park (20 specimens: 14 ♀♀, 1 juvenile, and 1 larva on slides, and 4 specimens used for DNA extraction); coll. 04.12.2015, Paulina Kosztyła.

Literature:
- Original description: Fontoura (1982).
- Later records: Binda & Pilato (1995a), Fontoura *et al*. (2008), Gąsiorek *et al*. (2019a).

Shortened description. Body plump, with short stout limbs (Fig. 82A–B, 83). Light yellow to dark orange body and small red eyes; body colour and eyes disappeared soon after mounting in Hoyer’s medium. Dactyloid cephalic papillae (Fig. 84A). Body appendage formula *A-C-D-D^{d}-E*. Dorsal sculpturing of the *E. spinulosus* type, pores with the endocuticular rings (Fig. 84B–C). Median plates 1, 3 unipartite (m3 reduced to the tiny triangular surface with pores covered by the paired segmental plate II and caudal plate), but m2 bipartite with the anterior smooth portion. Lateral, non-porous portions of the scapular and paired segmental plates present. Faceting of the caudal plate delineated by epicuticular ridges/sutures (Fig. 82–83). Ventral plates absent. Pedal plates absent. Pulvini present (Fig. 82A). External claws spurless, but internal ones with thin acute spurs positioned at *ca.* 25% of the claw branch (Fig. 85).

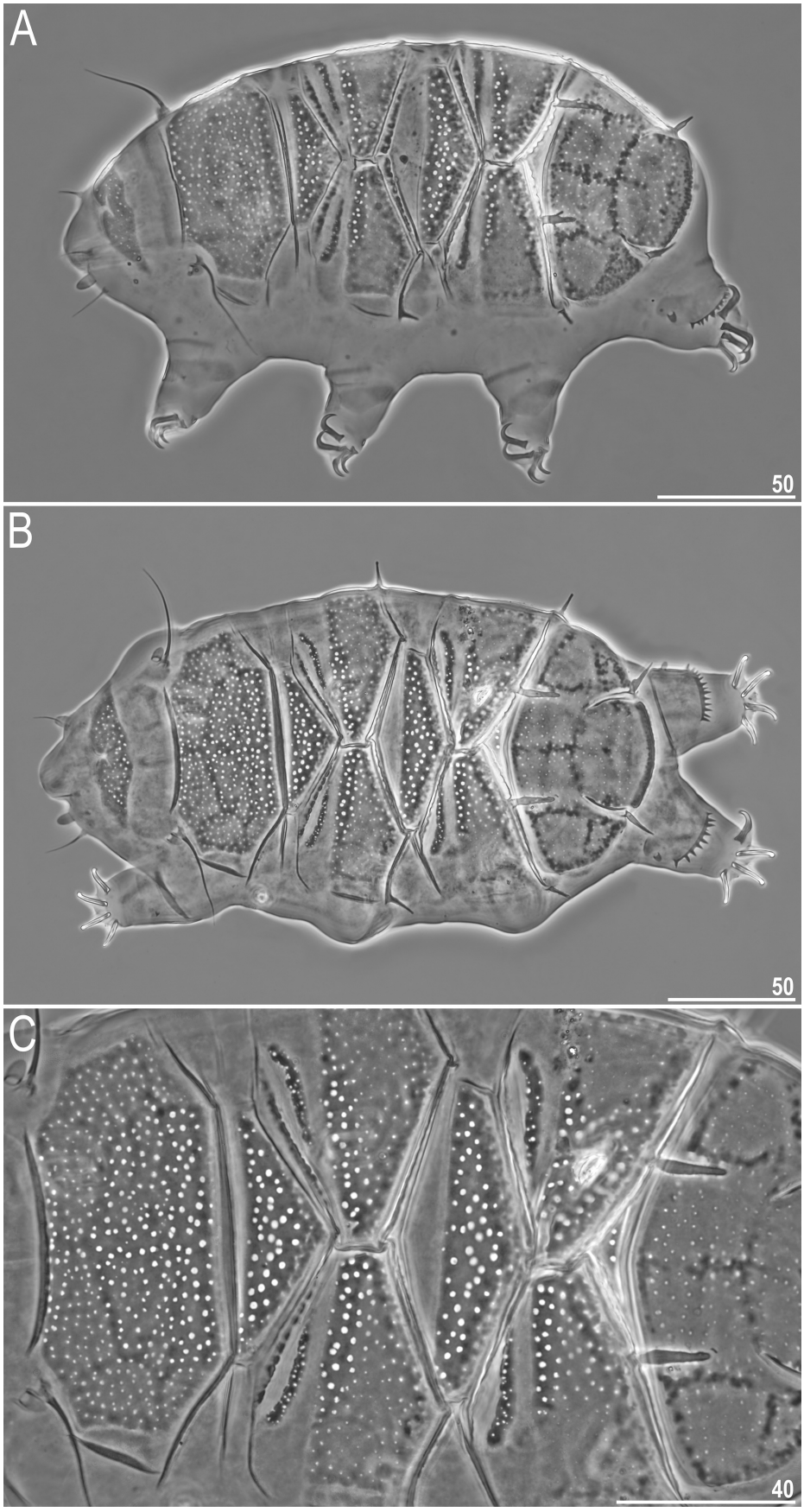

FIGURE 82. Habitus (A–B, females in dorsolateral and dorsal view) and dorsal sculpturing (C) of *Echiniscus scabrospinosus* Fontoura, 1982 (PCM). Scale bars in μm.

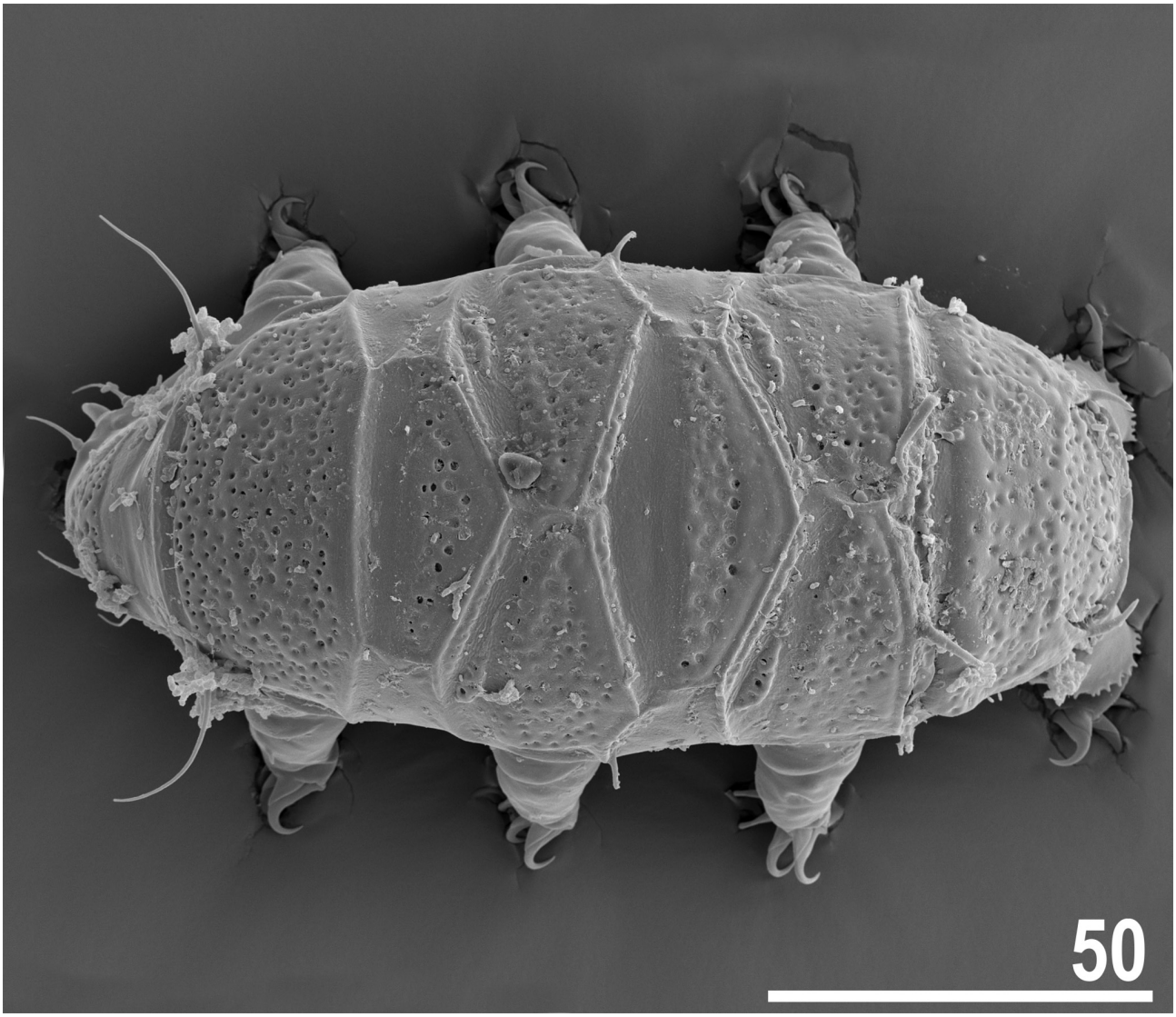

FIGURE 83. Habitus of *Echiniscus scabrospinosus* (SEM, female in dorsal view). Scale bar = 50 μm.

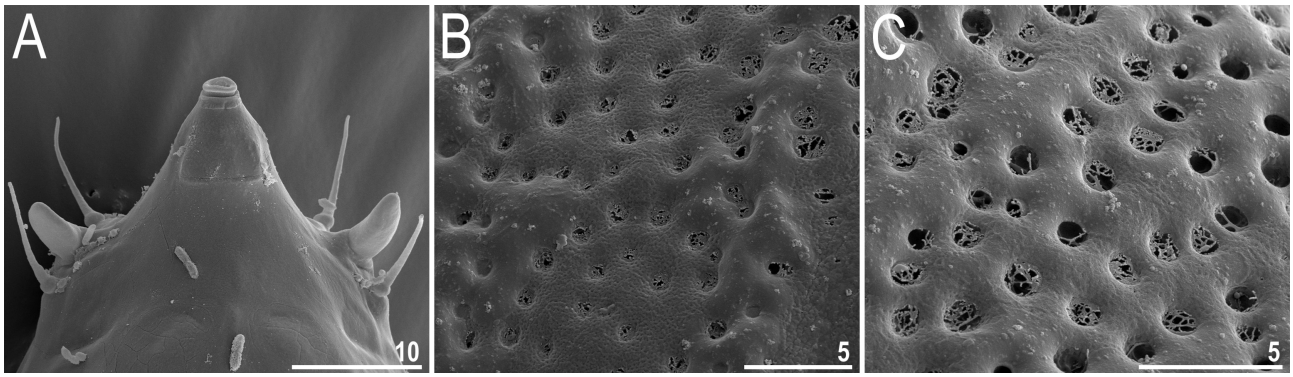

FIGURE 84. Morphology of *Echiniscus scabrospinosus* (SEM, females): A—cephalic appendages, B, C—pores in close-up. Scale bars in μm.

DNA markers and phylogenetic position. *Echiniscus scabrospinosus* is the sister species of *E. oreas* **sp. nov.** within the *E. spinulosus* complex (Fig. 117). The species closest in COI is *E. cavagnaroi* (p-distance = 15.2–16.2%), in ITS-1 and ITS-2—*E. oreas* **sp. nov.** (0.3–1.4% and 0.3–0.6%, respectively). The ranges of intraspecific variability in all three sequenced fast evolving markers were as follows: COI: 0.6–2.4%, ITS-1: 0.3–2.0%, and ITS-2: 0.3%.

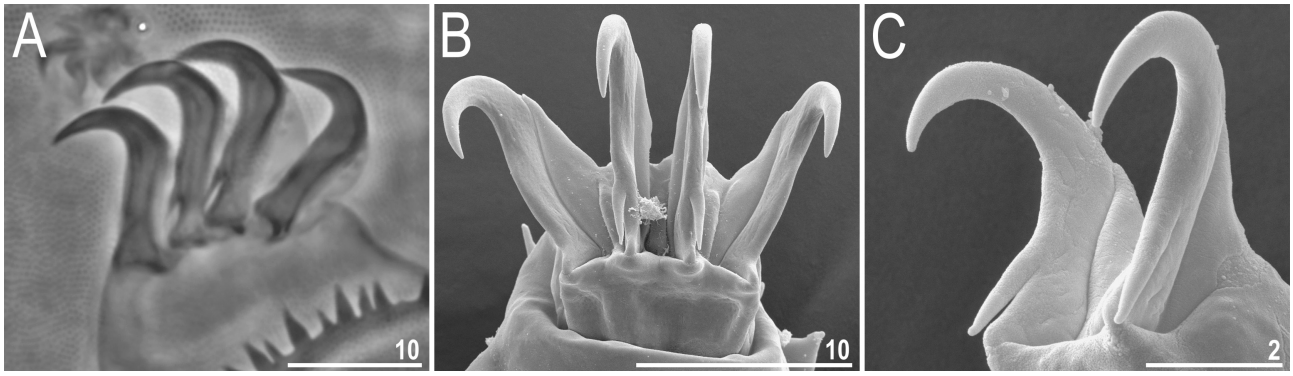

FIGURE 85. Claws of *Echiniscus scabrospinosus*: A—claws IV (PCM, female), B—claws IV (SEM, female), C—larval claws (SEM). Scale bars in μm.

Geographic distribution. The species was originally described from the Iberian Peninsula (Portugal; Fontoura 1982) and subsequently reported from the Atlantic Ocean (Azores; Fontoura *et al*. 2008) and Central Africa (Tanzania; Binda & Pilato 1995a). The species is ubiquitous in South Africa (Fig. 120E), although it is most often represented by small populations of several individuals. Given that genetic data are available for both the Iberian (Gąsiorek *et al*. 2019a) and the South African populations (the present study), it can be stated with confidence that the range of *E. scabrospinosus* encompasses the south-western Palaearctic and the Afrotropic. The ubiquity of the species in South Africa may suggest natural dispersal that occurred a long time ago. Alternatively, the wide distribution of *E. scabrospinosus* in the region may be explained by recent anthropogenic dispersal if the species exhibits high reproductive rate and good short distance dispersal abilities (these alternative hypotheses could be tested by investigating genetic structure of a number of European and African populations).

Remarks. Parthenogenetic. The morphological and ontogenetic variability are considerable in *E. scabrospinosus* (Pilato *et al*. 2008), but the phylogenetic analysis confirmed the species identity of the Portuguese (Gąsiorek *et al*. 2019a) and African populations (Fig. 117).

26. Echiniscus setaceus sp. nov. Gąsiorek, Vončina, Morek & Michalczyk

urn:lsid:zoobank.org:act:55AB5DCF-9AFC-4478-8CA4-D1277B4A07DB
Figures 86–93, Tables 46–49

Data source:

A total of 309 specimens (146 ♀♀, 23 ♂♂, 59 juveniles, 13 larvae, and 68 specimens of unknown instar/sex):

- Sample ZA.015: 36 specimens (27 ♀♀, 3 ♂♂, 1 larva and 1 specimen of unknown sex on slides, and 4 specimens used for DNA extraction and secured as hologenophores); found with *Echiniscus attenboroughi* **sp. nov**., *E. draconis* **sp. nov.**, *E. lichenorum*, and *E. virginicus*.
- Sample ZA.020: 12 specimens (5 ♀♀, 5 juveniles and 2 larvae on slides); found with *Echiniscus dentatus* **sp. nov.**, *E. draconis* **sp. nov.**, *E. lichenorum*, and *E. longispinosus*.
- Sample ZA.022: 1 specimen (1 ♀ on a slide); found with *Echiniscus attenboroughi* **sp. nov**., *E. dentatus* **sp. nov.**, *E. gracilis* **sp. nov.**, *E. lichenorum*, and *E. longispinosus*.
- Sample ZA.026: 5 specimens (4 ♀♀ and 1 ♂ on slides).
- Sample ZA.029: 45 specimens (14 ♀♀, 11 ♂♂ and 2 juveniles on slides, 10 specimens on SEM stub 19.04, and 8 specimens used for DNA extraction, including 7 hologenophores).
- Sample ZA.089: 1 specimen (1 ♀ on a slide).
- Sample ZA.096: 1 specimen (1 ♀ on a slide); found with *Echiniscus gracilis* **sp. nov.** and *E. longispinosus*.
- Sample ZA.436: 1 specimen (1 ♀ on a slide); found with *Echiniscus attenboroughi* **sp. nov**., *E. draconis* **sp. nov.**, and *E. scabrocirrosus* **sp. nov.**
- Sample ZA.490: 25 specimens (9 ♀♀, 2 ♂♂, 1 larva and 3 specimens of unknown sex on slides, and 10 specimens used for DNA extraction, including 6 hologenophores); found with *Echiniscus scabrospinosus*.
- Sample ZA.493: 8 specimens (6 ♀♀, 1 ♂ and 1 juvenile on slides).

- Sample ZA.495: 2 specimens (2 ♀♀ on a slide); found with *Echiniscus dentatus* **sp. nov.**
- Sample ZA.502: 3 specimens (1 larva on a slide, and 2 specimens used for DNA extraction, including 1 hologenophore); found with *Cornechiniscus madagascariensis*, *Echiniscus dentatus* **sp. nov.**, *E. irroratus*, and *E. latruncularis* **sp. nov.**
- Sample ZA.505: 3 specimens (2 juveniles and 1 specimen of unknown sex on slides); found with *Echiniscus dentatus* **sp. nov.**
- Sample ZA.506: 11 specimens (7 ♀♀, 3 juveniles and 1 specimens of unknown sex on slides).
- Sample ZA.507: 2 specimens (2 ♀♀ on slides); found with *Echiniscus dentatus* **sp. nov.** and *E. longispinosus*.
- Sample ZA.509: 25 specimens (16 ♀♀, 2 ♂♂ and 7 juveniles on slides).
- Sample ZA.510: 6 specimens (6 ♀♀ on slides).
- Sample ZA.513: 45 specimens (28 ♀♀ and 3 juveniles on slides, 10 specimens on SEM stub 19.03, and 4 specimens used for DNA extraction, including 3 hologenophores); found with *Echiniscus gracilis* **sp. nov.**, *E. latruncularis* **sp. nov.**, and *E. scabrospinosus*.
- Sample ZA.517: 1 specimen (1 juvenile on a slide).
- Sample ZA.529: 4 specimens (1 ♀, 2 ♂♂, 1 juvenile on slides); found with *Echiniscus merokensis*, *E. scabrospinosus*, and *Pseudechiniscus (P.)* cf. *ehrenbergi*.
- Sample ZA.530: 1 specimen (1 larva on a slide).
- Sample ZA.532: 61 specimens (5 ♀♀, 1 ♂, 34 juveniles and 7 larvae on slides, 10 specimens on SEM stub 19.06, and 4 specimens used for DNA extraction, including 3 hologenophores); found with *Echiniscus scabrospinosus*.
- Sample ZA.537: 2 specimens (2 ♀♀ on slides); found with *Echiniscus dentatus* **sp. nov.**
- Sample ZA.538: 3 specimens (3 ♀♀ on slides); found with *Pseudechiniscus (P.)* cf. *ehrenbergi*.
- Sample ZA.540: 3 specimens (3 ♀♀ on a slide); found with *Pseudechiniscus (P.)* cf. *ehrenbergi*.
- Sample ZA.541: 1 specimen (1 ♀♀ on a slide); found with *Pseudechiniscus (P.)* cf. *ehrenbergi*.
- Sample ZA.542: 1 specimen (1 ♀♀ on a slide); found with *Echiniscus latruncularis* **sp. nov.** and *E. longispinosus*.

Description. Mature females (*i.e*. from the third instar onwards; measurements and statistics in Table 46). Medium-sized *Echiniscus* with a very wide spectrum of morphological variability. Light yellow to dark orange body and large red eyes; body colour and eyes disappeared soon after mounting in Hoyer's medium. Body massive, with thick limbs (Fig. 86A, 87–88). Dactyloid cephalic papillae (secondary clavae) and (primary) clavae (Fig. 86A, 87, 91A, D); cirri growing out from bulbous cirrophores. Cirri *A* short. Body appendage configuration *A-C-C^{d}-D-(D^{d})-(E)*. Appendage *C^{d}* formed as a cirrus longer than other trunk appendages, which are short flexible spines (Fig. 86A, 87–88, 90). Aberrant asymmetric appendage *B* (17.6 μm) in the holotype. The configuration is very unstable, and single asymmetries are common.

Dorsal plates with a variable sculpture: typically, pores and pseudopores (visible as bright dots under PCM) are randomly distributed in plates between minute epicuticular granules (visible as dark dots under PCM) (Fig. 86–91). However, epicuticular granules may merge into a mostly smooth plate surface (Fig. 87B, 90). The cephalic plate with a large chalice-shaped anterior incision (Fig. 86A, 87A). The cervical (neck) plate visible only under SEM as a thin belt embedded on the anterior margin of the scapular plate (Fig. 91A, D). The scapular plate large, with lateral sutures demarcating lateral trapezoid portions (Fig. 86A, 87B, 90), and belts without pores in the central portion identifiable under SEM (Fig. 91A, D). Thin transverse belts on the paired segmental plates I–II (Fig. 90), with delicate epicuticular sculpturing identifiable under SEM (Fig. 91B, E). Median plate 1 and the posterior portion of m2 or equal in size; the anterior portion of m2 smooth, narrow and very reduced (Fig. 91B, E). Median plate 3 absent. The caudal (terminal) plate with two unsclerotised incisions, and with facets formed by weakly developed epicuticular ridges (Fig. 91C, F). Ventral cuticle with minute endocuticular pillars distributed throughout the whole venter; ventral plates absent. Sexpartite gonopore placed anteriorly to legs IV, and a trilobed anus between legs IV.

Pedal plates in the form of darker unsculptured areas in the central portions of all legs under PCM (Fig. 87A), not visible under SEM (Fig. 89C). Pulvini narrow but clearly marked (Fig. 86B, 87A, 89C). A minuscule spine on leg I and a tiny papilla on leg IV (Fig. 86A, 87). Dentate collar IV with a variable number of minute teeth. Claws I–IV similar in size. All external claws spurless. All internal claws with large, long spurs positioned at *ca.* 25%–30% of the branch height and highly divergent from it (Fig. 92).

Mature males and sexually dimorphic traits (*i.e.* from the third instar onwards; measurements and statistics in Table 47). Qualitatively like females, excluding the circular gonopore (Fig. 92B). On average smaller and less massive than females (Fig. 86B, 89). Body size differences: mean body length ±SD: 225 ±28 µm *vs* 272 ±22 µm (one-tailed Welch's *t*-test with N♀♀=10 and N♂♂=10: t_{13}=3.92; p<0.001); mean scapular plate length: 42.3 ±3.5 µm *vs* 54.6 ±7.1 µm (t_{13}=4.66; p<0.001).

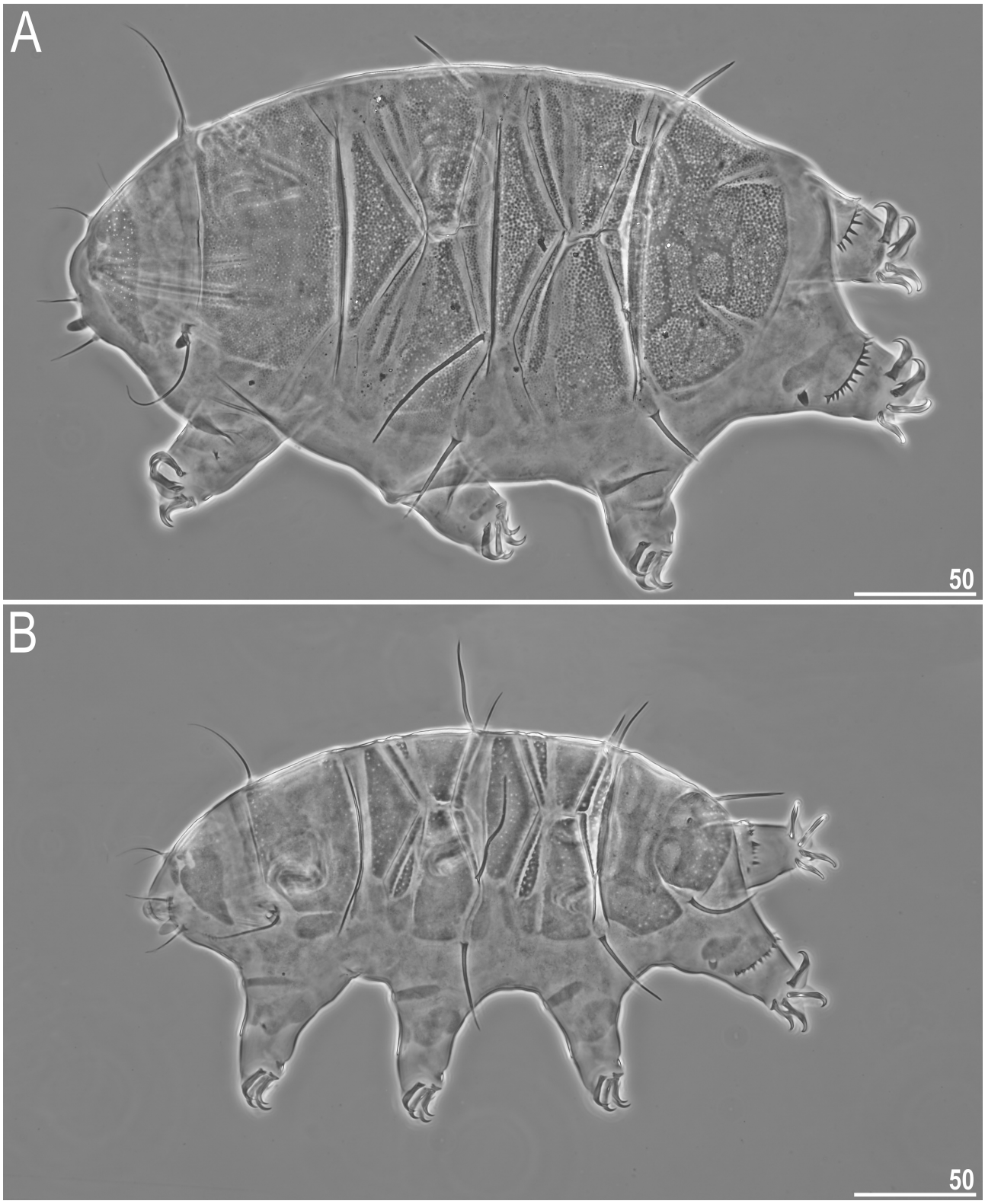

FIGURE 86. Habitus of *Echiniscus setaceus* **sp. nov.** (PCM): A—holotype, female in dorsolateral view, B—allotype, male in dorsolateral view. Scale bars = 50 µm.

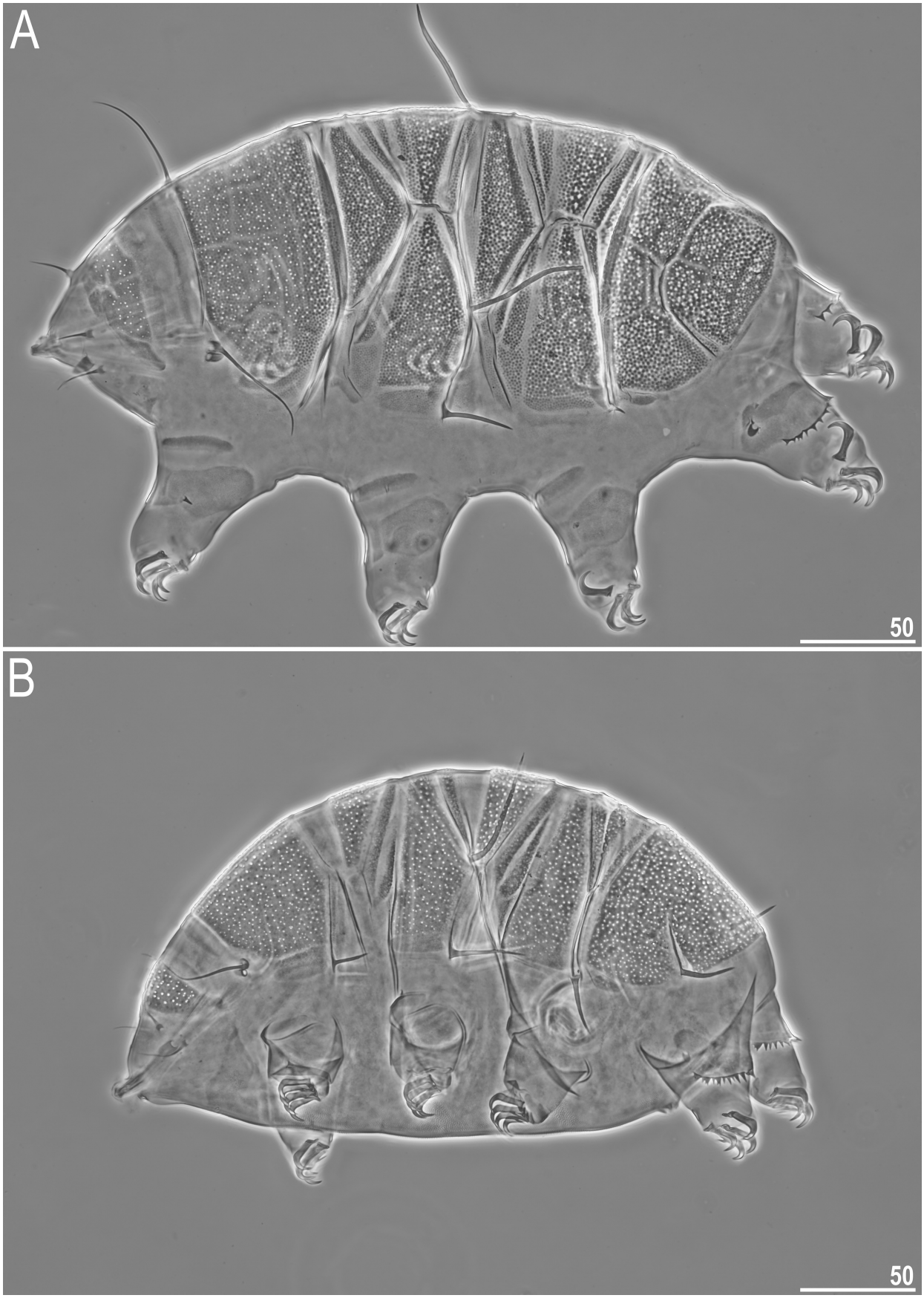

FIGURE 87. Variability of females of *Echiniscus setaceus* **sp. nov.** (PCM): A—dorsolateral view, B—lateral view. Scale bars = 50 μm.

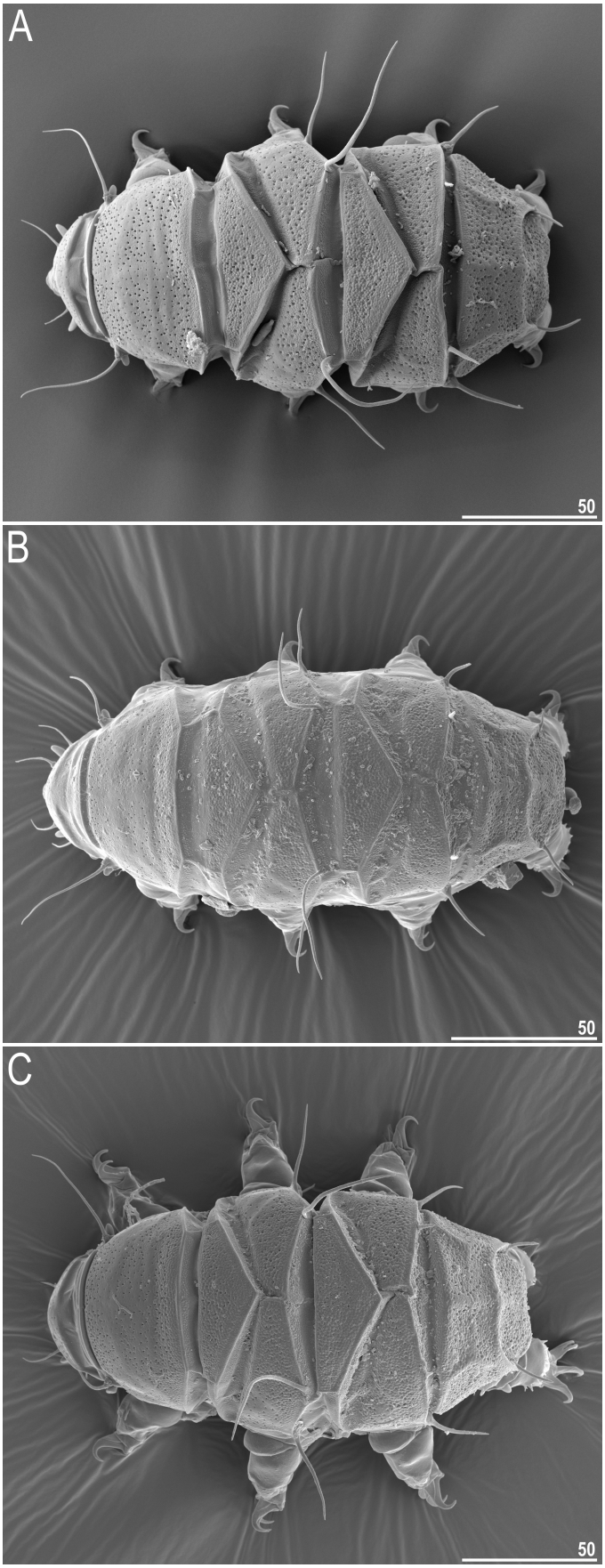

FIGURE 88. Variability of females of *Echiniscus setaceus* **sp. nov.** (SEM, dorsal view). Scale bars = 50 μm.

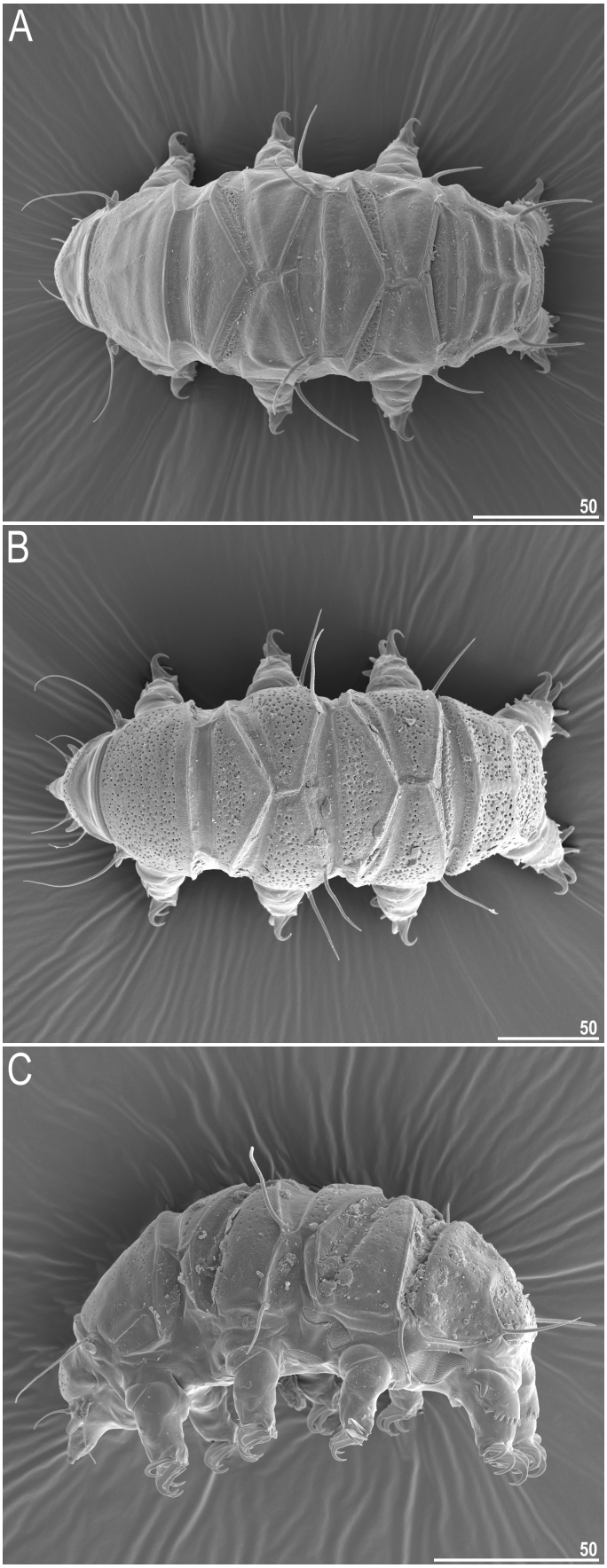

FIGURE 89. Variability of males of *Echiniscus setaceus* **sp. nov.** (SEM, dorsal and lateral view). Scale bars = 50 µm.

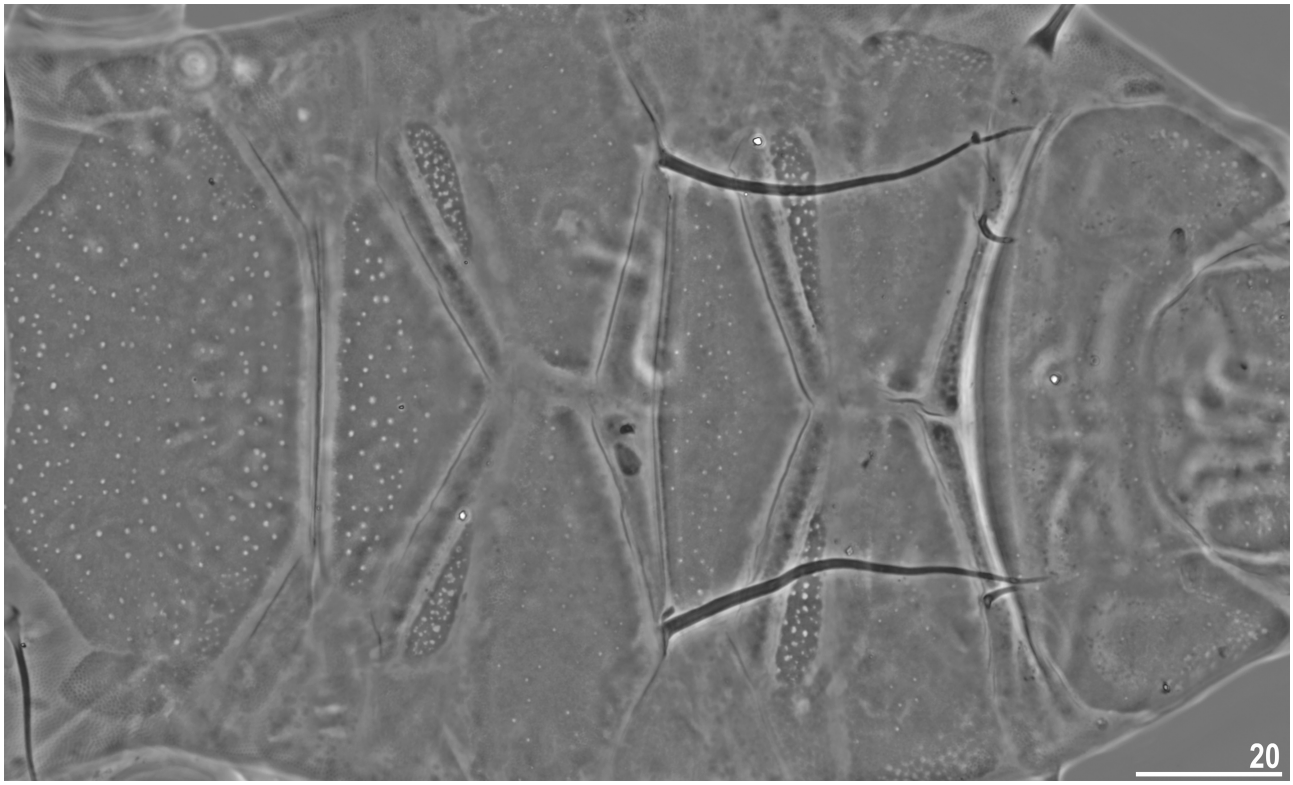

FIGURE 90. Dorsal sculpturing of *Echiniscus setaceus* **sp. nov.** in close-up (PCM, female). Scale bar = 20 μm.

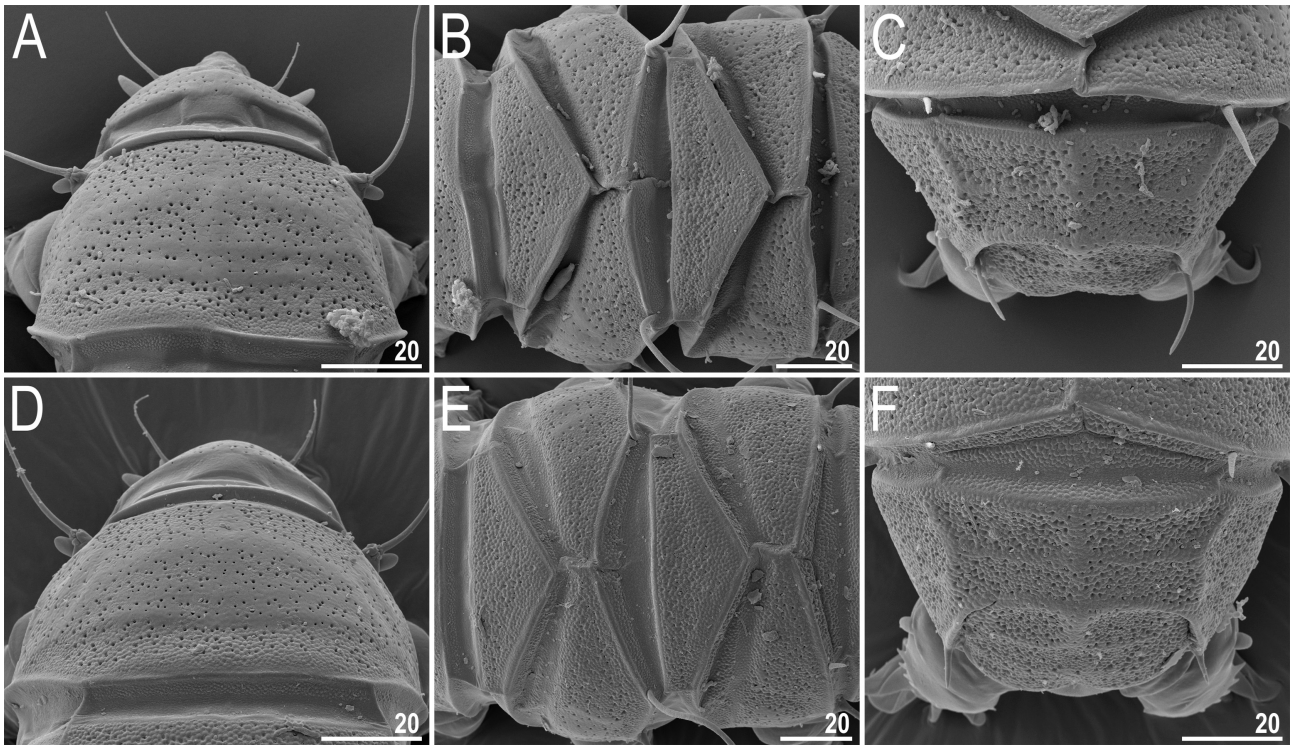

FIGURE 91. Dorsal sculpturing of *Echiniscus setaceus* **sp. nov.** in close-up (SEM, females): A, D—scapular plate, B, E—paired segmental and median plates, C, F—caudal (terminal) plate. Scale bars in μm.

Juveniles (*i.e.* the second instar; measurements and statistics in Table 48). No gonopore. Qualitatively like adults, but the dorsal sculpturing may be weakly developed (Fig. 93A). Morphometric gap between juveniles and adults present.

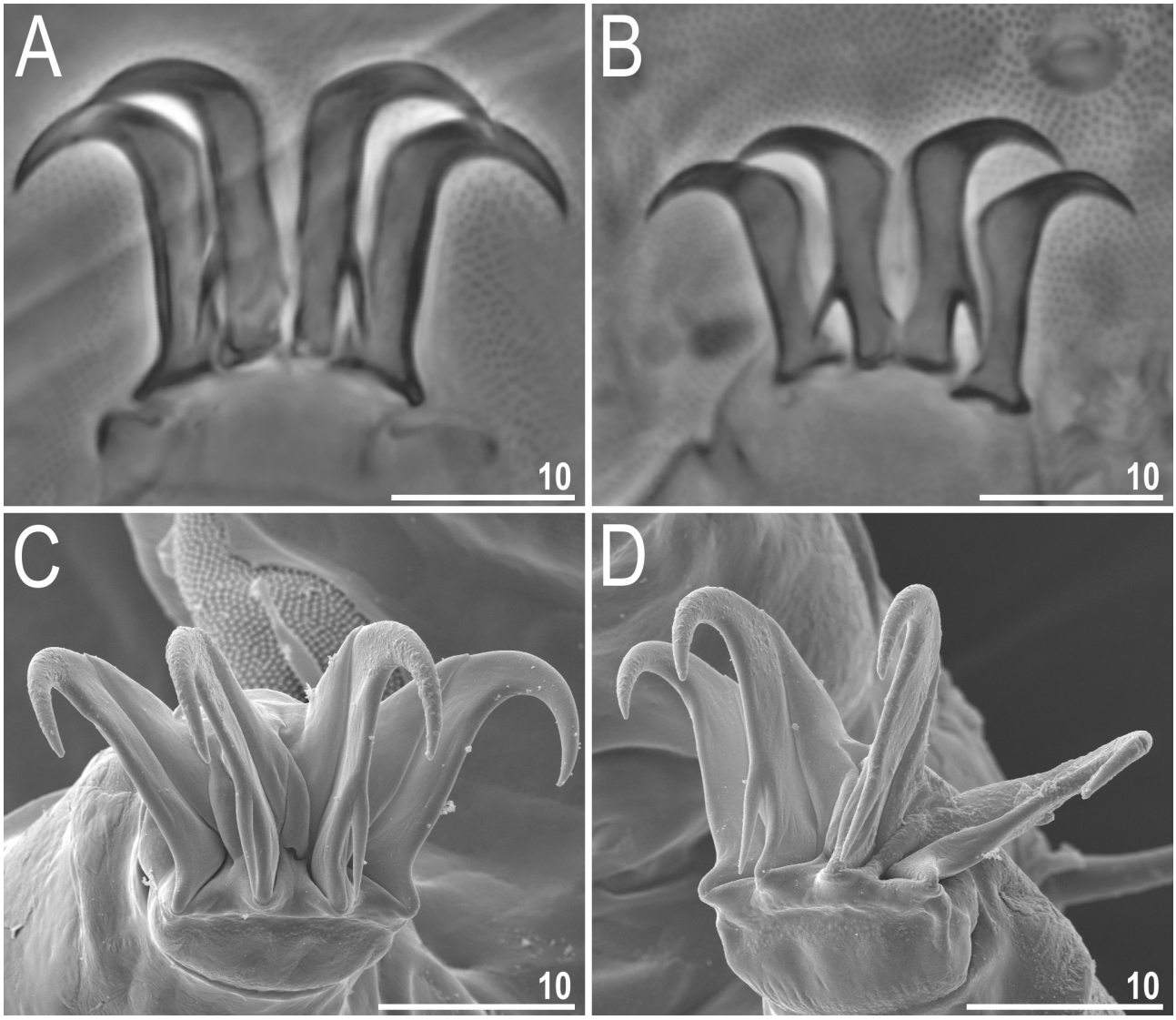

FIGURE 92. Claws of *Echiniscus setaceus* **sp. nov.**: A—claws II (PCM, female), B—claws IV (PCM, male), C—claws II (SEM, female), D—claws III (SEM, female). Scale bars = 10 μm.

Larvae (*i.e*. the first instar; measurements and statistics in Table 49). Gonopore and anus absent. The dorsal sculpturing developed as in some adults, which lack epicuticular granules (Fig. 93B). The body size overlaps with juveniles.

Eggs. Up to five yellow eggs per exuvia were found.

DNA markers and phylogenetic position. The new species is sister to all other representatives of the South-African endemic clade (Fig. 117). The species closest in ITS-1 is *E. lichenorum* (p-distance = 5.7–7.1%), and in ITS-2—*E. gracilis* **sp. nov.** (3.8–4.1%). The ranges of intraspecific variability are narrow in both ITS: ITS-1—0.3–1.4%, and ITS-2—0.3–1.2%.

Type material. 14 ♀♀, 11 ♂♂ and 2 juveniles on slides ZA.029.01–7; holotype: mature ♀ on slide ZA.029.05, allotype: mature ♂ on slide ZA.029.06. 10 specimens on SEM stub 19.04, 8 specimens used for DNA extraction, including 7 secured as hologenophores.

Type locality. 33°34’23.5’’S, 19°08’10.6’’E, 345 m asl: Republic of South Africa, Western Cape, Bain’s Kloof Pass; fynbos, lichen from rock (sample ZA.029).

Etymology. From Latin *saeta* = hair, referring to the cirrous appendage C^d usually longer than other trunk appendages. An adjective in the nominative singular.

Geographic distribution. The new species is widely distributed in South Africa (Fig. 120J) and the populations are often large (>20 specimens).

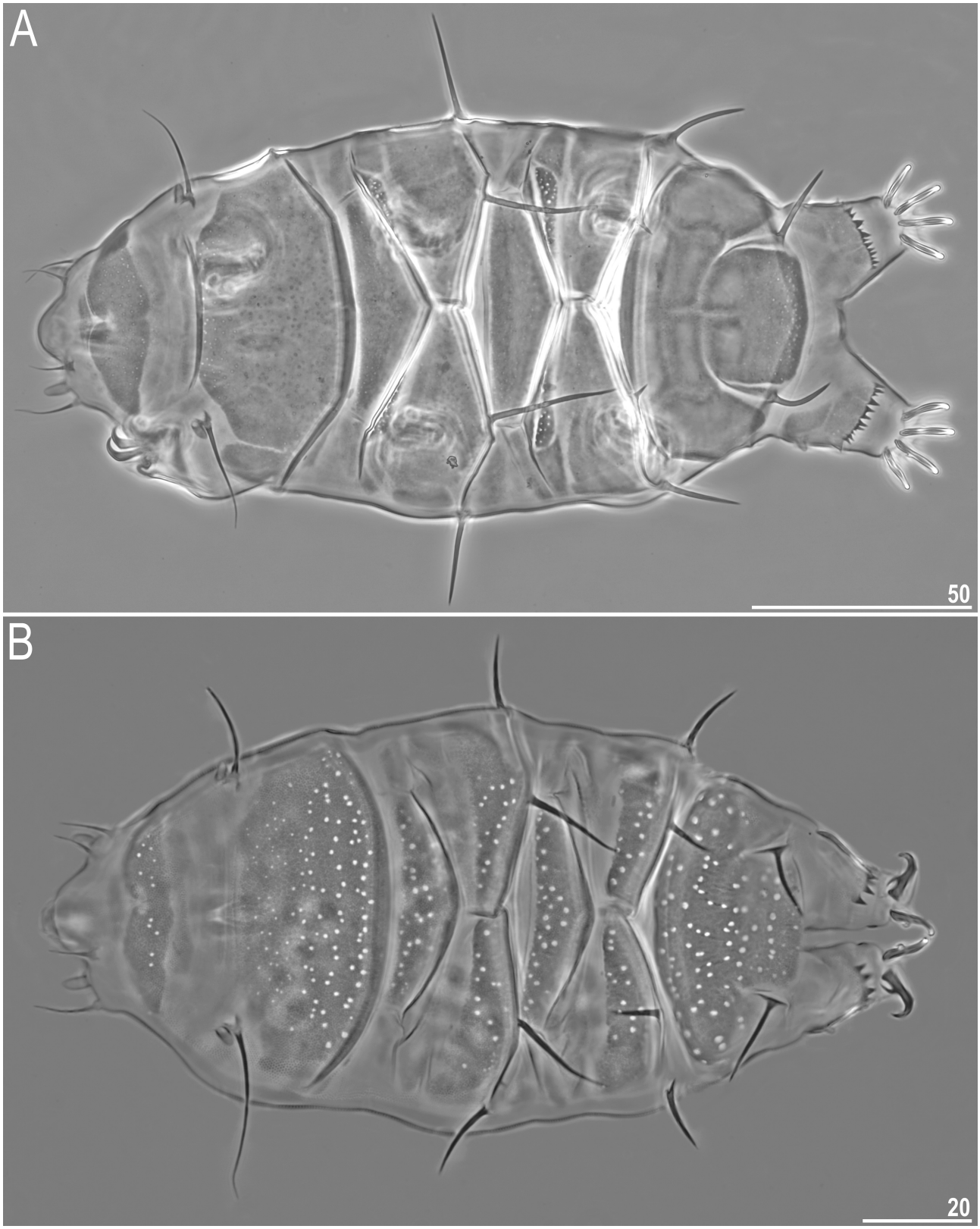

FIGURE 93. Habitus of sexually immature stages of *Echiniscus setaceus* **sp. nov.** (PCM): A—juvenile, dorsal view, B—larva, dorsal view. Scale bars in μm.

Remarks. This morphologically variable echiniscid may form both monospecific populations and be mixed with other echiniscids.

Differential diagnosis. The combination of body appendage configuration *A-C-C^{d}-D-(D^{d})-(E)* and the dissimi-

larity in the length of appendages (with the cirrus C^d much longer than spines in other positions) makes *E. setaceus* **sp. nov.** unique among all known *Echiniscus* spp.

Raw measurements. Supplementary Materials (SM.03) and Tardigrada Register (www.tardigrada.net/register/0096.htm).

TABLE 46. Measurements [in µm] of selected morphological structures of the adult females of *Echiniscus setaceus* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Holotype	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	11	247	–	310	*448*	–	*667*	272	*504*	22	*66*	285	*462*
Scapular plate length	11	42.5	–	63.6		–		54.6	–	7.1	–	61.7	–
Head appendages lengths													
Cirrus *internus*	10	14.2	–	21.8	*23.0*	–	*34.7*	16.7	*30.0*	2.2	*3.6*	14.2	*23.0*
Cephalic papilla	11	7.0	–	11.2	*14.1*	–	*22.6*	9.3	*17.1*	1.3	*2.3*	8.7	*14.1*
Cirrus *externus*	10	18.5	–	29.4	*33.9*	–	*50.2*	22.9	*41.2*	3.0	*5.0*	22.4	*36.3*
Clava	11	5.1	–	8.4	*8.8*	–	*14.7*	6.4	*11.8*	1.2	*2.1*	5.6	*9.1*
Cirrus *A*	11	31.1	–	54.6	*52.9*	–	*110.4*	45.2	*83.9*	7.5	*16.8*	50.3	*81.5*
Cirrus *A*/Body length ratio	11	11%	–	20%		–		17%	–	3%	–	18%	–
Body appendages lengths													
Appendage *C*	11	27.8	–	38.9	*44.3*	–	*72.2*	33.3	*61.8*	3.4	*8.4*	33.6	*54.5*
Cirrus C^d	11	43.5	–	66.2	*82.2*	–	*136.7*	57.3	*106.2*	6.5	*15.7*	56.0	*90.8*
Appendage *D*	11	12.2	–	34.5	*23.0*	–	*73.4*	27.2	*50.8*	6.0	*14.4*	25.2	*40.8*
Appendage D^d	6	7.3	–	11.3	*11.8*	–	*26.6*	9.3	*18.3*	1.7	*6.2*	7.3	*11.8*
Appendage *E*	10	14.1	–	29.8	*22.5*	–	*68.5*	24.9	*45.8*	5.5	*13.7*	27.1	*43.9*
Spine on leg I length	11	2.0	–	5.8	*3.4*	–	*10.6*	3.5	*6.4*	1.0	*1.8*	3.8	*6.2*
Papilla on leg IV length	11	3.9	–	6.1	*7.6*	–	*13.9*	5.2	*9.6*	0.6	*1.6*	4.7	*7.6*
Number of teeth on the collar	11	7	–	16		–		11.7	–	2.5	–	16	–
Claw I heights													
Branch	10	12.6	–	18.4	*25.6*	–	*38.4*	16.1	*29.7*	1.5	*3.6*	15.8	*25.6*
Spur	10	2.5	–	5.5	*5.8*	–	*8.8*	4.1	*7.4*	0.9	*1.2*	5.4	*8.8*
Spur/branch height ratio	10	20%	–	34%		–		25%	–	5%	–	34%	–
Claw II heights													
Branch	11	11.3	–	18.6	*25.5*	–	*42.1*	15.3	*28.2*	2.0	*4.9*	16.0	*25.9*
Spur	11	3.3	–	4.4	*6.3*	–	*8.2*	3.8	*7.0*	0.3	*0.6*	4.4	*7.1*
Spur/branch height ratio	11	20%	–	29%		–		25%	–	3%	–	28%	–
Claw III heights													
Branch	10	11.4	–	17.5	*24.0*	–	*40.2*	15.3	*28.3*	1.8	*4.5*	14.8	*24.0*
Spur	8	3.0	–	4.3	*5.8*	–	*9.2*	3.7	*6.9*	0.4	*1.0*	3.6	*5.8*
Spur/branch height ratio	8	23%	–	26%		–		24%	–	1%	–	24%	–
Claw IV heights													
Branch	10	13.1	–	19.9	*28.0*	–	*45.2*	17.8	*32.7*	2.1	*4.6*	17.3	*28.0*
Spur	8	3.7	–	5.7	*6.6*	–	*13.4*	4.6	*8.7*	0.7	*2.2*	?	*?*
Spur/branch height ratio	8	20%	–	31%		–		26%	–	4%	–	?	–

TABLE 47. Measurements [in µm] of selected morphological structures of the adult males of *Echiniscus setaceus* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	**RANGE**						**MEAN**		**SD**		**Allotype**	
		µm			***sp***			**µm**	***sp***	**µm**	***sp***	**µm**	***sp***
Body length	10	184	–	258	*460*	–	*602*	225	*533*	28	*47*	189	*460*
Scapular plate length	10	36.8	–	49.1		–		42.3	–	3.5	–	41.1	–
Head appendages lengths													
Cirrus *internus*	9	10.2	–	18.3	*27.7*	–	*41.9*	14.8	*34.9*	2.4	*4.1*	13.7	*33.3*
Cephalic papilla	10	7.3	–	9.9	*18.1*	–	*23.0*	8.6	*20.3*	0.7	*1.4*	7.9	*19.2*
Cirrus *externus*	9	15.7	–	23.6	*38.2*	–	*57.2*	20.6	*48.9*	3.0	*6.6*	15.7	*38.2*
Clava	10	4.2	–	8.9	*10.2*	–	*20.4*	6.8	*16.0*	1.4	*2.7*	4.2	*10.2*
Cirrus *A*	10	25.2	–	44.6	*61.3*	–	*96.3*	34.0	*79.9*	7.6	*13.7*	25.2	*61.3*
Cirrus *A*/Body length ratio	10	10%	–	18%		–		15%	–	3%	–	13%	–
Body appendages lengths													
Appendage *C*	10	19.4	–	41.4	*46.3*	–	*100.7*	32.2	*76.0*	6.8	*15.0*	34.7	*84.4*
Cirrus C^d	10	31.3	–	54.9	*83.3*	–	*125.6*	43.3	*102.3*	8.3	*17.6*	49.0	*119.2*
Appendage *D*	9	12.7	–	39.3	*30.3*	–	*95.6*	29.0	*69.2*	10.1	*24.1*	39.3	*95.6*
Appendage D^d	8	5.5	–	34.5	*12.6*	–	*83.9*	13.9	*33.7*	9.9	*24.1*	34.5	*83.9*
Appendage *E*	10	13.1	–	53.6	*26.7*	–	*130.4*	26.7	*63.4*	12.5	*29.8*	33.3	*81.0*
Spine on leg I length	10	1.6	–	3.0	*3.7*	–	*6.6*	2.3	*5.4*	0.5	*1.0*	2.0	*4.9*
Papilla on leg IV length	10	3.5	–	5.8	*9.2*	–	*13.3*	4.7	*11.2*	0.8	*1.3*	4.7	*11.4*
Number of teeth on the collar	10	10	–	17		–		13.5	–	2.1	–	13	–
Claw I heights													
Branch	7	11.1	–	15.1	*27.0*	–	*33.8*	13.2	*31.0*	1.4	*2.2*	11.1	*27.0*
Spur	7	2.9	–	3.9	*6.9*	–	*8.8*	3.2	*7.5*	0.4	*0.7*	3.6	*8.8*
Spur/branch height ratio	7	21%	–	32%		–		25%	–	4%	–	32%	–
Claw II heights													
Branch	9	11.9	–	14.5	*28.8*	–	*34.6*	13.2	*31.2*	0.9	*2.1*	?	*?*
Spur	9	2.9	–	3.7	*6.6*	–	*9.4*	3.3	*7.9*	0.3	*1.0*	?	*?*
Spur/branch height ratio	9	23%	–	30%		–		25%	–	2%	–	?	–
Claw III heights													
Branch	8	10.6	–	14.4	*25.8*	–	*35.0*	12.5	*30.6*	1.1	*2.9*	10.6	*25.8*
Spur	8	2.7	–	3.5	*6.6*	–	*8.5*	3.0	*7.3*	0.3	*0.8*	3.5	*8.5*
Spur/branch height ratio	8	19%	–	33%		–		24%	–	4%	–	33%	–
Claw IV heights													
Branch	7	11.8	–	14.8	*28.7*	–	*35.8*	13.7	*32.8*	1.1	*2.5*	11.8	*28.7*
Spur	7	3.0	–	3.6	*7.3*	–	*9.8*	3.3	*7.8*	0.2	*0.9*	3.0	*7.3*
Spur/branch height ratio	7	20%	–	28%		–		24%	–	2%	–	25%	–

TABLE 48. Measurements [in µm] of selected morphological structures of the juveniles of *Echiniscus setaceus* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD	
		µm			*sp*			µm	*sp*	µm	*sp*
Body length	5	151	–	182	*446*	–	*511*	167	*479*	11	*24*
Scapular plate length	5	29.5	–	38.3		–		35.0	–	3.4	–
Head appendages lengths											
Cirrus *internus*	5	9.3	–	12.9	*27.9*	–	*34.9*	11.0	*31.5*	1.6	*2.5*
Cephalic papilla	5	4.8	–	6.9	*16.3*	–	*18.0*	6.0	*17.2*	0.8	*0.8*
Cirrus *externus*	5	11.8	–	19.6	*37.5*	–	*53.0*	14.9	*42.3*	3.0	*6.2*
Clava	4	2.7	–	5.8	*9.2*	–	*15.7*	4.4	*12.4*	1.4	*3.1*
Cirrus *A*	5	27.4	–	33.9	*87.3*	–	*95.0*	31.6	*90.4*	2.7	*3.4*
Cirrus *A*/Body length ratio	5	18%	–	20%		–		19%	–	1%	–
Body appendages lengths											
Appendage *C*	5	11.8	–	34.4	*31.3*	–	*93.0*	17.9	*50.8*	9.8	*25.2*
Cirrus C^d	5	18.7	–	54.6	*48.8*	–	*147.6*	31.7	*89.7*	15.2	*39.0*
Appendage *D*	5	11.6	–	30.2	*30.3*	–	*81.6*	16.6	*47.1*	7.8	*20.0*
Appendage D^d	5	4.2	–	16.7	*11.0*	–	*45.1*	8.3	*23.4*	5.1	*13.3*
Appendage *E*	3	12.1	–	24.2	*31.6*	–	*65.4*	16.1	*46.0*	7.0	*17.4*
Spine on leg I length	5	0.9	–	3.1	*3.1*	–	*8.4*	2.1	*5.9*	0.8	*1.9*
Papilla on leg IV length	5	2.6	–	4.3	*6.8*	–	*11.8*	3.5	*10.0*	0.8	*2.2*
Number of teeth on the collar	4	8.0	–	11.0	*23.3*	–	*33.9*	9.8	*28.2*	1.3	*4.6*
Claw I heights											
Branch	5	8.5	–	12.0	*22.2*	–	*32.4*	9.7	*27.9*	1.5	*3.9*
Spur	5	1.7	–	2.8	*4.8*	–	*7.6*	2.2	*6.4*	0.5	*1.3*
Spur/branch height ratio	5	18%	–	25%		–		23%	–	3%	–
Claw II heights											
Branch	4	7.7	–	11.5	*20.1*	–	*31.1*	9.2	*26.4*	1.8	*4.7*
Spur	4	2.2	–	3.0	*6.0*	–	*8.1*	2.5	*7.1*	0.4	*1.0*
Spur/branch height ratio	4	22%	–	30%		–		27%	–	4%	–
Claw III heights											
Branch	5	7.3	–	10.8	*19.1*	–	*29.2*	8.9	*25.5*	1.5	*4.0*
Spur	5	1.9	–	3.1	*5.3*	–	*8.4*	2.4	*6.8*	0.5	*1.4*
Spur/branch height ratio	5	20%	–	33%		–		27%	–	6%	–
Claw IV heights											
Branch	4	8.9	–	11.6	*23.2*	–	*33.7*	9.8	*28.7*	1.3	*4.4*
Spur	4	2.1	–	2.5	*5.9*	–	*7.8*	2.3	*6.7*	0.2	*0.9*
Spur/branch height ratio	4	21%	–	26%		–		24%	–	3%	–

TABLE 49. Measurements [in µm] of selected morphological structures of the larvae of *Echiniscus setaceus* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD	
		µm			*sp*			µm	*sp*	µm	*sp*
Body length	5	154	–	169	*446*	–	*569*	159	*527*	7	*50*
Scapular plate length	5	27.0	–	34.5		–		30.3	–	3.1	–
Head appendages lengths											
Cirrus *internus*	5	7.9	–	10.7	*25.2*	–	*36.3*	9.3	*30.9*	1.0	*4.2*
Cephalic papilla	5	4.5	–	5.0	*13.0*	–	*17.8*	4.8	*16.0*	0.2	*1.9*
Cirrus *externus*	5	10.6	–	13.2	*37.4*	–	*46.0*	12.0	*39.9*	1.0	*3.5*
Clava	5	2.5	–	4.3	*8.7*	–	*15.6*	3.4	*11.3*	0.7	*2.7*
Cirrus *A*	5	25.1	–	33.4	*85.8*	–	*106.7*	28.7	*94.9*	3.2	*8.0*
Cirrus *A*/Body length ratio	5	16%	–	20%		–		18%	–	1%	–
Body appendages lengths											
Appendage *C*	5	16.1	–	20.9	*54.5*	–	*66.8*	18.3	*60.4*	1.8	*4.6*
Cirrus C^d	5	21.2	–	27.2	*67.7*	–	*88.5*	23.6	*78.2*	2.4	*7.4*
Appendage *D*	5	15.4	–	21.7	*53.6*	–	*69.3*	18.3	*60.6*	2.3	*7.3*
Appendage D^d	5	10.6	–	13.6	*35.3*	–	*43.5*	12.1	*39.8*	1.4	*3.1*
Appendage *E*	5	15.1	–	17.1	*43.8*	–	*60.9*	16.1	*53.5*	0.8	*6.7*
Spine on leg I length	4	1.3	–	1.6	*4.1*	–	*5.8*	1.4	*4.8*	0.1	*0.7*
Papilla on leg IV length	4	2.5	–	7.0	*8.1*	–	*25.9*	3.7	*12.9*	2.2	*8.7*
Number of teeth on the collar	5	3	–	9		–		6.9	–	2.5	–
Claw I heights											
Branch	5	7.7	–	8.7	*22.9*	–	*30.1*	8.2	*27.4*	0.4	*2.7*
Spur	5	2.1	–	2.8	*7.0*	–	*10.1*	2.5	*8.4*	0.3	*1.2*
Spur/branch height ratio	5	27%	–	34%		–		31%	–	3%	–
Claw II heights											
Branch	4	7.8	–	8.1	*23.5*	–	*28.9*	8.0	*26.6*	0.2	*2.5*
Spur	4	1.8	–	2.2	*6.4*	–	*8.1*	2.1	*6.9*	0.2	*0.8*
Spur/branch height ratio	4	23%	–	28%		–		26%	–	2%	–
Claw III heights											
Branch	5	7.3	–	8.6	*22.6*	–	*31.2*	8.0	*26.7*	0.5	*3.9*
Spur	5	2.0	–	2.5	*7.0*	–	*8.5*	2.3	*7.5*	0.2	*0.6*
Spur/branch height ratio	5	23%	–	32%		–		28%	–	3%	–
Claw IV heights											
Branch	4	8.6	–	9.1	*27.5*	–	*31.9*	8.8	*30.1*	0.2	*2.2*
Spur	4	2.1	–	2.8	*7.6*	–	*10.4*	2.5	*8.6*	0.3	*1.3*
Spur/branch height ratio	4	24%	–	33%		–		29%	–	4%	–

27. Echiniscus similaris sp. nov. Gąsiorek, Vončina, Morek & Michalczyk

urn:lsid:zoobank.org:act:C57AB055-4F5B-4549-BE32-F8777517A53E

Figure 94, Tables 50–51

Data source:

A total of 16 specimens (8 ♀♀, 3 ♂♂, and 5 specimens of unknown instar/sex):

- Sample ZA.449: 16 specimens (8 ♀♀ and 3 ♂♂ on slides, and 5 specimens used for DNA extraction, all secured as hologenophores).

Description. Mature females (*i.e.* from the third instar onwards; measurements and statistics in Table 50). Large *Echiniscus* with a massive, plump body and short thick limbs (Fig. 94A). Dark orange body and large red eyes; body colour and eyes disappeared soon after mounting in Hoyer's medium. Dactyloid cephalic papillae (secondary clavae) and (primary) clavae; cirri growing out from bulbous cirrophores. Cirri *A* short. Body appendage configuration *A*-*B*-*C*-*C*^{d}-*D*-*D*^{d}. All trunk appendages in the form of short cirri of similar lengths. The configuration is stable, and single asymmetries uncommon.

Dorsal plates with a simple sculpture: pores of diverse size irregularly distributed in plates. Posterior portions of median plates 1–2 and paired segmental plates I–II unsculptured. The cephalic plate with a small anterior incision. The cervical (neck) plate developed as a wide belt adjacent to the anterior margin of the scapular plate. The scapular plate large, with lateral sutures demarcating lateral trapezoid poreless portions (Fig. 94A). Thin transverse belts on the paired segmental plates I–II poorly developed. Median plate 1 and the posterior portion of m2 equal in size; the anterior portion of m2 smooth, but of a similar size as the posterior fragment. Median plate 3 present as a narrow triangular surface with pores. The caudal (terminal) plate with two extremely poorly developed incisions. Ventral cuticle with minute endocuticular pillars distributed throughout the whole venter. Ventral plates absent. Sexpartite gonopore placed anteriorly to legs IV, and a trilobed anus between legs IV.

Pedal plates in the form of slightly darker unsculptured areas in the central portions of all legs (Fig. 94A). Pulvini clearly visible (Fig. 94A). A minuscule spine on the anterior margin of the pedal plate I and a papilla on leg IV. Dentate collar IV with numerous large teeth. Claws IV much longer than claws I–III. All external claws spurless. All internal claws with small spurs positioned at *ca.* 25% of the branch height (Fig. 94B, insert).

Mature males and sexually dimorphic traits (*i.e.* from the third instar onwards; measurements and statistics in Table 51). Quantitatively and qualitatively like females (Fig. 94B), excluding the circular gonopore.

Juveniles. Unknown.

Larvae. Unknown.

Eggs. Unknown.

DNA markers and phylogenetic position. The species is the sister taxon of *E. lichenorum* (Fig. 117). The species closest in COI and ITS-1 is *E. lichenorum* (p-distance = 1.2–1.8% and 1.4–1.7%, respectively), and in ITS-2—*E. draconis* **sp. nov.**, *E. imitans* **sp. nov.**, and *E. lichenorum* (0.9–1.8%).

Type material. 8 ♀♀ and 3 ♂♂ on slides ZA.449.01–3; holotype: mature ♀ on slide ZA.449.03, allotype: mature ♂ on slide ZA.449.03. 5 specimens used for DNA extraction and secured as hologenophores.

Type locality. 33°20'32"S, 21°53'31"E, 1025 m asl: Republic of South Africa, Western Cape, Groot Swartberg Nature Reserve; renosterveld, lichen from rock (sample ZA.449).

Etymology. From Latin *similaris* = similar, referring to the similarity to *E. lichenorum*. An adjective in the nominative singular.

Geographic distribution. The species is likely endemic to the Swartberg range (Fig. 120I).

Remarks. Relatively low genetic disparity between *E. similaris* **sp. nov.** and *E. lichenorum* suggests that their lineages split recently.

Differential diagnosis. *E. similaris* **sp. nov.** shares body appendage configuration *A*-*B*-*C*-*C*^{d}-*D*-*D*^{d} and similar dorsal sculpturing with *E. lichenorum*, but the two species can be distinguished by: body size (body length 306–395 µm in *E. similaris* **sp. nov.** *vs* 226–315 µm in *E. lichenorum*/the upper value after Maucci 1983), the scapular plate length (58.0–72.5 µm in *E. similaris* **sp. nov.** *vs* 44.8–58.7 µm in *E. lichenorum*), the cephalic papilla length (7.9–10.2 µm in *E. similaris* **sp. nov.** *vs* 5.5–8.2 µm in *E. lichenorum*), and by the appendage *C*^{d} and *D*^{d} lengths (34.1–59.1 µm and 43.4–64.8 µm long and in the form of cirri similar in length to lateral cirri in *E. similaris* **sp. nov.** *vs* 12.7–27.2 µm and 11.1–31.5 µm and in the form of spines shorter than lateral cirri in *E. lichenorum*).

Raw measurements. Supplementary Materials (SM.03) and Tardigrada Register (www.tardigrada.net/register/0097.htm).

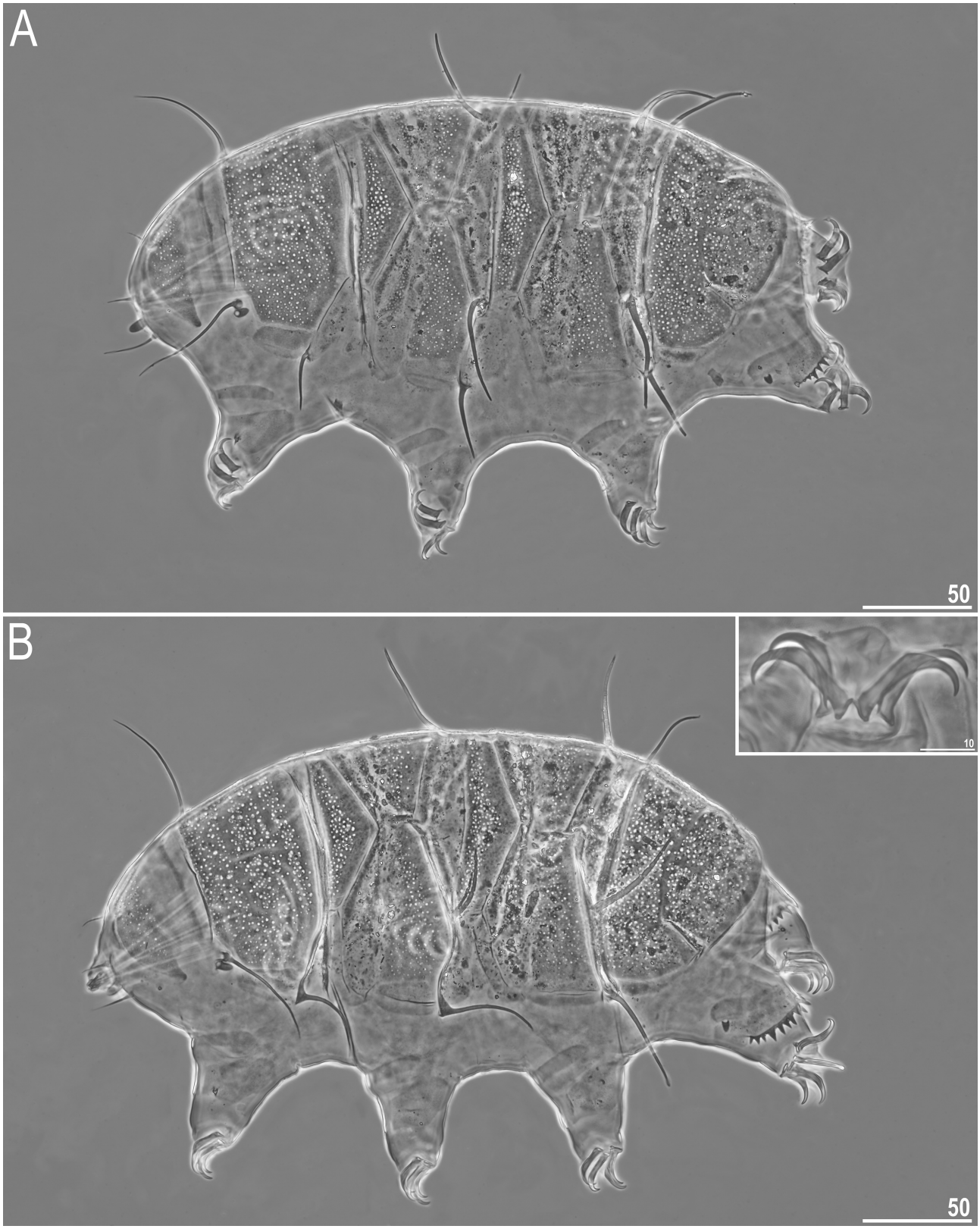

FIGURE 94. Habitus of *Echiniscus similaris* **sp. nov.** (PCM): A—holotype, female in dorsolateral view, B—allotype, male in dorsolateral view (insert shows claws III). Scale bars in μm.

TABLE 50. Measurements [in µm] of selected morphological structures of the adult females of *Echiniscus similaris* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Holotype	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	8	308	–	395	*502*	–	*545*	347	*524*	31	*16*	308	*518*
Scapular plate length	8	59.3	–	72.5		–		66.2	–	5.0	–	59.5	–
Head appendages lengths													
Cirrus *internus*	8	10.5	–	15.7	*15.8*	–	*22.1*	12.3	*18.5*	1.9	*1.9*	11.1	*18.7*
Cephalic papilla	8	8.5	–	10.2	*12.4*	–	*15.7*	9.3	*14.1*	0.7	*1.1*	9.0	*15.1*
Cirrus *externus*	7	16.6	–	33.9	*25.9*	–	*46.8*	26.8	*39.9*	5.2	*7.0*	26.8	*45.0*
Clava	8	7.0	–	9.2	*10.3*	–	*14.1*	8.1	*12.3*	0.8	*1.1*	7.3	12.3
Cirrus *A*	7	30.2	–	71.9	*50.9*	–	*112.0*	56.5	*83.7*	14.2	*19.8*	?	*?*
Cirrus *A*/Body length ratio	7	10%	–	22%		–		16%	–	4%	–	?	–
Body appendages lengths													
Cirrus *B*	8	18.6	–	45.8	*31.4*	–	*70.2*	35.2	*52.7*	9.1	*11.5*	27.3	*45.9*
Cirrus *C*	7	35.3	–	60.6	*59.3*	–	*92.9*	47.6	*72.7*	9.1	*13.1*	35.3	*59.3*
Cirrus C^d	7	34.1	–	59.1	*57.5*	–	*92.1*	49.8	*76.3*	7.7	*11.7*	52.5	*88.2*
Cirrus *D*	7	35.2	–	69.1	*59.2*	–	*107.6*	52.7	*80.3*	10.8	*15.4*	35.2	*59.2*
Cirrus D^d	8	43.4	–	64.8	*73.2*	–	*94.5*	55.8	*84.1*	7.0	*7.6*	53.4	*89.7*
Spine on leg I length	7	3.7	–	5.8	*5.8*	–	*8.0*	4.8	*7.2*	0.8	*0.9*	3.9	*6.6*
Papilla on leg IV length	7	5.3	–	7.2	*8.3*	–	*10.4*	6.2	*9.5*	0.7	*0.8*	5.9	*9.9*
Number of teeth on the collar	7	8	–	13		–		10.3	–	1.9	–	?	–
Claw I heights													
Branch	5	18.1	–	21.8	*29.6*	–	*30.5*	19.3	*30.2*	1.5	*0.4*	18.1	*30.4*
Spur	5	2.9	–	3.5	*4.3*	–	*5.9*	3.2	*5.0*	0.2	*0.6*	2.9	*4.9*
Spur/branch height ratio	5	14%	–	19%		–		16%	–	2%	–	16%	–
Claw II heights													
Branch	5	17.2	–	20.8	*28.2*	–	*30.2*	19.3	*28.9*	1.4	*0.8*	17.2	*28.9*
Spur	5	3.0	–	3.4	*4.5*	–	*5.0*	3.2	*4.8*	0.2	*0.2*	3.0	*5.0*
Spur/branch height ratio	5	15%	–	17%		–		17%	–	1%	–	17%	–
Claw III heights													
Branch	6	17.5	–	20.7	*27.9*	–	*31.4*	19.4	*29.6*	1.2	*1.4*	17.5	*29.4*
Spur	6	2.8	–	3.7	*4.5*	–	*5.6*	3.3	*5.0*	0.4	*0.4*	2.8	*4.7*
Spur/branch height ratio	6	14%	–	18%		–		17%	–	1%	–	16%	–
Claw IV heights													
Branch	7	19.6	–	28.1	*30.1*	–	*40.8*	23.1	*35.1*	3.3	*3.7*	21.3	*35.8*
Spur	7	3.2	–	4.1	*5.0*	–	*6.4*	3.7	*5.7*	0.4	*0.5*	3.5	*5.9*
Spur/branch height ratio	7	15%	–	17%		–		16%	–	1%	–	16%	–

TABLE 51. Measurements [in µm] of selected morphological structures of the adult males of *Echiniscus similaris* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Allotype	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	3	306	–	323	*504*	–	*552*	317	*520*	9	*28*	306	*504*
Scapular plate length	3	58.0	–	64.1		–		61.0	–	3.1	–	60.8	–
Head appendages lengths													
Cirrus *internus*	3	11.8	–	12.9	*19.7*	–	*20.3*	12.2	*20.1*	0.6	*0.3*	12.0	*19.7*
Cephalic papilla	3	7.9	–	9.3	*13.1*	–	*15.3*	8.5	*14.0*	0.7	*1.1*	9.3	*15.3*
Cirrus *externus*	3	18.2	–	28.0	*31.4*	–	*43.7*	22.9	*37.4*	4.9	*6.2*	22.5	*37.0*
Clava	3	8.3	–	8.4	*12.9*	–	*14.3*	8.3	*13.7*	0.1	*0.7*	8.4	*13.8*
Cirrus *A*	3	30.0	–	56.2	*46.8*	–	*96.9*	46.0	*76.4*	14.1	*26.2*	51.9	*85.4*
Cirrus *A*/Body length ratio	3	9%	–	18%		–		15%	–	5%	–	17%	–
Body appendages lengths													
Cirrus *B*	3	26.1	–	34.8	*44.5*	–	*57.2*	29.8	*48.9*	4.5	*7.2*	34.8	*57.2*
Cirrus *C*	3	40.8	–	46.9	*66.6*	–	*77.1*	43.5	*71.4*	3.1	*5.3*	46.9	*77.1*
Cirrus C^d	3	34.9	–	47.6	*57.4*	–	*82.1*	40.5	*66.7*	6.5	*13.4*	34.9	*57.4*
Cirrus *D*	2	47.0	–	52.6	*77.3*	–	*82.1*	49.8	*79.7*	4.0	*3.4*	47.0	77.3
Cirrus D^d	3	42.5	–	49.1	*72.4*	–	*76.6*	45.2	*74.1*	3.5	*2.2*	44.0	*72.4*
Spine on leg I length	3	3.7	–	4.6	*6.1*	–	*7.6*	4.1	*6.7*	0.5	*0.8*	4.6	*7.6*
Papilla on leg IV length	3	5.0	–	6.0	*7.8*	–	*9.9*	5.5	*9.1*	0.5	*1.1*	6.0	*9.9*
Number of teeth on the collar	3	10	–	11		–		10.3	–	0.6	–	10	–
Claw I heights													
Branch	2	17.6	–	18.4	*28.7*	–	*30.3*	18.0	*29.5*	0.6	*1.2*	?	*?*
Spur	2	3.2	–	3.8	*5.0*	–	*6.6*	3.5	*5.8*	0.4	*1.1*	?	*?*
Spur/branch height ratio	2	17%	–	22%		–		19%	–	3%	–	?	–
Claw II heights													
Branch	3	18.3	–	19.4	*28.5*	–	*33.1*	19.0	*31.2*	0.6	*2.4*	19.4	*31.9*
Spur	3	3.0	–	3.2	*5.0*	–	*5.2*	3.1	*5.1*	0.1	*0.1*	3.1	*5.1*
Spur/branch height ratio	3	16%	–	17%		–		16%	–	1%	–	16%	–
Claw III heights													
Branch	2	19.5	–	19.6	*30.4*	–	*32.2*	19.6	*31.3*	0.1	*1.3*	19.6	*32.2*
Spur	2	3.0	–	3.4	*4.7*	–	*5.6*	3.2	*5.1*	0.3	*0.6*	3.4	*5.6*
Spur/branch height ratio	2	15%	–	17%		–		16%	–	1%	–	17%	–
Claw IV heights													
Branch	3	20.1	–	23.1	*34.3*	–	*38.0*	21.7	*35.7*	1.5	*2.0*	23.1	*38.0*
Spur	3	3.4	–	3.9	*5.3*	–	*6.4*	3.6	*5.9*	0.3	*0.6*	3.9	*6.4*
Spur/branch height ratio	3	15%	–	17%		–		16%	–	1%	–	17%	–

28. Echiniscus tetraspinosus sp. nov. Gąsiorek, Vončina, Morek & Michalczyk

urn:lsid:zoobank.org:act:398ED64B-8194-44B3-91E7-1BD3885CBA82

Figure 95, Tables 52–53

Data source:

A total of 18 specimens (11 ♀♀, 3 juveniles, and 4 specimens of unknown instar/sex):

- Sample ZA.130: 12 specimens (8 ♀♀ on slides and 4 specimens used for DNA extraction, including 1 hologenophore); found with *Echiniscus intricatus* **sp. nov.**
- Sample ZA.201: 5 specimens (2 ♀♀ and 3 juveniles on slides); found with *Echiniscus intricatus* **sp. nov.**, *E. oreas* **sp. nov.**, and *E. tristis*.
- Sample ZA.218: 1 specimen (1 ♀ on a slide); found with *Echiniscus draconis* **sp. nov.**, *E. intricatus* **sp. nov.**, *E. lichenorum*.

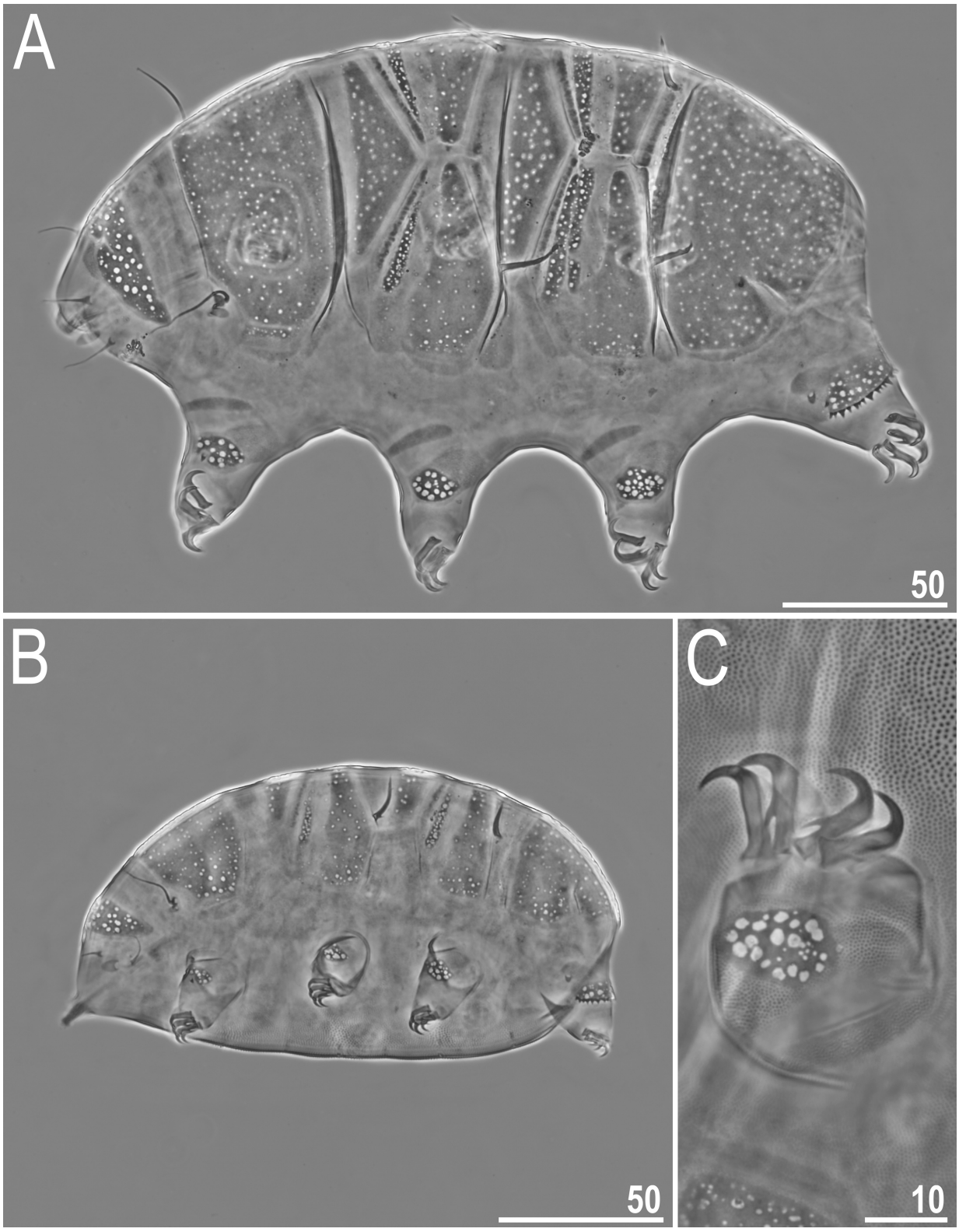

FIGURE 95. Detailed morphology of *Echiniscus tetraspinosus* **sp. nov.** (PCM): A—holotype, female in dorsolateral view, B—paratype, juvenile in lateral view, C—claws II. Scale bars in μm.

Description. Mature females (*i.e*. from the third instar onwards; measurements and statistics in Table 52). A medium-sized *Echiniscus* with a plump body and short thick limbs (Fig. 95A). Dark orange body and large red eyes; body colour and eyes disappeared soon after mounting in Hoyer's medium. Dactyloid cephalic papillae (secondary clavae) and (primary) clavae; cirri growing out from bulbous cirrophores. Cirri *A* very short. Body appendage configuration *A*-C^d-D^d. All trunk appendages in the form of short smooth spines. The configuration is stable, and single asymmetries do not occur.

Dorsal plates with a heteromorphic sculpture of the *spinulosus* type: (I) sparsely distributed, somehow faint pores in the scapular plate, median plates 1–2, posterior portions of paired segmental plates I–II, and the caudal (terminal) plate, and (II) larger and densely arranged pores with clear edges, penetrating much darker (= thicker) endocuticular matrix of the cephalic plate, narrow anterior portions of paired segmental plates I–II, and the evident pedal plates I–IV (Fig. 95A). The cephalic plate with a chalice-shaped anterior incision; the cervical (neck) plate absent. The scapular plate uniform, without a median groove, but with poorly marked lateral sutures separating small rectangular lateral portions. Wide transverse belts on the paired segmental plates I–II present, with single pores. Median plate 1 and the posterior portion of m2 equal in size; the anterior portion of m2 smooth and narrow. Median plate 3 absent. The caudal (terminal) plate with two extremely poorly developed and short incisions. Ventral cuticle with minute endocuticular pillars distributed throughout the whole venter. Ventral plates absent. Sexpartite gonopore placed anteriorly to legs IV, and a trilobed anus between legs IV.

Pulvini present and well-marked (Fig. 95A). Minuscule spine on the anterior margin of the pedal plate I and a papilla on leg IV present. Dentate collar IV formed by numerous minute teeth. Claws I–IV similar in size. All external claws spurless. All internal claws with large spurs positioned at *ca.* 30–50% of the branch height (Fig. 95C).

Juveniles (*i.e*. the second instar; measurements and statistics in Table 53). No gonopore. Phenotypically indistinguishable from adult females (Fig. 95B), but there was a clear morphometric gap between the few juveniles and adult females analysed in this study.

Larvae. Unknown.

Eggs. Unknown.

DNA markers and phylogenetic position. The species constitutes a separate lineage within the *E. spinulosus* group (Fig. 117), but, in the Maximum Likelihood phylogeny, *E. tetraspinosus* **sp. nov.** is the sister species to all other representatives of the *E. spinulosus* complex (bootstrap value = 100%). The species closest in ITS-1 is *E. oreas* **sp. nov.** (p-distance = 5.1%), and in ITS-2—*E. oreas* **sp. nov.** and *E. tristis* (3.5%).

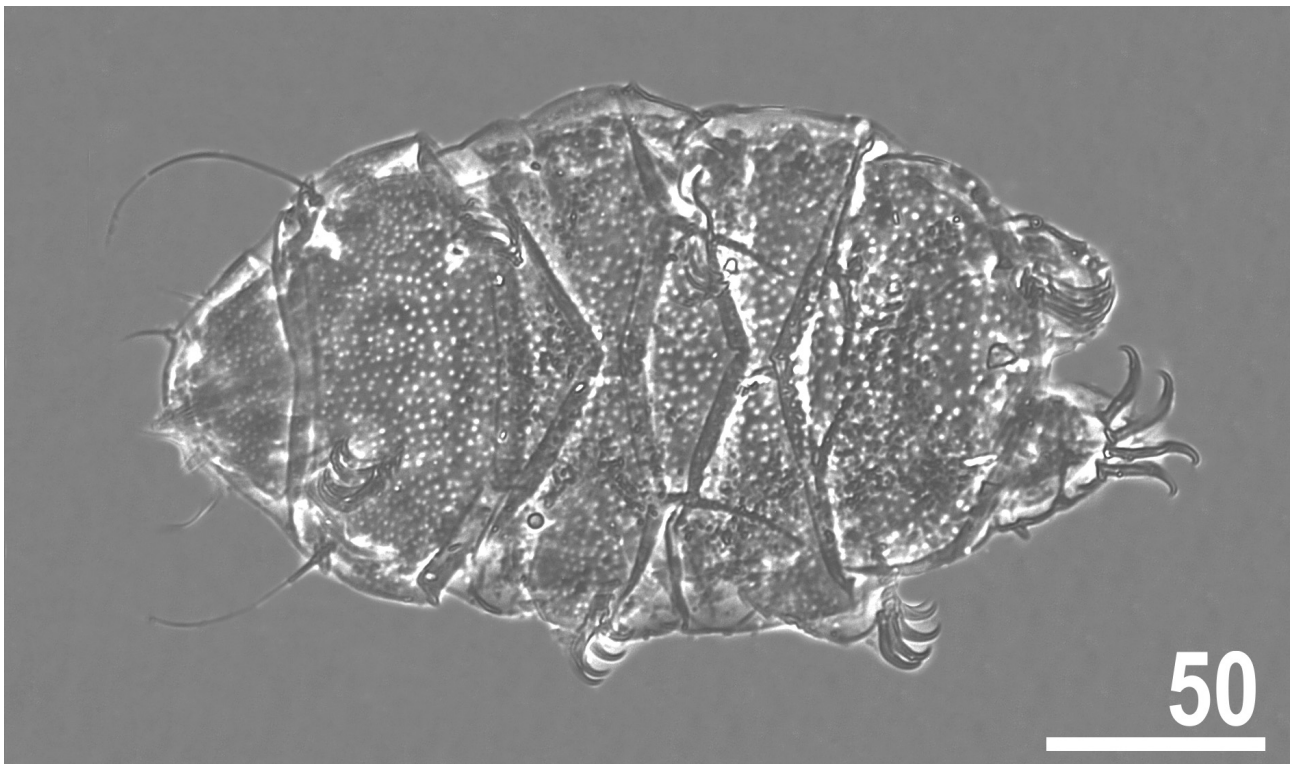

FIGURE 96. Habitus of *Echiniscus murrayi* Iharos, 1969 (PCM, syntype). Scale bar = 50 µm.

TABLE 52. Measurements [in µm] of selected morphological structures of the adult females of *Echiniscus tetraspinosus* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Holotype	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	9	198	–	272	*435*	–	*553*	241	*520*	22	*37*	249	*539*
Scapular plate length	10	29.2	–	49.8		–		44.6	–	5.8	–	46.2	–
Head appendages lengths													
Cirrus *internus*	10	8.6	–	15.8	*18.6*	–	*45.9*	12.9	*29.5*	2.0	*7.0*	12.8	*27.7*
Cephalic papilla	10	6.0	–	8.4	*12.8*	–	*24.0*	7.4	*16.9*	0.7	*3.0*	8.3	*18.0*
Cirrus *externus*	10	14.5	–	20.4	*32.5*	–	*50.7*	17.7	*40.0*	2.2	*5.5*	19.0	41.1
Clava	9	3.6	–	7.0	*7.9*	–	*20.2*	5.5	*12.8*	1.1	*3.5*	6.6	*14.3*
Cirrus *A*	10	21.7	–	33.5	*47.7*	–	*108.2*	29.3	*67.3*	3.8	*16.1*	25.1	*54.3*
Cirrus *A*/Body length ratio	9	10%	–	14%		–		12%	–	1%	–	10%	–
Body appendages lengths													
Cirrus C^d	10	17.0	–	22.3	*37.3*	–	*62.3*	19.2	*43.7*	1.5	*7.2*	20.2	*43.7*
Cirrus D^d	9	13.3	–	18.2	*31.2*	–	*45.5*	16.0	*36.7*	1.8	*4.5*	15.3	*33.1*
Spine on leg I length	9	2.6	–	3.5	*5.4*	–	*10.6*	3.0	*6.9*	0.3	*1.5*	2.6	*5.6*
Papilla on leg IV length	10	2.9	–	3.9	*6.2*	–	*11.6*	3.4	*7.7*	0.3	*1.6*	3.1	*6.7*
Number of teeth on the collar	6	11	–	15		–		14.2	–	1.6	–	15	–
Claw I heights													
Branch	10	11.1	–	14.7	*24.9*	–	*38.0*	12.7	*28.8*	1.2	*3.8*	12.3	*26.6*
Spur	7	3.1	–	4.5	*6.9*	–	*9.0*	3.6	*7.8*	0.5	*0.7*	3.8	*8.2*
Spur/branch height ratio	7	22%	–	31%		–		28%	–	3%	–	31%	–
Claw II heights													
Branch	10	11.3	–	14.5	*24.8*	–	*39.0*	12.8	*29.0*	1.1	*3.9*	12.4	*26.8*
Spur	8	2.4	–	3.7	*4.9*	–	*10.6*	3.2	*7.5*	0.4	*1.6*	3.6	*7.8*
Spur/branch height ratio	8	17%	–	29%		–		25%	–	4%	–	29%	–
Claw III heights													
Branch	10	11.3	–	14.8	*25.5*	–	*41.1*	12.8	*29.1*	1.1	*4.6*	11.8	*25.5*
Spur	6	2.5	–	3.7	*5.7*	–	*11.0*	3.1	*7.3*	0.5	*2.0*	?	?
Spur/branch height ratio	6	20%	–	28%		–		24%	–	3%	–	?	–
Claw IV heights													
Branch	10	12.8	–	15.4	*27.5*	–	*44.5*	13.9	*31.7*	0.8	*4.8*	14.4	*31.2*
Spur	6	3.5	–	4.4	*7.5*	–	*13.0*	3.8	*9.1*	0.3	*2.1*	3.7	*8.0*
Spur/branch height ratio	6	26%	–	31%		–		28%	–	2%	–	26%	–

TABLE 53. Measurements [in µm] of selected morphological structures of the juveniles of *Echiniscus tetraspinosus* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD	
		µm			*sp*			µm	*sp*	µm	*sp*
Body length	2	156	–	171	*520*	–	*529*	163	*525*	11	*7*
Scapular plate length	2	29.4	–	32.9		–		31.2	–	2.5	–
Head appendages lengths											
Cirrus *internus*	2	5.3	–	6.6	*16.1*	–	*22.4*	6.0	*19.3*	0.9	*4.5*
Cephalic papilla	2	5.7	–	5.8	*17.6*	–	*19.4*	5.8	*18.5*	0.1	*1.2*
Cirrus *externus*	2	9.6	–	10.4	*29.2*	–	*35.4*	10.0	*32.3*	0.6	*4.4*
Clava	2	2.9	–	3.1	*8.8*	–	*10.5*	3.0	*9.7*	0.1	*1.2*
Cirrus *A*	2	15.1	–	18.1	*51.4*	–	*55.0*	16.6	*53.2*	2.1	*2.6*
Cirrus *A*/Body length ratio	2	10%	–	11%		–		10%	–	1%	–
Body appendages lengths											
Cirrus C^d	2	9.8	–	15.0	*33.3*	–	*45.6*	12.4	*39.5*	3.7	*8.7*
Cirrus D^d	2	9.6	–	11.8	*32.7*	–	*35.9*	10.7	*34.3*	1.6	*2.3*
Spine on leg I length	2	1.6	–	2.0	*4.9*	–	*6.8*	1.8	*5.8*	0.3	*1.4*
Papilla on leg IV length	2	2.3	–	2.9	*7.0*	–	*9.9*	2.6	*8.4*	0.4	*2.0*
Number of teeth on the collar	0		?			–		?	–	?	–
Claw I heights											
Branch	2	7.5	–	7.8	*23.7*	–	*25.5*	7.7	*24.6*	0.2	*1.3*
Spur	2	2.1	–	2.8	*7.1*	–	*8.5*	2.5	*7.8*	0.5	*1.0*
Spur/branch height ratio	2	28%	–	36%		–		32%	–	6%	–
Claw II heights											
Branch	2	6.2	–	7.1	*21.1*	–	*21.6*	6.7	*21.3*	0.6	*0.3*
Spur	1	2.4	–	2.4	*7.3*	–	*7.3*	2.4	*7.3*	?	*?*
Spur/branch height ratio	1	34%	–	34%		–		34%	–	?	–
Claw III heights											
Branch	2	6.6	–	7.5	*22.4*	–	*22.8*	7.1	*22.6*	0.6	*0.2*
Spur	1	2.2	–	2.2	*6.7*	–	*6.7*	2.2	*6.7*	?	*?*
Spur/branch height ratio	1	29%	–	29%		–		29%	–	?	–
Claw IV heights											
Branch	2	8.3	–	8.8	*26.7*	–	*28.2*	8.6	*27.5*	0.4	*1.0*
Spur	0		?			?		?	*?*	?	*?*
Spur/branch height ratio	0		?			–		?	–	?	–

Type material. 8 ♀♀ on slides ZA.130.01–5; holotype: mature ♀ on slide ZA.130.05. Mounted together with 29 ♀♀, 2 ♂♂, 4 juveniles of *E. intricatus* **sp. nov.** 4 specimens used for DNA extraction, including 1 secured as a hologenophore.

Type locality. 33°37'33.4"S, 25°26'4.6"E, 210 m asl: Republic of South Africa, Eastern Cape, Valley Bushveld Country Lodge; shrubland, lichen from rock (sample ZA.130).

Etymology. The name refers to the four dorsal spines in the new species. An adjective in the nominative singular.

Geographic distribution. Only a few small populations of the new species were found in South Africa (Fig. 120L).

Remarks. The three samples, in which the new species was found, were co-habited by *E. intricatus* **sp. nov.**

Differential diagnosis. The body appendage configuration *A-C^d-D^d* and the dorsal sculpturing of the *E. spinulosus* type constitute a combination of characters present only in *E. tetraspinosus* **sp. nov.** and in *E. murrayi*, known only from the Andean Altiplano (Iharos 1969). Nevertheless, the two species cane be differentiated by: the dorsal sculpture (heteromorphic in *E. tetraspinosus* **sp. nov.** *vs* uniform in *E. murrayi*, see Fig. 96), the cirrus *A* length (15.1–33.5 µm in *E. tetraspinosus* **sp. nov.** *vs* 55 µm in *E. murrayi*), the lengths of spines *C^d* and *D^d* (9.8–22.3 µm and 9.6–18.2 µm, respectively, in *E. tetraspinosus* **sp. nov.** *vs* 40 µm and 30 µm, respectively, in *E. murrayi*), and by the number of teeth in the dentate collar IV (11–15 in *E. tetraspinosus* **sp. nov.** *vs* 4–5 in *E. murrayi*).

Raw measurements. Supplementary Materials (SM.03) and Tardigrada Register (www.tardigrada.net/register/0098.htm).

29. Echiniscus tristis Gąsiorek & Kristensen, 2018

Data source:
A total of 103 specimens (57 ♀♀, 27 juveniles, 2 larvae, and 17 specimens of unknown instar/sex):
- Sample ZA.201: 103 specimens (57 ♀♀, 27 juveniles and 2 larvae on slides, 10 specimens on SEM stub 19.01, and 7 specimens used for DNA extraction, including 3 hologenophores); found with *E. intricatus* **sp. nov.**, *E. oreas* **sp. nov.**, and *E. tetraspinosus* **sp. nov.**

Literature:
- Original description: Gąsiorek & Kristensen (2018).
- Later records: Bartylak *et al*. (2019), Bochnak *et al*. (2020).

Shortened description. A medium-sized member of the *E. spinulosus* complex. Body appendage formula *A-(C)-D^d-E*. Median plate 3 developed as a reduced stripe covered under the paired segmental plate II and caudal (terminal) plate. Faceting of the caudal plate in the form of six rectangles demarcated by epicuticular ridges.

DNA markers and phylogenetic position. The analysed nuclear markers show that *E. tristis* is a sister species of *E. manuelae* (Fig. 117). Among species for which COI sequences are available, the closest species is *E. lineatus* (p-distance = 15.8–16.2%), whereas in the ITS-1 and ITS-2 dataset, *E. manuelae* is most similar (0.9% in both markers).

Geographic distribution. This likely Afrotropical endemic was found four times, always in the highlands: Afromontane rainforests in Tanzania and Madagascar (Gąsiorek & Kristensen 2018; Bartylak *et al*. 2019; Bochnak *et al*. 2020), and mountainous shrublands in South Africa (Fig. 120K).

Remarks. None.

30. Echiniscus virginicus Riggin, 1962
Figure 97

Data source:
A total of 83 specimens (70 ♀♀ and 13 juveniles):
- Sample ZA.015: 2 specimens (2 ♀♀ used for DNA extraction); found with *Echiniscus attenboroughi* **sp. nov.**, *E. draconis* **sp. nov.**, *E. lichenorum*, and *E. setaceus* **sp. nov.**
- Sample ZA.152: 2 specimens (2 ♀♀ on slides); found with *Echiniscus longispinosus* and *E. oreas* **sp. nov.**
- Sample ZA.157: 1 specimen (1 ♀ on a slide); found with *Echiniscus scabrospinosus*, *Pseudechiniscus (Pseudechiniscus)* cf. *ehrenbergi*, and *P. (Meridioniscus) wallacei* **sp. nov.**
- Sample ZA.158: 9 specimens (9 ♀♀ on slides); found with *Echiniscus scabrospinosus* and *Pseudechiniscus (Meridioniscus) wallacei* **sp. nov.**
- Sample ZA.185: 1 specimen (1 juvenile on a slide); found with *Echiniscus oreas* **sp. nov.**, *E. regularis* **sp. nov.**, and *E. scabrospinosus*.
- Sample ZA.206: 20 specimens (16 ♀♀ on slides and 4 ♀♀ used for DNA extraction); found with *Echiniscus oreas* **sp. nov.**, *E. regularis* **sp. nov.**, and *E. scabrospinosus.*

- Sample ZA.214: 9 specimens (6 ♀♀ and 3 juveniles on slides); found with *Doryphoribius bindae*, *Echiniscus africanus*, *E. baius*, *E. oreas* **sp. nov.**, *E. perarmatus*, *Pseudechiniscus (Pseudechiniscus)* cf. *ehrenbergi*, and *Ramazzottius szeptycki*.
- Sample ZA.242: 2 specimens (2 ♀♀); found with *Cornechiniscus madagascariensis* and *Echiniscus blumi*.
- Sample ZA.245: 12 specimens (10 ♀♀ and 2 juveniles on slides); found with *Pseudechiniscus (Pseudechiniscus)* cf. *ehrenbergi*.
- Sample ZA.260: 3 specimens (2 ♀♀ and 1 juvenile on slides); found with *Doryphoribius bindae*, *Echiniscus baius*, *E. longispinosus*, *E. oreas* **sp. nov.**, *E. pellucidus*, and *E. scabrospinosus*.
- Sample ZA.302: 15 specimens (10 ♀♀ and 5 juveniles on slides).
- Sample ZA.321: 6 specimens (5 ♀♀ and 1 juvenile on slides).
- Sample ZA.360: 1 specimen (1 ♀ on a slide); found with *Echiniscus draconis* **sp. nov.**, *E. lichenorum*, *E. longispinosus*, and *E. scabrospinosus*.

Literature:
- Original description: Riggin (1962).
- Later trustworthy records: summarised in Gąsiorek *et al*. (2019b).

Shortened description. Small representative of the *E. virginicus* complex. Body appendage formula *A-C-C*^{d}*-D-D*^{d}*-E*. Dorsal epicuticular ornamentation overlapping with endocuticular pillars usually strongly developed and evident (Fig. 97). Pedal plates and pulvini I–III barely demarcated. All external claws spurless, all internal claws with spurs positioned at *ca.* 25% of the claw height and strongly bent downwards (Fig. 97, insert).

DNA markers and phylogenetic position. *E. virginicus* belongs in the *E. virginicus-perarmatus* clade at the base of the generic phylogeny, being the sister species of *E. lineatus* (Fig. 117). The species closest in all fast evolving markers is *E. lineatus* (COI p-distance = 14.7%, ITS-1: 1.1–1.7%, and ITS-2: 1.2%).

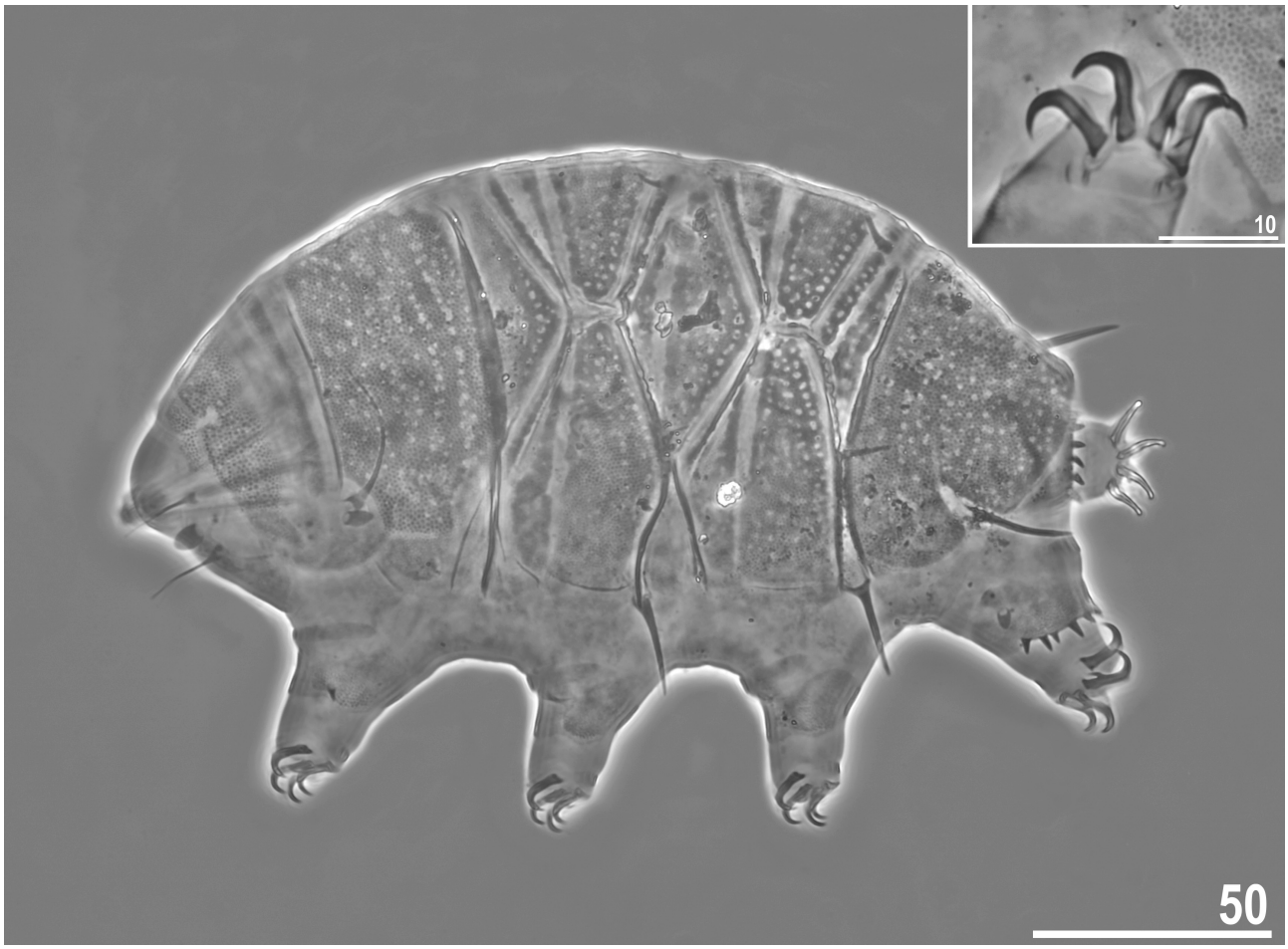

FIGURE 97. Habitus of *Echiniscus virginicus* Riggin, 1962 (PCM, dorsolateral view; insert shows claws II). Scale bars in µm.

Geographic distribution. Although widely distributed in South Africa (Fig. 120L), it is not common and forms small populations (usually below ten individuals). Given that all other confirmed records of *E. virginicus* are limited to the Eastern Nearctic (Gąsiorek *et al*. 2019b), we hypothesise that the presence of the species in the southernmost Afrotropic is a result of anthropogenic dispersal.

Remarks. All examined South African individuals lack spines *B*, which may be present in specimens from the Nearctic. Found accompanying much larger populations of other echiniscids, such as *E. oreas* **sp. nov.** (in the mountains) and *E. scabrospinosus* (in the lowlands).

Genus: *Hypechiniscus* Thulin, 1928

1. Hypechiniscus africanus sp. nov. Gąsiorek, Morek & Michalczyk

urn:lsid:zoobank.org:act:6757406E-43DE-4017-AAFC-7925305B0B73
Figures 98–100, Table 54

Data source:
A total of 7 specimens (2 ♀♀ and 2 ♂♂, and 3 specimens of unknown instar/sex):

- Sample ZA.246: 7 specimens (2 ♀♀ and 2 ♂♂ on slides, 3 specimens used for DNA extraction); found with *Pseudechiniscus (P.) aquatilis* **sp. nov.** and *P. (Meridioniscus) wallacei* **sp. nov.**

Description. Mature females (*i.e.* from the third instar onwards; measurements in Table 54). Body white and elongated, with ovoid black eyes that disappeared soon after mounting in Hoyer's medium (Fig. 98A). Elongated, dactyloid cephalic papillae (secondary clavae) and (primary) clavae; peribuccal cirri without cirrophores. Cirrus *A* very short, with cirrophore. *Cirrus dorsalis* absent.

Dorsal plates poorly sclerotised, with the *Pseudechiniscus*-type sculpturing, *i.e*. endocuticular pillars protruding through the epicuticle and visible as dark dots under PCM (Fig. 98A, 99A). Epicuticular ornamentation visible under PCM as darker ridges of plates and sutures (Fig. 99A). Generally, the sculpture is well-developed and evident in LCM. The cephalic plate is large and clearly sexpartite, with three small anterior portions, a central keel-like portion, and two significantly larger trapezoid portions (Fig. 100A). The cervical (neck) plate reduced to a thickening anterior to the scapular plate. The scapular plate divided in two parts by a central longitudinal suture (Fig. 98A, 100A). Three median plates, all weakly outlined: m1–2 bipartite, m3 unipartite; six lateral intersegmental platelets flanking their boarders (Fig. 99A, 100A). Two pairs of large segmental plates. Very large caudal (terminal) plate with short and weakly developed incisions (Fig. 99A, 100A).

Ventral cuticle with a clear species-specific pattern reaching the lateroventral sides of the body, and composed of endocuticular pillars of variable sizes; epicuticular thickenings absent (Fig. 100B). Larger accumulations of pillars present only in the centromedian portion of the venter, extending from the level slightly anterior to legs II towards the genital zone. Crescent-shaped accumulation of pillars surrounds the anus. Subcephalic zone smooth. Sexpartite gonopore located anteriorly of legs IV and a trilobed anus between legs IV.

Pedal plates and dentate collar IV absent, instead large patches of pillars are present centrally on each leg (Fig. 98A). Pulvini absent. Markedly sclerotised areas present on the inner side of each leg below the claws. A small spine or papilla on leg I absent, and a papilla on leg IV present (Fig. 98A). Claws IV longer than claws I–III. All external claws spurless. All internal claws with small spurs positioned at *ca.* 10–20% of the claw height and perpendicular to the branch (Fig. 98A, insert).

Mature males (*i.e*. from the third instar onwards; measurements in Table 54). No secondary sexual dimorphism except for the circular gonopore (Fig. 98, 99B).

Juveniles. Unknown.

Larvae. Unknown.

Eggs. Unknown.

DNA markers and phylogenetic position. The species is the only representative of the genus *Hypechiniscus* known from South Africa (Fig. 118). *Hypechiniscus africanus* **sp. nov.** belongs in the paraphyletic *H. exarmatus* morphogroup, being the sister species of the Taiwanese *H. crassus* Gąsiorek *et al*., 2021 (Fig. 118).

Type material. 2 ♀♀ and 2 ♂♂ on slides ZA.246.01–3; holotype: mature ♀ on slide ZA.246.03, allotype: mature ♂ on slide ZA.246.01. Mounted together with 4 ♀♀ of *Pseudechiniscus (P.) aquatilis* **sp. nov.** and 2 ♀♀ of *P. (M.) wallacei* **sp. nov.** 3 specimens used for DNA extraction.

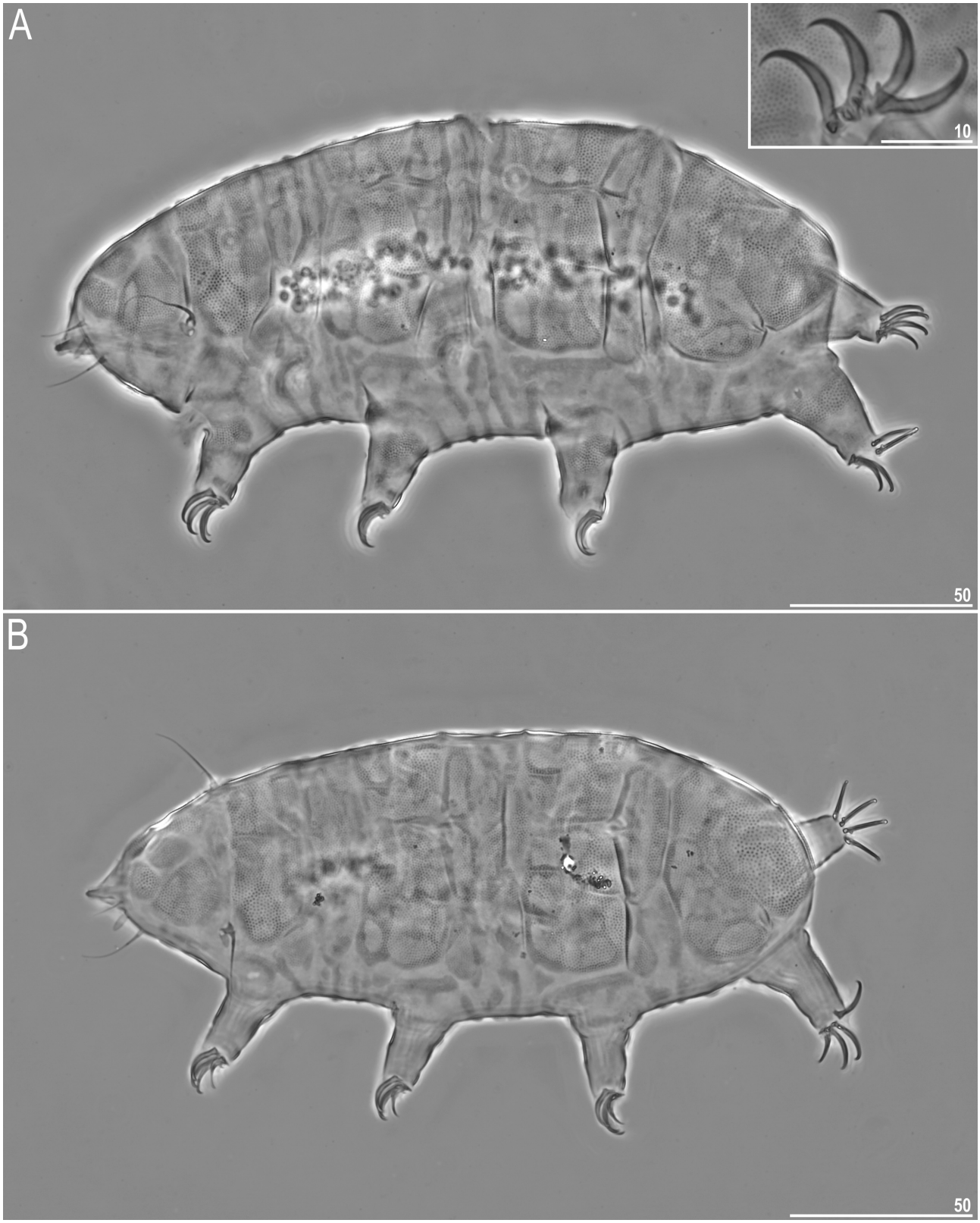

FIGURE 98. Habitus of *Hypechiniscus africanus* **sp. nov.** (PCM): A—holotype, female in dorsolateral view (insert shows claws III), B—allotype, male in dorsolateral view. Scale bars in μm.

Type locality. 29°45’13.7”S, 29°11’33.2”E, 1900 m asl: Republic of South Africa, KwaZulu-Natal, Drakensberg, Garden Castle Nature Reserve; river bank surrounded by mountainous grassland, moss from rock partially submerged by lotic water (sample ZA.246).

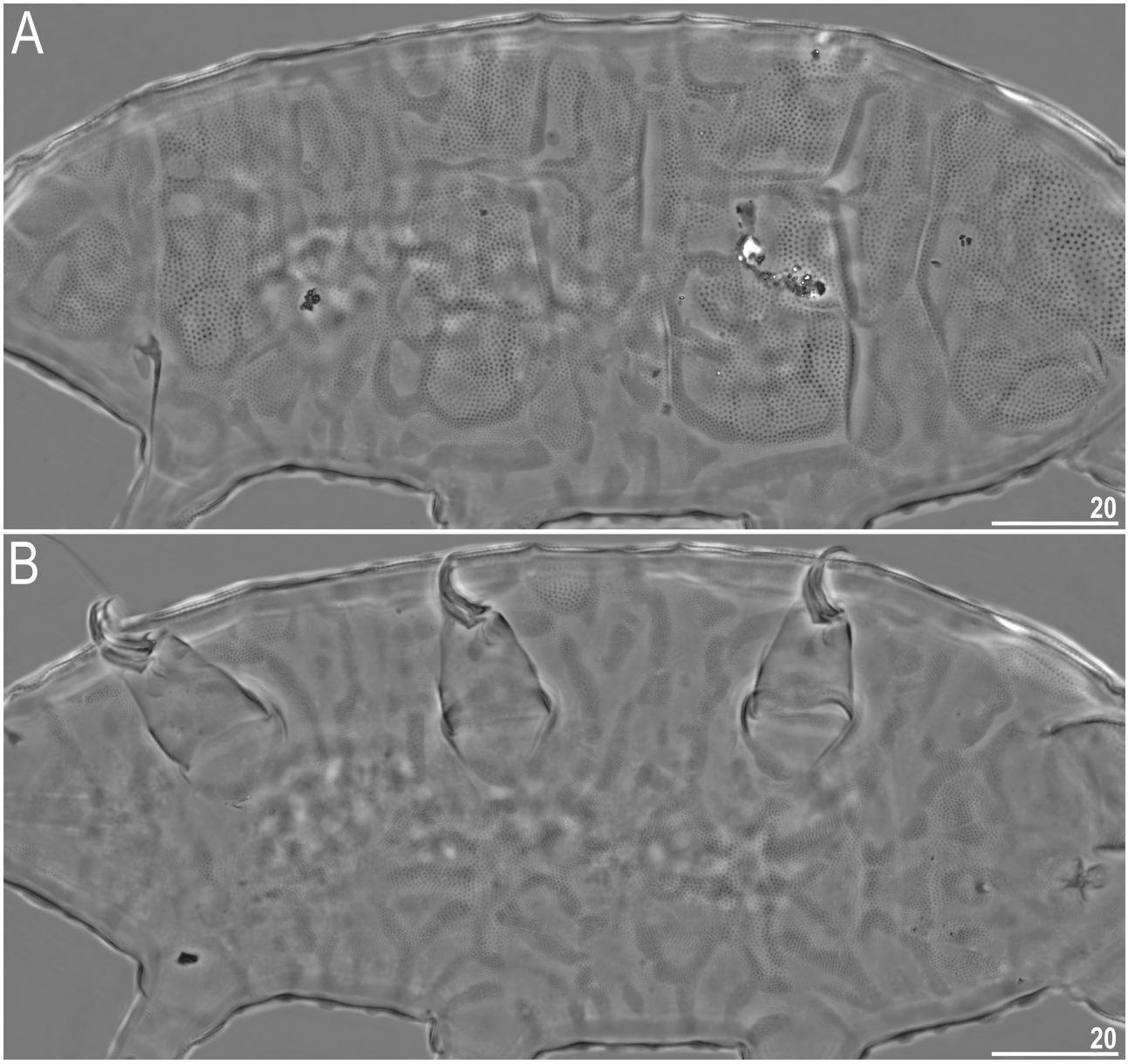

FIGURE 99. Sculpturing of *Hypechiniscus africanus* **sp. nov.** (PCM, allotype): A—dorsal view, B—ventral view. Scale bars = 20 μm.

Etymology. The name refers to the continent in which the species was discovered and underlines that it is the first *Hypechiniscus* species to be found in Africa. An adjective in the nominative singular.

Geographic distribution. Only recorded from the type locality in South Africa (Fig. 120B).

Remarks. This is the first report of the genus in Africa.

Differential diagnosis. The species belongs to the *Hypechiniscus exarmatus* morphogroup (*sensu* Gąsiorek *et al*. 2021b), but it differs from:

- *H. cataractus*, widely distributed in the Malay Archipelago, by the presence of dorsal sculpturing (minute, densely arranged endocuticular pillars appearing as dark dots under PCM in *H. africanus* **sp. nov.** *vs* uniform cuticular matrix appearing as smooth cuticle in *H. cataractus*);
- *H. crassus*, recently described from Taiwan (Gąsiorek *et al*. 2021d), by the presence of *striae* between pillars in dorsal plates (absent in *H. africanus* **sp. nov.** *vs* present in *H. crassus*);
- *H. exarmatus*, with reliable records from the Western Palaearctic, by the relative length of the cephalic papillae (*sp* values: ♀♀: *19.4–25.6*, ♂♂: *26.7–29.9* in *H. africanus* **sp. nov.** *vs* ♀♀: *13.3–19.6*, ♂♂: *22.1–25.1* in

H. exarmatus), and by the relative length of (primary) clavae (♀♀: *19.8–20.7* in *H. africanus* **sp. nov.** *vs* ♀♀: *10.8–17.9* in *H. exarmatus*);

- *H. flavus*, known only from Japan, by the body colour (white in *H. africanus* **sp. nov.** *vs* yellow in *H. flavus*). Moreover, the ventral pattern of pillars separates all five species (see Gąsiorek *et al*. 2021b, d for comparison). The main differences between *H. africanus* **sp. nov.** and the most similar *H. exarmatus*, *i.e*. the lengths of cephalic appendages and ventral sculpturing, are congruent with the analyses in Gąsiorek *et al*. (2021b), pinpointing these characters as crucial for correct species delineation in the genus.

Raw measurements. Supplementary Materials (SM.03) and Tardigrada Register (www.tardigrada.net/register/0099.htm).

TABLE 54. Measurements [in µm] of selected morphological structures of the adults of *Hypechiniscus africanus* **sp. nov.** mounted in Hoyer's medium. *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	♀ **(holotype)**		♀		♂ **(allotype)**		♂	
	µm	***sp***	**µm**	***sp***	**µm**	***sp***	**µm**	***sp***
Body length	217	*879*	205	*847*	200	*922*	223	*953*
Scapular plate length	24.7	–	24.2	–	21.7	–	23.4	–
Head appendages lengths								
Cirrus *internus*	7.2	*29.1*	10.6	*43.8*	8.4	*38.7*	10.7	*45.7*
Cephalic papilla	4.8	*19.4*	6.2	*25.6*	5.8	*26.7*	7.0	*29.9*
Cirrus *externus*	20.3	*82.2*	16.0	*66.1*	17.9	*82.5*	17.4	74.4
Clava	4.9	*19.8*	5.0	*20.7*	4.4	*20.3*	4.5	*19.2*
Cirrus *A*	26.4	*106.9*	23.8	*98.3*	23.8	*109.7*	23.7	*101.3*
Cirrus *A*/Body length ratio	12%	–	12%	–	12%	–	11%	–
Body appendages lengths								
Papilla on leg IV length	2.8	*11.3*	2.5	*10.3*	2.7	*12.4*	3.2	*13.7*
Claw I heights								
Branch	12.5	*50.6*	12.2	*50.4*	11.3	*52.1*	12.1	*51.7*
Spur	2.5	*10.1*	2.1	*8.7*	2.0	*9.2*	2.0	*8.5*
Spur/branch height ratio	20%	–	17%	–	18%	–	17%	–
Claw II heights								
Branch	11.9	*48.2*	11.8	*48.8*	10.5	*48.4*	10.5	*44.9*
Spur	2.2	*8.9*	2.2	*9.1*	2.1	*9.7*	?	*?*
Spur/branch height ratio	18%	–	19%	–	20%	–	?	–
Claw III heights								
Branch	11.3	*45.7*	12.2	*50.4*	11.1	*51.2*	10.8	*46.2*
Spur	2.4	*9.7*	2.0	*8.3*	1.8	*8.3*	?	*?*
Spur/branch height ratio	21%	–	16%	–	16%	–	?	–
Claw IV heights								
Branch	13.5	*54.7*	13.8	*57.0*	12.4	*57.1*	12.5	*53.4*
Spur	?	*?*	?	*?*	?	*?*	?	?
Spur/branch height ratio	?	–	?	–	?	–	?	–

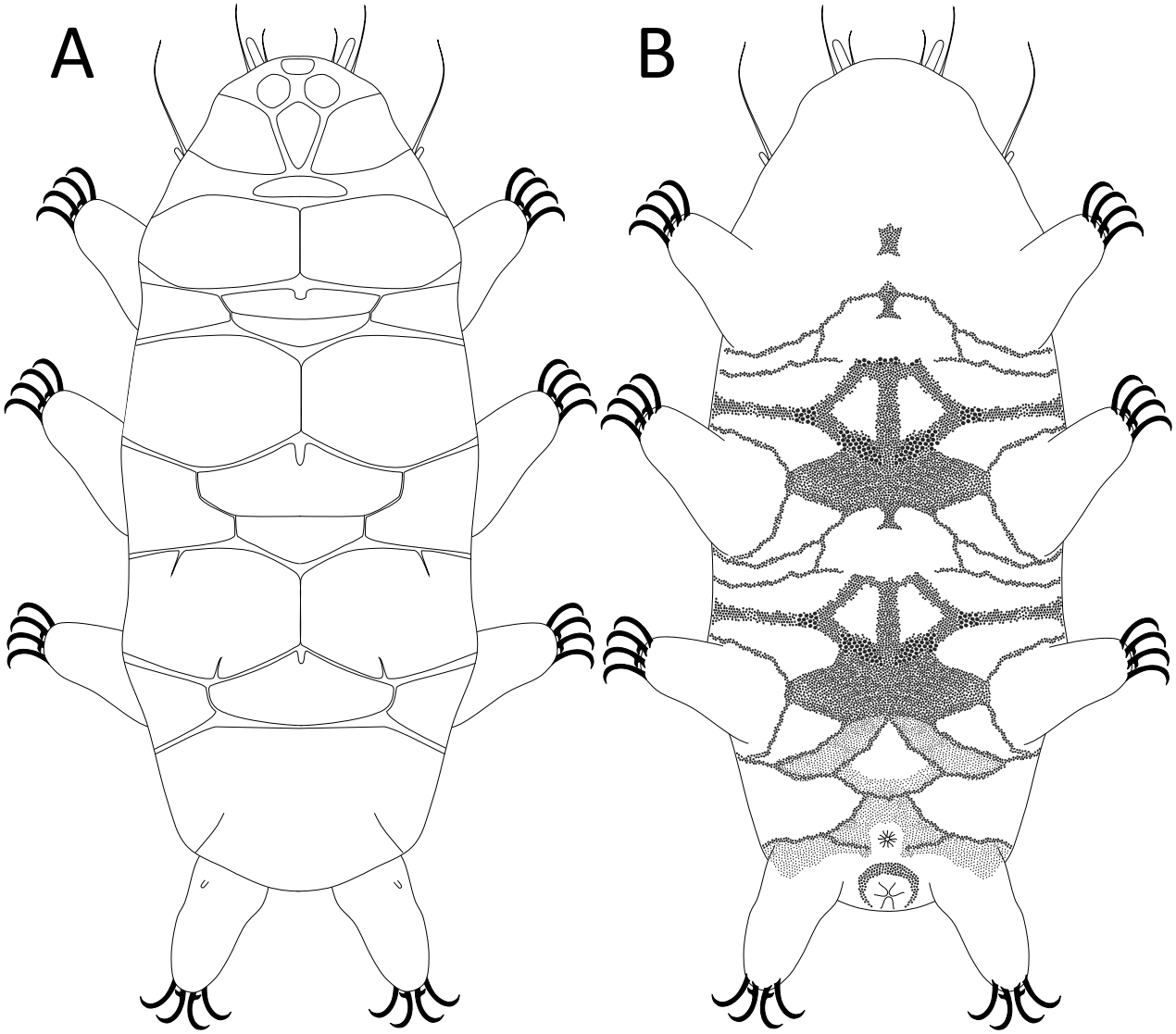

FIGURE 100. Schematic drawings of *Hypechiniscus africanus* **sp. nov.**: A—dorsal view, B—ventral view.

Genus: *Pseudechiniscus* Thulin, 1911

Subgenus: *Meridioniscus* Gąsiorek *et al*., 2021

***1. Pseudechiniscus* (*Meridioniscus*) *wallacei* sp. nov. Vončina, Gąsiorek, Morek & Michalczyk**

Pseudechiniscus cf. *angelusalas* in Gąsiorek *et al.* 2021a, d

urn:lsid:zoobank.org:act:2648337E-42EC-465C-996D-9EF63E7187C6

Figures 101–105, Tables 55–56

Data source:

A total of 134 specimens (74 ♀♀, 18 juveniles, 2 larvae, and 40 specimens of unknown instar/sex):

- Sample ZA.157: 4 specimens (4 ♀♀ on slides); found with *Echiniscus scabrospinosus* and *Pseudechiniscus* (*P.*) cf. *ehrenbergi*.
- Sample ZA.158: 4 specimens (4 ♀♀ on slides); found with *Echiniscus scabrospinosus and E. virginicus*.
- Sample ZA.169: 13 specimens (3 ♀♀ on slides, and 10 specimens on SEM stub 19.09).
- Sample ZA.177: 33 specimens (12 ♀♀, 5 juveniles and 2 larvae on slides, 10 specimens on SEM stub 19.03, and 4 specimens used for DNA extraction); found with *Pseudechiniscus* (*P.*) cf. *ehrenbergi*.

- Sample ZA.178: 3 specimens (1 ♀ on a slide and 2 specimens used for DNA extraction); found with *Pseudechiniscus* (*P.*) cf. *ehrenbergi*.
- Sample ZA.183: 16 specimens (13 ♀♀ and 3 juveniles on slides); found with *Doryphoribius maasaimarensis*, *Echiniscus oreas* **sp. nov.**, *E. regularis* **sp. nov.**, *E. scabrospinosus*, *Pseudechiniscus* (*P.*) cf. *ehrenbergi*, and *Ramazzottius szeptycki.*
- Sample ZA.216: 2 specimens (2 ♀♀ on a slide); found with *Echiniscus intricatus* **sp. nov.** and *Pseudechiniscus* (*P.*) cf. *ehrenbergi*.
- Sample ZA.237: 2 specimens (1 ♀ and 1 juvenile on a slide).
- Sample ZA.246: 2 specimens (2 ♀♀ on a slide); found with *Hypechiniscus africanus* **sp. nov.**, *Pseudechiniscus* (*P.*) *aquatilis* **sp. nov.**, and *P.* (*P.*) cf. *ehrenbergi*.
- Sample ZA.256: 14 specimens (9 ♀♀ and 1 juvenile on slides, and 4 specimens used for DNA extraction, including 2 hologenophores); found with *Doryphoribius bindae*, *Echiniscus cavagnaroi*, and *Ramazzottius szeptycki*.
- Sample ZA.261: 12 specimens (2 ♀♀ on a slide, and 10 specimens on SEM stub 18.20); found with *Bryodelphax* **sp. nov.** and *Pseudechiniscus* (*P.*) cf. *ehrenbergi***.**
- Sample ZA.263: 1 specimen (1 ♀ on a slide); found with *Echiniscus longispinosus*, *E. regularis* **sp. nov.**, and *Pseudechiniscus* (*P.*) cf. *ehrenbergi*.
- Sample ZA.346: 21 specimens (16 ♀♀ and 5 juveniles on slides).
- Sample ZA.364: 2 specimens (2 ♀♀ on a slide); found with *Echiniscus perarmatus*, *Pseudechiniscus* (*P.*) *linnaei* **sp. nov.**, and *P.* (*P.*) cf. *ehrenbergi*.
- Sample ZA.518: 4 specimens (1 ♀ and 3 juveniles on slides); found with *Echiniscus dentatus* **sp. nov.**, *E. irroratus* **sp. nov.**, *E. scabrospinosus*, and *Pseudechiniscus* (*P.*) cf. *ehrenbergi*.
- Sample ZA.531: 1 specimen (1 ♀ on a slide); found with *Echiniscus dentatus* **sp. nov.**

Description. Mature females (*i.e*. from the third instar onwards; measurements in Table 55). Body orange and more rounded than in typical *Pseudechiniscus* (Fig. 101A–B, 102), with round black eyes that disappeared after mounting in Hoyer's medium in some specimens. Dactyloid cephalic papillae (secondary clavae) and minute (primary) clavae (Fig. 101A–B, 103A, 104A); peribuccal cirri with poorly developed cirrophores. Cirrus *A* short, with cirrophore.

Dorsal plates poorly sclerotised, but well-demarcated, with the *Pseudechiniscus*-type sculpturing, *i.e*. endocuticular pillars protruding under the epicuticle, visible under PCM as dark dots (Fig. 101A–B, 103) and as granules under SEM (Fig. 102, 104A, C–E); additionally, pores may be identifiable under SEM (Fig. 104C–E). *Striae* present, best visible in the caudal plate (Fig. 103C–E), but typically not identifiable under SEM (Fig. 104C–E), only sometimes *striae* observable in the cephalic region (Fig. 104A); epicuticular ornamentation visible as darker belts in all dorsal plates (Fig. 101A–B, 103A, C–E). The cephalic plate tetrapartite, with the anterior bi-halved portion and three posterior portions roughly equal in size (Fig. 101A–B). The cervical (neck) plate absent. The scapular plate with sutures, separating elongated, rectangular posterior portion (Fig. 104C). Three median plates: m1–2 bipartite, with much reduced, narrow posterior portions, m3 unipartite (Fig. 104C–E); two pairs of lateral intersegmental platelets flanking the boarders of m1–2. Two pairs of large segmental plates with well-delineated median longitudinal suture. The pseudosegmental plate IV' divided by a median suture; the posterior margin of the plate wide, but without lobes (Fig. 101A–B, 103A, E, 104E). The caudal (terminal) plate with short longitudinal crests (Fig. 103A, E, 104E).

Ventral cuticle with a pronounced species-specific pattern reaching the lateroventral sides of the body (Fig. 103A–B, 105), being a typical *reticulum* composed of large multangular, longitudinal shapes; epicuticular thickenings absent. The subcephalic zone with a wide belt of pillars (Fig. 103B), but more frequently a pair of large lateroventral plates occur (Fig. 104A, 105). Sexpartite gonopore located anteriorly of legs IV and a trilobed anus between legs IV.

Pedal plates and dentate collar IV absent, but large patches of pillars are present centrally on each leg. Pulvini faint. Papilla on leg I absent and papilla on leg IV present (Fig. 101A–B, 102–103A, E). Claws I–IV similar in size, short and delicate (Fig. 101A, insert, 104B). All external claws spurless. All internal claws with minuscule, thin spurs positioned at *ca.* 10–20% of the claw height.

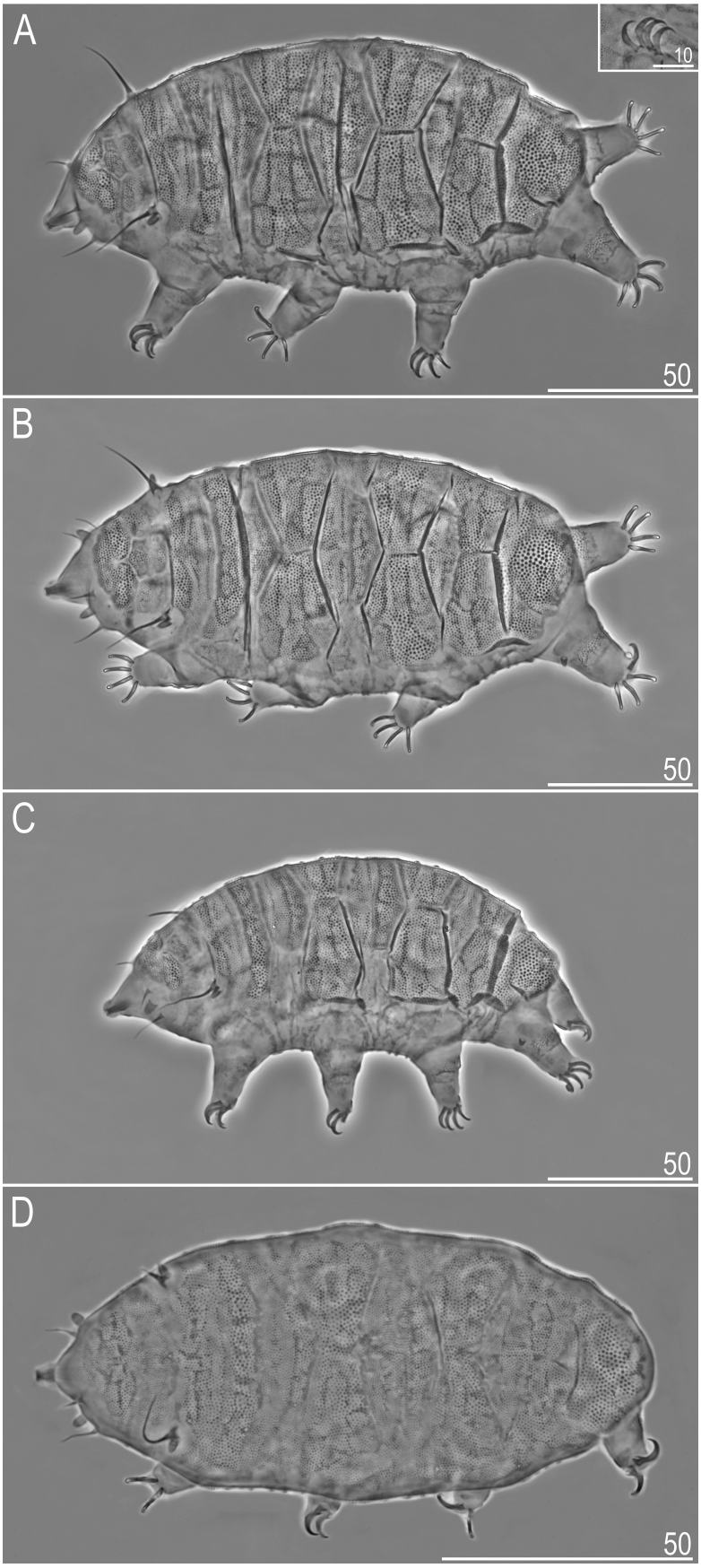

FIGURE 101. Habitus of *Pseudechiniscus* (*M.*) *wallacei* **sp. nov.** (PCM): A,—holotype, female in dorsolateral view (insert shows claws III), B—paratype, female in dorsolateral view, C—juvenile in dorsolateral view, D—larva in dorsal view. Scale bars in μm.

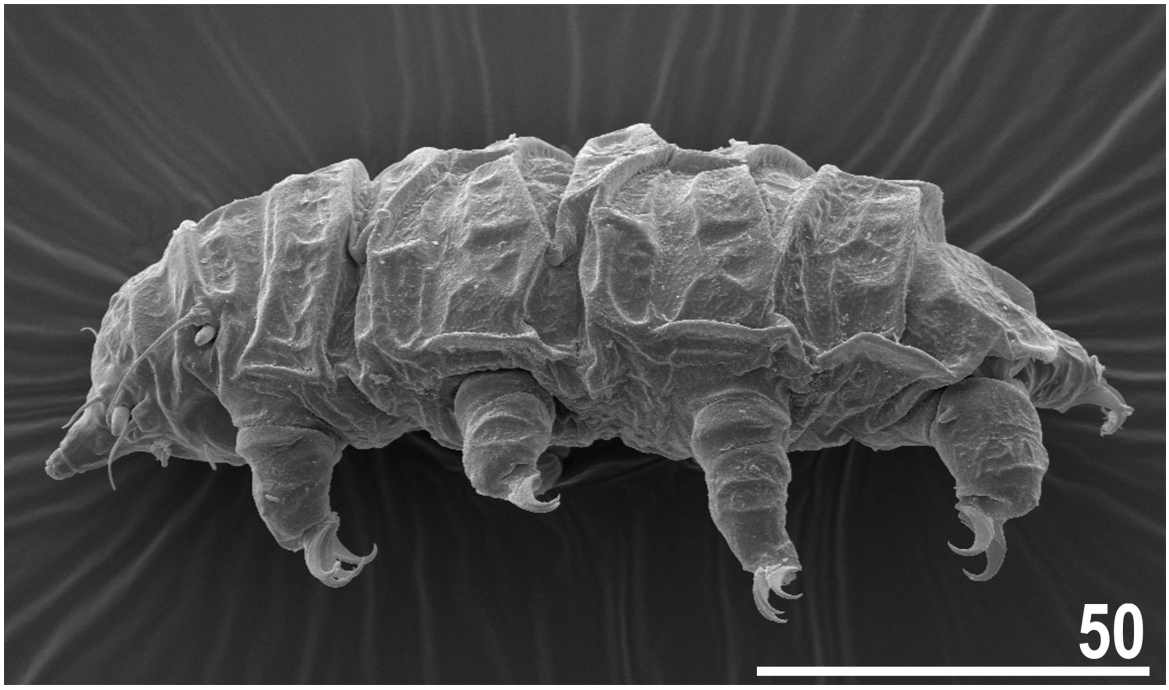

FIGURE 102. Habitus of *Pseudechiniscus* (*M.*) *wallacei* **sp. nov.** (SEM, female in lateral view). Scale bar = 50 µm.

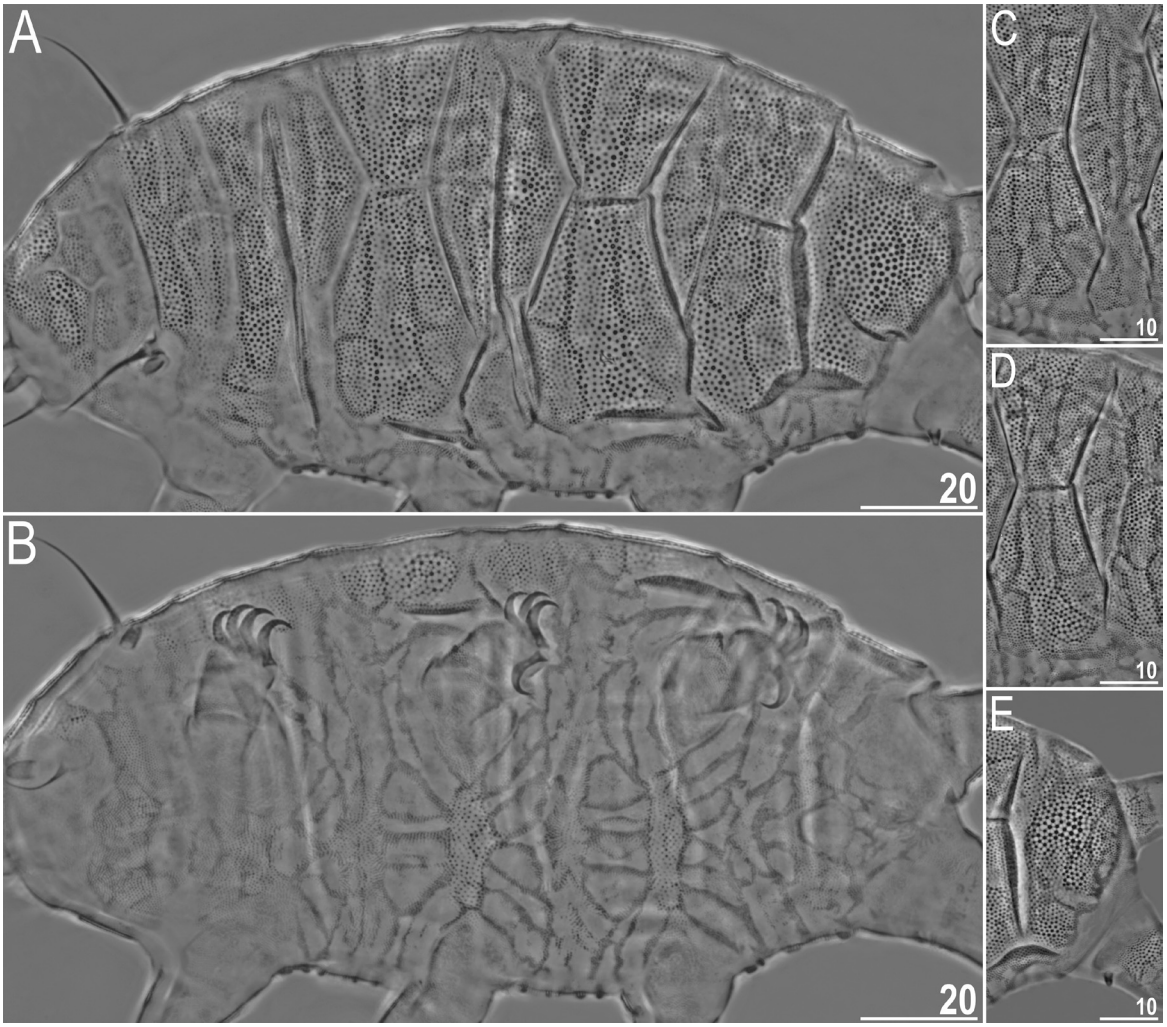

FIGURE 103. Sculpturing of *Pseudechiniscus* (*M.*) *wallacei* **sp. nov.** (PCM, females): A—dorsolateral view, B—ventral view, C–E—close-up on the parts of plates with discernible *striae*. Scale bars in µm.

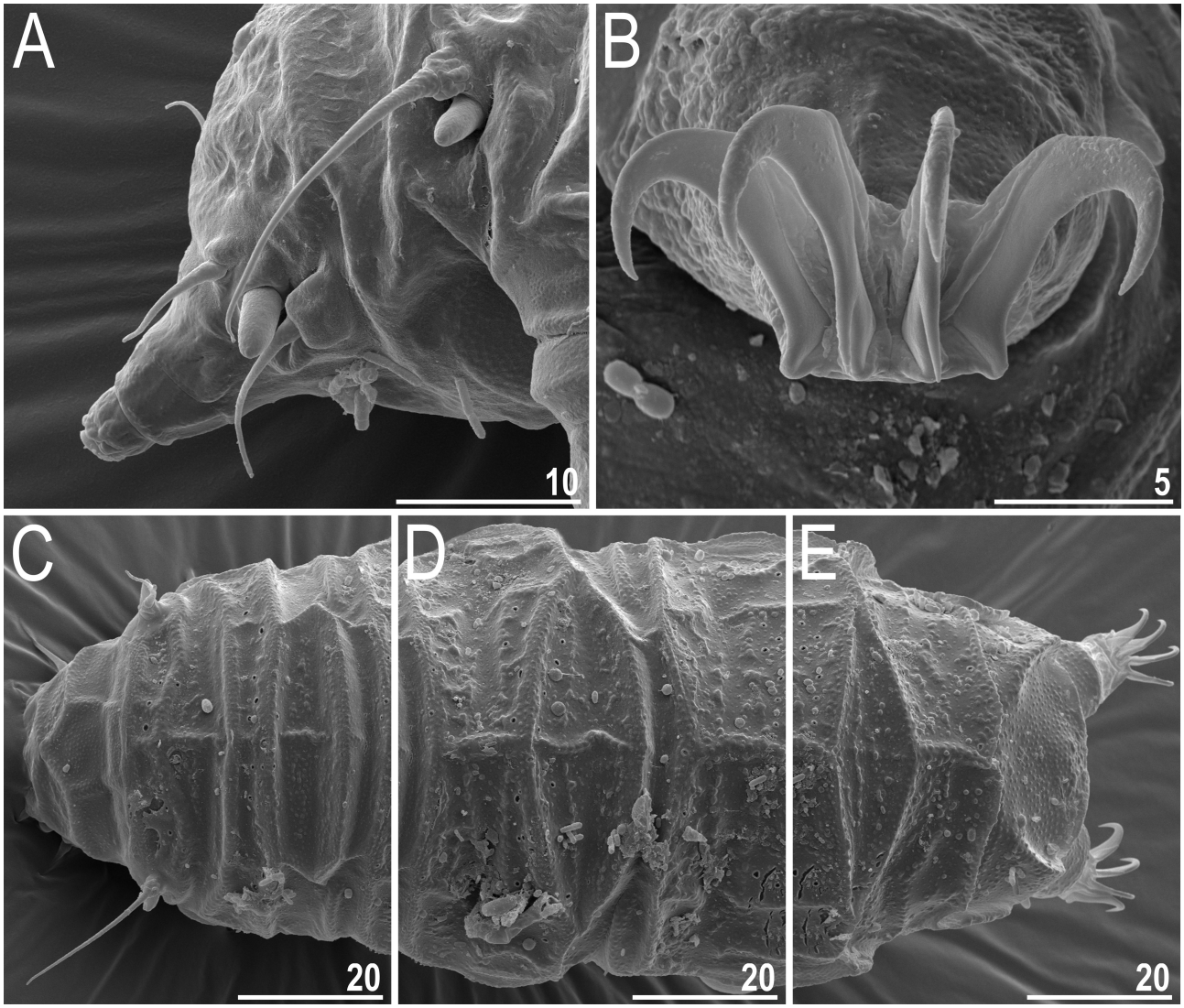

FIGURE 104. Morphology of *Pseudechiniscus* (*M.*) *wallacei* **sp. nov.** (SEM, females): A—cephalic appendages in lateral view, B—claws IV and papilla IV, C—anterior portion of the body, D—central portion of the body, E—posterior portion of the body. Scale bars in μm.

Juveniles (*i.e*. from the second instar onwards; measurements in Table 56). Phenotypically similar to females (Fig. 101C), beside of the lacking gonopore. On average smaller than females, but with no morphometric gap between juveniles and adult females.

Larvae (*i.e*. the first instar). No gonopore and anus. The distinction between dorsal plates blurred, so the armour seems uniform (Fig. 101D). Morphometric data for the two found larvae: body length 87–119 μm, the scapular plate length 14.6–16.8 μm; cephalic appendages: *cirrus internus* 3.6–4.6 μm, cephalic papilla 3.1–3.7 μm, *cirrus externus* 4.8–6.8 μm, (primary) clava 3.0–3.4 μm, cirrus *A* 11.7–15.1 μm; papilla IV length: 1.7–1.8 μm; claw heights 5.2–6.7 μm, claw spurs 1.0–1.2 μm.

DNA markers and phylogenetic position. The sister species of yet undescribed *Meridioniscus* species from the Malay Archipelago (*Pseudechiniscus* sp. 6 in Fig. 119; p-distance = 19.3–21.8% in ITS-1), conforming to the data presented in Gąsiorek *et al*. (2021a, d).

Type material. 12 ♀♀, 5 juveniles and 2 larvae on slides ZA.177.03–7; holotype: mature ♀ on slide ZA.177.04. Mounted together with 9 ♀♀ and 8 juveniles of *P.* (*P.*) cf. *ehrenbergi*, 4 specimens used for DNA extraction.

Type locality. 29°02’57.4’’S, 29°24’18.2’’E, 1415 m asl: Republic of South Africa, KwaZulu-Natal, Drakensberg, Giants Castle Game Reserve; secondary forest, mosses and lichens from rocks (sample ZA.177).

Etymology. The name honours Alfred Russel Wallace, the father of biogeography and an independent conceiver of the theory of evolution by natural selection. A noun in the genitive singular.

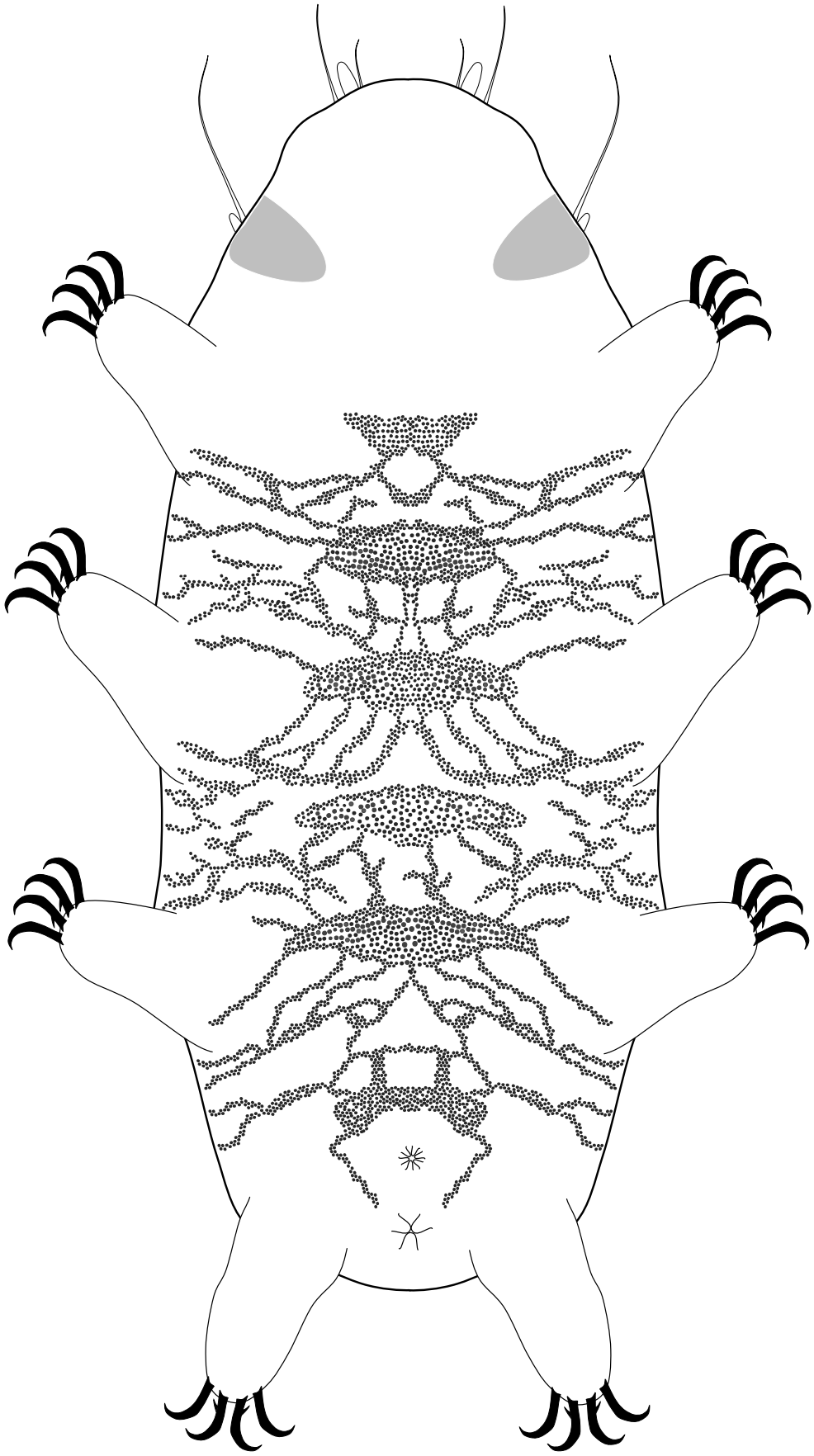

FIGURE 105. Schematic drawing of the venter of *Pseudechiniscus* (*M.*) *wallacei* **sp. nov.**

TABLE 55. Measurements [in µm] of selected morphological structures of the adult females of *Pseudechiniscus wallacei* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Holotype	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	20	138	–	197	*592*	–	*816*	173	*702*	15	*55*	162	*631*
Scapular plate length	20	21.0	–	29.1		–		24.7	–	2.0	–	25.7	–
Head appendages lengths													
Cirrus *internus*	19	5.3	–	8.7	*22.6*	–	*35.4*	7.4	*29.7*	1.0	*3.4*	7.2	*28.0*
Cephalic papilla	20	3.4	–	6.1	*12.9*	–	*25.1*	4.5	*18.4*	0.6	*2.7*	5.2	*20.2*
Cirrus *externus*	19	8.5	–	13.0	*36.3*	–	*53.7*	11.0	*44.4*	1.3	*4.9*	10.4	*40.5*
Clava	20	3.4	–	6.1	*14.0*	–	*24.5*	4.8	*19.5*	0.7	*2.8*	4.8	*18.7*
Cirrus *A*	17	17.5	–	24.0	*71.3*	–	*102.9*	21.4	*86.9*	1.7	*9.2*	20.6	*80.2*
Cirrus *A*/Body length ratio	17	10%	–	16%		–		12%	–	1%	–	13%	–
Body appendages lengths													
Papilla on leg IV length	20	2.3	–	4.3	*9.3*	–	*18.9*	3.1	*12.5*	0.5	*2.3*	3.1	*12.1*
Claw I heights													
Branch	18	6.6	–	9.4	*26.9*	–	*38.8*	8.4	*34.0*	0.7	*3.2*	9.3	*36.2*
Spur	11	1.0	–	2.1	*4.0*	–	*8.2*	1.5	*6.2*	0.3	*1.2*	2.1	*8.2*
Spur/branch height ratio	11	11%	–	23%		–		18%	–	3%	–	23%	–
Claw II heights													
Branch	20	6.1	–	9.4	*24.9*	–	*37.5*	8.3	*33.5*	0.8	*2.9*	9.2	*35.8*
Spur	14	0.9	–	1.8	*3.6*	–	*6.8*	1.2	*4.9*	0.3	*1.0*	1.5	*5.8*
Spur/branch height ratio	14	10%	–	20%		–		14%	–	3%	–	16%	–
Claw III heights													
Branch	20	6.6	–	9.2	*26.9*	–	*39.0*	8.5	*34.4*	0.6	*3.0*	8.6	*33.5*
Spur	15	0.8	–	2.0	*3.1*	–	*9.5*	1.2	*5.1*	0.4	*1.7*	1.2	*4.7*
Spur/branch height ratio	15	9%	–	24%		–		15%	–	4%	–	14%	–
Claw IV heights													
Branch	13	8.4	–	10.1	*8.0*	–	*41.7*	9.2	*35.3*	0.4	*8.5*	?	*?*
Spur	11	1.0	–	2.0	*1.5*	–	*9.5*	1.5	*5.8*	0.3	*2.1*	?	*?*
Spur/branch height ratio	11	12%	–	23%		–		16%	–	4%	–	?	–

Geographic distribution. Widely distributed in South Africa (Fig. 120M) and Asia: Malay Archipelago and Vietnam (Gąsiorek *et al*. 2021a).

Remarks. *P. wallacei* **sp. nov.** is the second most common *Pseudechiniscus* species in South Africa (Fig. 120M). It often inhabits the same moss cushions/lichen thalli, as *P.* cf. *ehrenbergi* does.

Differential diagnosis. To date, this is the only *Meridioniscus* species found in South Africa and it can be distinguished from the most similar species (lacking appendages on the pseudosegmental plate IV' and lateral hemispherical projections) of the subgenus:

- *P. angelusalas* Roszkowska *et al*., 2020, described from Madagascar, by the presence of males (absent in *P. wallacei* **sp. nov.** *vs* present in *P. angelusalas*), by dorsal sculpturing (darker belts in all dorsal plates present in *P. wallacei* **sp. nov.** *vs* evenly distributed, uniform pillars in *P. angelusalas*), and by the body size (138–197 µm in *P. wallacei* **sp. nov.** *vs* 113–143 µm in *P. angelusalas*);
- *P. dastychi* Roszkowska *et al*., 2020, described from Antarctica, by the length of cephalic appendages: *cirrus internus* (5.3–8.7 µm in *P. wallacei* **sp. nov.** *vs* 10.4–12.7 µm in *P. dastychi*), *cirrus externus* (8.5–13.0 µm in *P. wallacei* **sp. nov.** *vs* 15.9–19.1 µm in *P. dastychi*), cirrus *A* (17.5–25.0 µm in *P. wallacei* **sp. nov.** *vs* 40.0–40.5

μm in *P. dastychi*), and by the dorsal sculpturing (epicuticular ornamentation visible as dark transversal belts in *P. wallacei* **sp. nov.** *vs* uniformly distributed pillars in *P. dastychi*);

- *P. dreyeri* Gąsiorek *et al*., 2021, described from Taiwan, by the length of papilla IV (2.3–4.3 μm in *P. wallacei* **sp. nov.** *vs* 1.5–2.3 μm in *P. dreyeri*) and comparatively larger spurs with regard to claw branches (spur/branch height ratios I–III: 9–24% in *P. wallacei* **sp. nov.** *vs* 23–34% in *P. dreyeri*);
- *P. indistinctus* Roszkowska *et al*., 2020, described from the Scandinavian Peninsula, by the shorter cirrus *A* (17.5–25.0 μm in *P. wallacei* **sp. nov.** *vs* 27.6–34.2 μm in *P. indistinctus*), by the presence of the longitudinal suture dividing the scapular plate in *P. indistinctus*, and the distribution of the pillars on the dorsum (epicuticular ornamentation visible as darker belts in all dorsal plates in *P. wallacei* **sp. nov.** *vs* evenly distributed pillars in *P. indistinctus*);
- *P. mascarenensis* Kiosya *et al.*, 2021, described from Mauritius, by the length of papilla IV (2.3–4.3 μm in *P. wallacei* **sp. nov.** *vs* 1.5–2.4 μm in *P. mascarenensis*) and the presence of epicuticular ornamentation (present in *P. wallacei* **sp. nov.** *vs* absent in *P. mascarenensis*);

TABLE 56. Measurements [in μm] of selected morphological structures of the juveniles of *Pseudechiniscus wallacei* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD	
		μm			*sp*			μm	*sp*	μm	*sp*
Body length	5	120	–	155	*654*	–	*714*	137	*694*	16	*23*
Scapular plate length	5	17.1	–	22.0		–		19.7	–	2.1	–
Head appendages lengths											
Cirrus *internus*	5	6.5	–	8.2	*31.4*	–	*38.6*	7.0	*35.5*	0.7	*3.2*
Cephalic papilla	5	3.7	–	4.4	*18.9*	–	*21.6*	4.0	*20.3*	0.3	*1.2*
Cirrus *externus*	5	7.7	–	11.2	*39.3*	–	*51.9*	9.4	*47.4*	1.7	*5.5*
Clava	5	3.7	–	4.3	*17.7*	–	*24.6*	4.0	*20.3*	0.3	*2.6*
Cirrus *A*	5	15.0	–	24.0	*82.0*	–	*109.1*	19.3	*97.5*	3.6	*10.0*
Cirrus *A*/Body length ratio	5	12%	–	16%		–		14%	–	1%	–
Body appendages lengths											
Papilla on leg IV length	5	1.8	–	2.6	*9.8*	–	*12.9*	2.3	*11.8*	0.3	*1.2*
Claw I heights											
Branch	4	6.2	–	8.3	*32.1*	–	*38.8*	6.9	*35.8*	1.0	*2.7*
Spur	4	0.9	–	1.1	*4.6*	–	*5.3*	1.0	*5.0*	0.1	*0.3*
Spur/branch height ratio	4	13%	–	15%		–		14%	–	1%	–
Claw II heights											
Branch	5	5.7	–	7.9	*29.1*	–	*36.9*	6.8	*34.4*	0.9	*3.1*
Spur	4	0.8	–	1.1	*4.1*	–	*5.8*	1.0	*5.0*	0.1	*0.7*
Spur/branch height ratio	4	14%	–	16%		–		15%	–	1%	–
Claw III heights											
Branch	5	6.0	–	7.7	*30.6*	–	*37.4*	6.8	*34.5*	0.6	*3.1*
Spur	3	1.0	–	1.2	*5.1*	–	*5.6*	1.1	*5.4*	0.1	*0.3*
Spur/branch height ratio	3	15%	–	17%		–		16%	–	1%	–
Claw IV heights											
Branch	3	6.8	–	8.2	*35.9*	–	*39.8*	7.6	*38.0*	0.7	*1.9*
Spur	1	1.5	–	1.5	*7.0*	–	*7.0*	1.5	*7.0*	?	*?*
Spur/branch height ratio	1	18%	–	18%		–		18%	–	?	–

- *P. santomensis* Fontoura *et al*., 2010, described from São Tomé Island, Gulf of Guinea, by the presence of small projections on the pseudosegmental plate IV' (posterior margin with the plate wide, but without any projections in *P. wallacei* **sp. nov.** *vs* small projections variously developed in *P. santomensis*, generally tooth-shaped), and by the dorsal sculpturing (ornamentation visible as darker belts of the pillars in *P. wallacei* **sp. nov.** *vs* densely and regularly distributed pillars in *P. santomensis*).

Moreover, all abovementioned species can be also differentiated by the ventral sculpturing pattern.

Raw measurements. Supplementary Materials (SM.03) and Tardigrada Register (www.tardigrada.net/register/0100.htm).

Subgenus: *Pseudechiniscus* Thulin, 1911 in Gąsiorek *et al*. (2021a)

2. Pseudechiniscus (*Pseudechiniscus*) *aquatilis* sp. nov. Vončina, Gąsiorek, Morek & Michalczyk

Pseudechiniscus sp. 11 in Gąsiorek *et al.* 2021a, d

urn:lsid:zoobank.org:act:685B76AA-8733-415E-A256-A0B5708F9E49

Figures 106–108, Table 57

Data source:

A total of 6 specimens (4 ♀♀ and 2 specimens of unknown instar/sex):

- Sample ZA.246: 6 specimens (4 ♀♀ on slides, 2 specimens used for DNA extraction); found with and *Hypechiniscus africanus* **sp. nov.**, *Pseudechiniscus* (*P.*) cf. *ehrenbergi, P.* (*M.*) *wallacei* **sp. nov.**

Description. Mature females (*i.e*. from the third instar onwards; measurements in Table 57). Body light yellow and elongated, with ovoid black eyes that disappeared soon after mounting in Hoyer's medium (Fig. 106). Pseudohemispherical cephalic papillae (secondary clavae) and minute (primary) clavae; peribuccal cirri with poorly developed cirrophores. Cirrus *A* short, with cirrophore.

Dorsal plates poorly sclerotised and barely demarcated, with the *Pseudechiniscus*-type sculpturing, *i.e*. endocuticular pillars protruding under the epicuticle as granules, visible under PCM as dark dots (Fig. 106–107). *Striae* or epicuticular ornamentation absent (Fig. 107A). The cephalic plate pentapartite, with two small anterior portions and three larger posterior portions (Fig. 106). The cervical (neck) plate absent. The scapular plate uniform, without grooves or sutures (Fig. 106–107A). Three median plates: m1–2 bipartite, m3 unipartite; a pair of lateral intersegmental platelets flanking the boarders of m1–2 (Fig. 107A). Two pairs of large segmental plates with weakly delineated median longitudinal suture. Single pseudosegmental plate IV', undivided by a median suture; appendages on the posterior margin of the plate absent. The caudal (terminal) plate with short and weakly developed longitudinal crests (Fig. 106–107A).

Ventral cuticle with a clear species-specific pattern reaching the lateroventral sides of the body (Fig. 107–108), and composed of endocuticular pillars of similar size; epicuticular thickenings absent (Fig. 108). Belts of pillars thin and forming an intricate reticulum between three larger accumulations of pillars: at the levels of legs II, III, and in the genital zone, where pillars uniformly surround gonopore and anus. Sexpartite gonopore located anteriorly of legs IV and a trilobed anus between legs IV.

Pedal plates and dentate collar IV absent, instead large patches of pillars are present centrally on each leg (Fig. 107A). Pulvini weakly developed. A small spine or papilla on leg I absent, and a papilla on leg IV present (Fig. 107A). Claws I–IV similar in size, rather elongated. All external claws spurless. All internal claws with moderately large spurs positioned at *ca.* 20–25% of the claw height (Fig. 106A, insert).

DNA markers and phylogenetic position. The species is the sister taxon to *P. linnaei* **sp. nov.** (Fig. 119; p-distance = 2.9% in ITS-1).

Type material. 4 ♀♀ on slides ZA.246.01–2; holotype: mature ♀ on slide ZA.246.01. Two specimens used for DNA extraction.

Type locality. 29°45'13.7"S, 29°11'33.2"E, 1900 m asl: Republic of South Africa, KwaZulu-Natal, Drakensberg, Garden Castle Nature Reserve; river bank surrounded by mountainous grassland, moss from rock partially submerged by lotic water (sample ZA.246).

FIGURE 106. Habitus of *Pseudechiniscus* (*P.*) *aquatilis* **sp. nov.** (PCM, holotype, female in dorsolateral view). Insert shows claws III. Scale bars in μm.

Etymology. From Latin *aquatilis* = aquatic, underlying the limno-terrestrial habitat, in which the new species was found. An adjective in the nominative singular.

Geographic distribution. Recorded only in South Africa (Fig. 120M).

Remarks. None.

Differential diagnosis. The species can be distinguished from other *Pseudechiniscus* spp. inhabiting South Africa based on the pattern of ventral sculpturing. Moreover, it is differentiated from:

- *P. beasleyi*, described from China (Li *et al*. 2007), by the faceting of the scapular plate (almost indiscernible in *P. aquatilis* **sp. nov.** *vs* present and well-developed in *P. beasleyi*);
- *P. chengi*, described from China (Xue *et al*. 2017), by the presence of longitudinal fold dividing the pseudosegmental plate IV' (absent in *P. aquatilis* **sp. nov.** *vs* present in *P. chengi*) and by the dorsal sculpturing (pillars arranged more sparsely and less pronounced in *P. aquatilis* **sp. nov.** *vs* densely arranged and more pronounced in *P. chengi*);
- *P.* cf. *ehrenbergi*, by a relatively longer *cirrus internus* (*36.6–50.8* in *P. aquatilis* **sp. nov.** *vs 19.8–34.6* in *P.* cf. *ehrenbergi*) and a relatively shorter primary clava (*13.8–15.1* in *P. aquatilis* **sp. nov.** *vs 16.1–22.7* in *P.* cf. *ehrenbergi*), and longer claws (I–III: 8.9–9.7 μm, IV: 10.1 μm in *P. aquatilis* **sp. nov.** *vs* I–III: 6.8–9.0 μm, IV: 7.4–9.8 μm in *P.* cf. *ehrenbergi*);
- *P. ehrenbergi*, described from Italy (Roszkowska *et al*. 2020) and reported from Mongolia (Cesari *et al*. 2020), by the subdivision of the scapular plate (absence of the median longitudinal suture in *P. aquatilis* **sp. nov**. *vs* with the median longitudinal suture in *P. ehrenbergi*), and by the presence of a rudimentary papilla I (absent in *P. aquatilis* **sp. nov.** *vs* present in *P. ehrenbergi*) and by the presence of males (absent in *P. aquatilis* **sp. nov.** *vs* present in *P. ehrenbergi*);
- *P. formosus*, described from Taiwan (Gąsiorek *et al*. 2021d), by the size of granules on the central portions of paired segmental plates and the pseudosegmental plate IV' (similar to other granules in the dorsum in *P. aquatilis* **sp. nov.** *vs* much larger than other granules in the dorsum in *P. formosus*) and slenderer, higher claws (8.3–10.1 μm in *P. aquatilis* **sp. nov.** *vs* 7.9–8.4 μm in *P. formosus*);
- *P. lacyformis*, described from Norway (Roszkowska *et al*. 2020), by the presence of males (absent in *P. aquatilis* **sp. nov.** *vs* present in *P. lacyformis*) and by the presence of longitudinal fold dividing the scapular plate (absent in *P. aquatilis* **sp. nov.** *vs* present in *P. lacyformis*);

- *P. lalitae*, described from the Azores (Kayastha *et al*. 2020), by the presence of epicuticular ornamentation (absent in *P. aquatilis* **sp. nov.** *vs* present in *P. lalitae*) and slenderer, higher claws (I–III: 8.3–9.7 μm, IV: 9.3–10.1 μm in *P. aquatilis* **sp. nov.** *vs* I–III: 5.4–7.6 μm, IV: 6.5–8.8 μm in *P. lalitae*);
- *P. linnaei* **sp. nov.**, by the shape of the posterior margin of pseudosegmental plate IV' (smooth in *P. aquatilis* **sp. nov.** *vs* with an eminent lobe overlapping with the caudal plate in *P. linnaei* **sp. nov.**);
- *P. shintai*, described from Honshu, Japan (Vončina *et al*. 2020), by the presence of epicuticular ornamentation (absent in *P. aquatilis* **sp. nov.** *vs* present in *P. shintai*);
- *P. suillus* (Ehrenberg, 1853), redescribed from Italy (Grobys *et al*. 2020), by the longer claws (8.3–10.1 μm in *P. aquatilis* **sp. nov.** *vs* 6.3–8.7 μm in *P. suillus*);
- *P. totoro*, described from Taiwan (Gąsiorek *et al*. 2021d), by slenderer, higher claws (8.3–10.1 μm in *P. aquatilis* **sp. nov.** *vs* 6.1–8.0 μm in *P. totoro*);
- *P. xiai*, described from China (Wang *et al*. 2018), by the dorsal sculpturing (more pronounced and denser in *P. xiai* than in *P. aquatilis* **sp. nov.**) and by the presence of males (absent in *P. aquatilis* **sp. nov.** *vs* present in *P. xiai*).

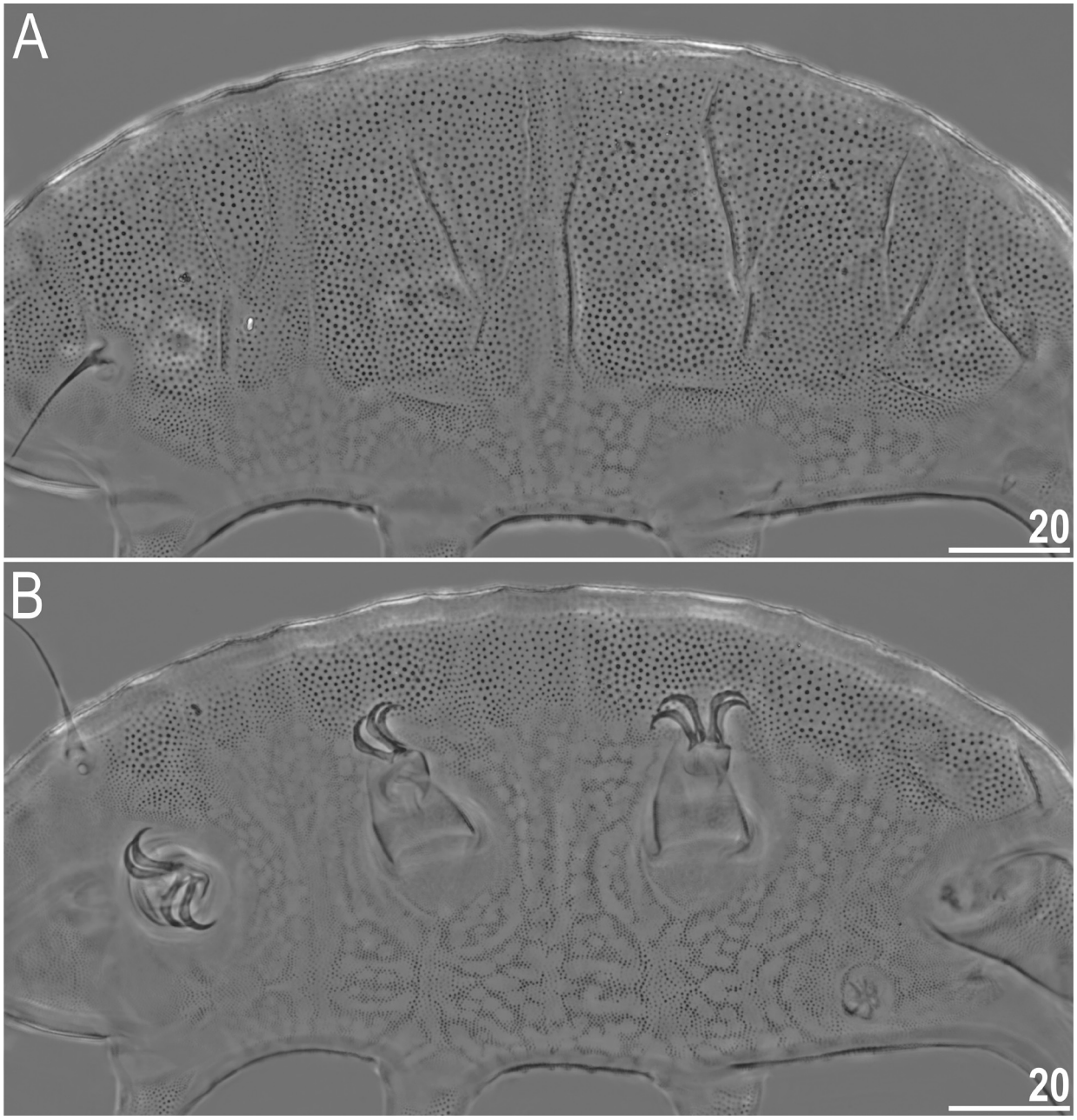

FIGURE 107. Sculpturing of *Pseudechiniscus* (*P.*) *aquatilis* **sp. nov.** (PCM, paratype): A—dorsolateral view, B—ventrolateral view. Scale bars = 20 μm.

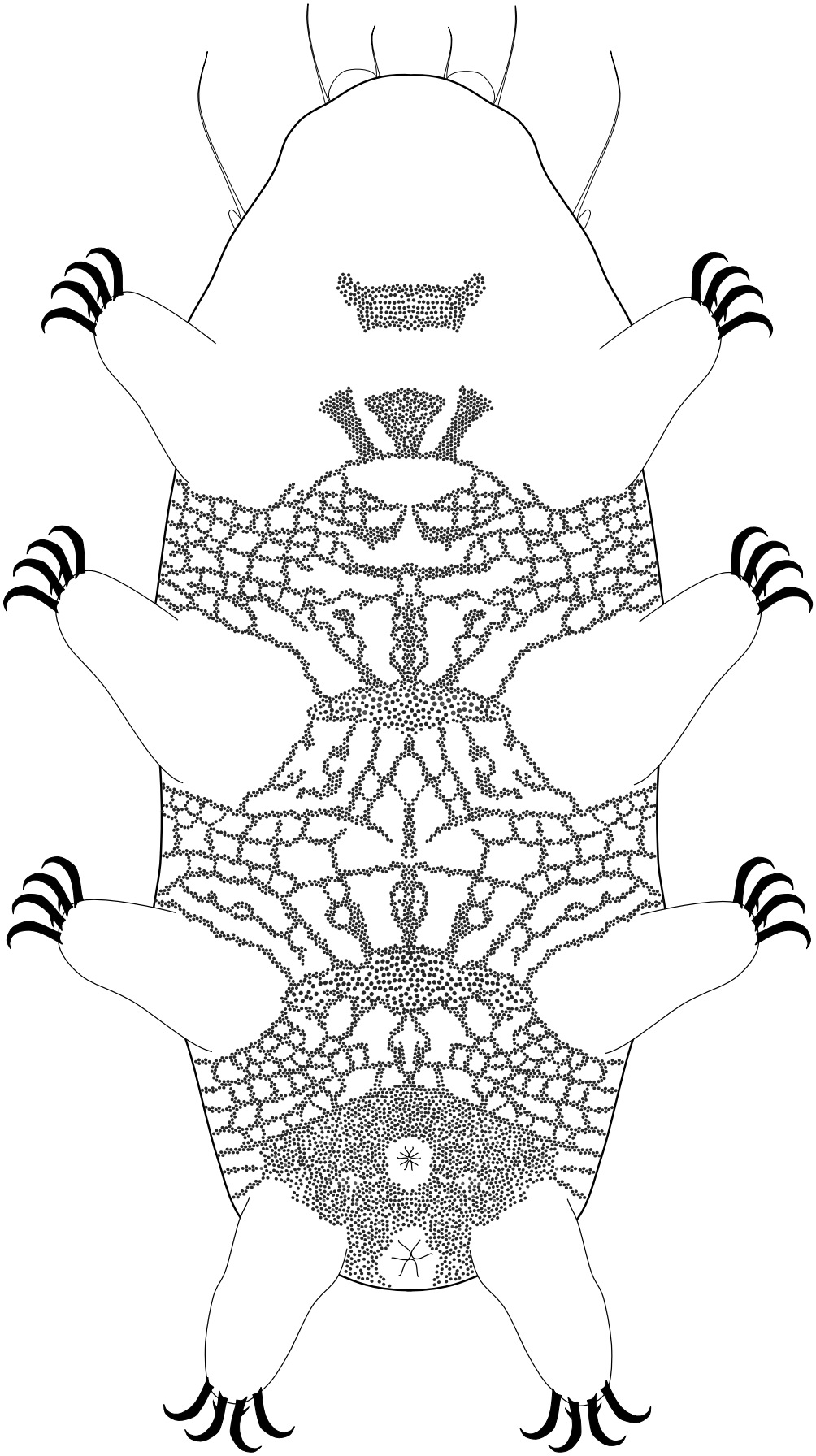

FIGURE 108. Schematic drawing of the venter of *Pseudechiniscus* (*P.*) *aquatilis* **sp. nov.**

Raw measurements. Supplementary Materials (SM.03) and Tardigrada Register (www.tardigrada.net/register/0101.htm).

TABLE 57. Measurements [in µm] of selected morphological structures of the adult females of *Pseudechiniscus aquatilis* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Holotype	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	4	174	–	195	*657*	–	*810*	184	*738*	10	*70*	188	*810*
Scapular plate length	4	23.2	–	26.5		–		25.0	–	1.4	–	23.2	–
Head appendages lengths													
Cirrus *internus*	4	6.9	–	12.7	*27.3*	–	*50.8*	9.7	*38.6*	2.5	*9.7*	8.5	*36.6*
Cephalic papilla	4	2.7	–	4.6	*10.7*	–	*19.8*	3.9	*15.6*	0.8	*3.8*	4.6	*19.8*
Cirrus *externus*	4	11.6	–	15.2	*45.8*	–	*60.8*	13.3	*53.0*	1.9	*6.5*	11.6	*50.0*
Clava	4	3.2	–	4.0	*13.8*	–	*15.1*	3.6	*14.5*	0.3	*0.5*	3.2	*13.8*
Cirrus *A*	4	25.1	–	30.3	*99.2*	–	*121.2*	27.7	*110.9*	2.7	*9.0*	25.8	*111.2*
Cirrus *A*/Body length ratio	4	14%	–	17%		–		15%	–	2%	–	14%	–
Body appendages lengths													
Papilla on leg IV length	4	3.2	–	3.8	*12.1*	–	*15.0*	3.4	*13.6*	0.3	*1.4*	3.4	*14.7*
Claw I heights													
Branch	2	9.2	–	9.5	*38.0*	–	*39.7*	9.4	*38.8*	0.2	*1.2*	9.2	*39.7*
Spur	2	2.1	–	2.6	*9.1*	–	*10.4*	2.4	*9.7*	0.4	*1.0*	2.1	*9.1*
Spur/branch height ratio	2	23%	–	27%		–		25%	–	3%	–	23%	–
Claw II heights													
Branch	4	8.3	–	9.7	*32.8*	–	*39.2*	9.0	*36.2*	0.6	*3.3*	9.1	39.2
Spur	4	1.7	–	2.5	*6.7*	–	*10.0*	2.2	*8.8*	0.4	*1.4*	2.2	*9.5*
Spur/branch height ratio	4	20%	–	27%		–		24%	–	3%	–	24%	–
Claw III heights													
Branch	4	8.9	–	9.6	*35.5*	–	*38.4*	9.2	*37.0*	0.3	*1.7*	8.9	*38.4*
Spur	4	2.0	–	2.6	*7.9*	–	*10.4*	2.2	*8.8*	0.3	*1.1*	2.0	*8.6*
Spur/branch height ratio	4	22%	–	27%		–		24%	–	2%	–	22%	–
Claw IV heights													
Branch	2	9.3	–	10.1	*36.8*	–	*38.1*	9.7	*37.4*	0.6	*1.0*	?	*?*
Spur	2	1.8	–	2.7	*7.1*	–	*10.2*	2.3	*8.7*	0.6	*2.2*	?	*?*
Spur/branch height ratio	2	19%	–	27%		–		23%	–	5%	–	?	–

3. Pseudechiniscus (*Pseudechiniscus*) cf. *ehrenbergi* Roszkowska *et al*., 2020

Pseudechiniscus cf. ehrenbergi in Gąsiorek *et al*. 2021a, d

Figures 109–113, Tables 58–59

Data source:

A total of 275 specimens (174 ♀♀, 34 juveniles and 67 specimens of unknown instar/sex):

- Sample ZA.153: 2 specimens (2 ♀♀ on a slide).
- Sample ZA.157: 16 specimens (12 ♀♀ on slides, and 4 specimens used for DNA extraction, including 2 retrieved as hologenophores); found with *Echiniscus scabrospinosus* and *Pseudechiniscus* (*Meridioniscus*) *wallacei* **sp. nov.**
- Sample ZA.173: 10 specimens (4 juveniles on slides and 6 specimens used for DNA extraction).

- Sample ZA.177: 23 specimens (12 ♀♀ and 11 juveniles on slides); found with *Pseudechiniscus* (*M.*) *wallacei* **sp. nov.**
- Sample ZA.178: 1 specimen (1 ♀ on a slide); found with *Pseudechiniscus* (*M.*) *wallacei* **sp. nov.**
- Sample ZA.183: 30 specimens (14 ♀♀ and 2 juveniles on slides, 10 specimens on SEM stub no. 18.07, and 4 specimens used for DNA extraction); found with *Doryphoribius maasaimarensis*, *Echiniscus oreas* **sp. nov.**, *E. regularis* **sp. nov.**, *E. scabrospinosus*, *Pseudechiniscus* (*M.*) *wallacei* **sp. nov.**, and *Ramazzottius szeptycki.*
- Sample ZA.190: 8 specimens (4 ♀♀ on slides and 4 specimens used for DNA extraction); found with *Echiniscus oreas* **sp. nov.**, *E. scabrospinosus*.
- Sample ZA.202: 89 specimens (55 ♀♀ and 6 juveniles on slides, 20 specimens on SEM stub no. 18.16, and 8 specimens used for DNA extraction); found with *Echiniscus scabrospinosus*.
- Sample ZA.205: 1 specimen (1 ♀ on a slide); found with *Echiniscus longispinosus*.
- Sample ZA.214: 3 specimens (2 ♀♀ and 1 juvenile on slides); found with *Diphascon zaniewi*, *Doryphoribius bindae*, *Echiniscus africanus*, *E. baius*, *E. oreas* **sp. nov.**, *E. perarmatus*, *E. virginicus*, and *Ramazzottius szeptycki*.
- Sample ZA.216: 8 specimens (6 ♀♀ and 2 juveniles on slides); found with *Echiniscus intricatus* **sp. nov.** and *Pseudechiniscus* (*M.*) *wallacei* **sp. nov.**
- Sample ZA.231: 1 specimen (1 ♀ on a slide); found with *Echiniscus scabrospinosus*.
- Sample ZA.246: 9 specimens (9 specimens used for DNA extraction); found with *Hypechiniscus africanus* **sp. nov.**, *Pseudechiniscus* (*P.*) *aquatilis* **sp. nov.**, and *P.* (*M.*) *wallacei* **sp. nov.**
- Sample ZA.249: 3 specimens (2 ♀♀ and 1 juvenile); found with *Echiniscus oreas* **sp. nov.** and *E. regularis* **sp. nov.**
- Sample ZA.254: 1 specimen (1 juvenile on a slide).
- Sample ZA.258: 10 specimens (10 ♀♀ on slides); found with *Echiniscus blumi*, *E. longispinosus*, and *E. oreas* **sp. nov.**
- Sample ZA.259: 2 specimens (2 ♀♀ on slides); found with *Echiniscus pellucidus* and *E. scabrospinosus*.
- Sample ZA.261: 7 specimens (2 ♀♀, 3 juveniles and 2 adults of unknown sex on slides); found with *Bryodelphax* **sp. nov.** and *Pseudechiniscus* (*M.*) *wallacei* **sp. nov.**
- Sample ZA.262: 1 specimen (1 ♀ on a slide).
- Sample ZA.263: 22 specimens (20 ♀♀ and 2 juveniles on slides); found with *Echiniscus longispinosus*, *E. regularis* **sp. nov.**, and *Pseudechiniscus* (*M.*) *wallacei* **sp. nov.**
- Sample ZA.265: 7 specimens (7 ♀♀ on slides); found with *Echiniscus regularis* **sp. nov.** and *E. scabrospinosus*.
- Sample ZA.266: 1 specimen (1 ♀ on a slide); found with *Echiniscus scabrospinosus*.
- Sample ZA.364: 1 specimen (1 juvenile on a slide); found with *Echiniscus perarmatus*, *Pseudechiniscus* (*P.*) *linnaei* **sp. nov.**, and *P.* (*M.*) *wallacei* **sp. nov.**
- Sample ZA.518: 1 specimen (1 ♀ on a slide); found with *Echiniscus dentatus* **sp. nov.**, *E. irroratus* **sp. nov.**, *E. scabrospinosus*, and *Pseudechiniscus* (*M.*) *wallacei* **sp. nov.**
- Sample ZA.524: 6 specimens (6 ♀♀ on slides); found with *Diphascon zaniewi*, *Echiniscus dentatus* **sp. nov.**, and *E. scabrospinosus*.
- Sample ZA.529: 1 specimen (1 ♀ on a slide); found with *Echiniscus merokensis*, *E. scabrospinosus*, and *E. setaceus* **sp. nov.**
- Sample ZA.538: 10 specimens (10 ♀♀ on slides); found with *Echiniscus setaceus* **sp. nov.**
- Sample ZA.540: 1 specimen (1 ♀ on a slide); found with *Echiniscus setaceus* **sp. nov.**

Literature:

- Original description of *Pseudechiniscus* (*P.*) *ehrenbergi*: Roszkowska *et al*. (2020), containing type COI sequences (MN528470).
- Other studies: Cesari *et al*. (2020) with COI sequence from Mongolia (MK804906), Gąsiorek *et al.* (2021a) containing DNA sequences from the Oriental region (Burma, Indonesia, and Vietnam), identified as representing *Pseudechiniscus* (*P.*) cf. *ehrenbergi* (MW031174–5, MW031183–4, MW031186–7, MW031201, MW031215–6).

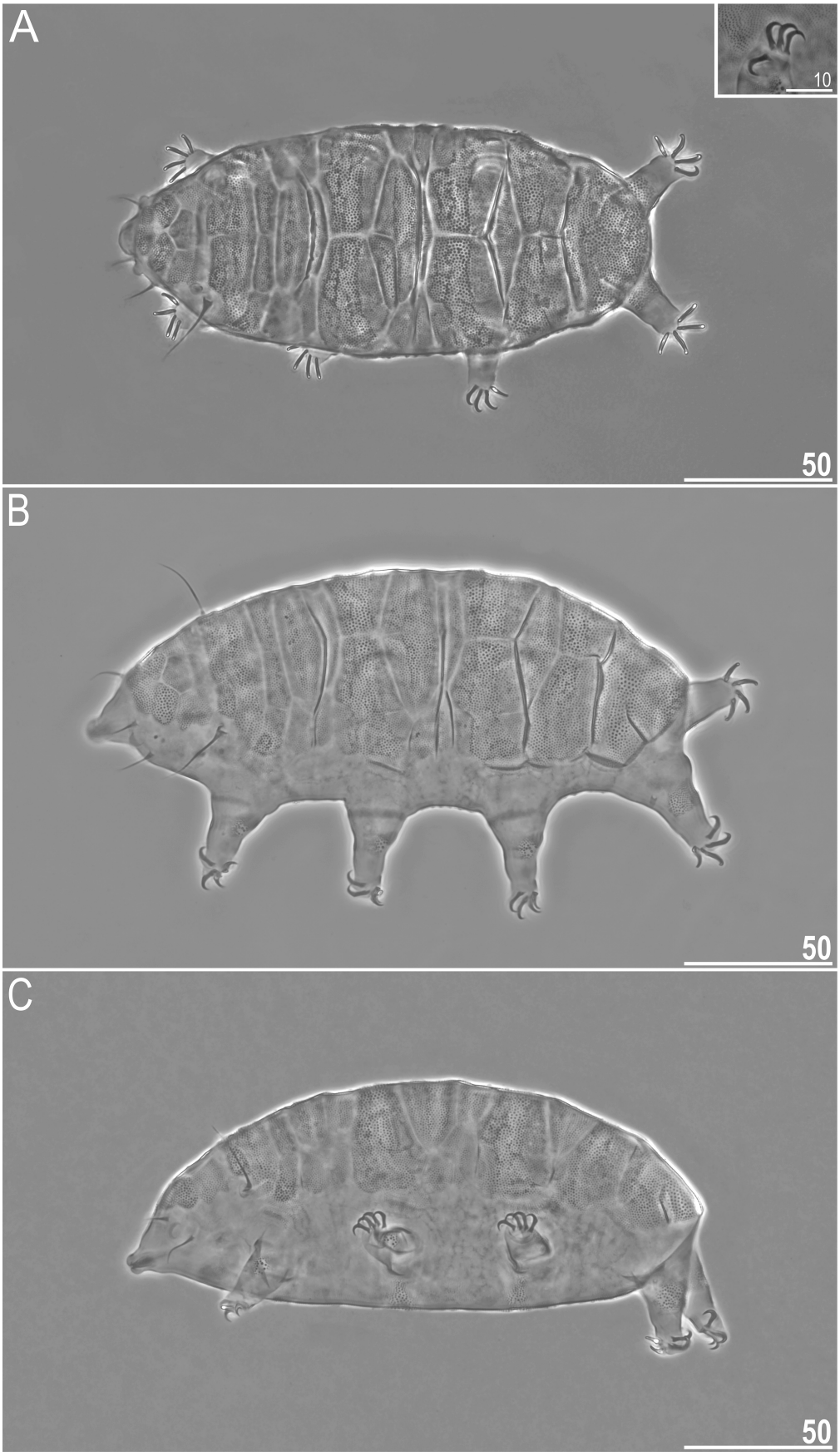

FIGURE 109. Habitus of females of *Pseudechiniscus* (*P.*) cf. *ehrenbergi* (PCM): A—dorsal view (insert shows claws II), B—dorsolateral view, C—lateral view. Scale bars in μm.

Description. Mature females (*i.e*. from the third instar onwards; measurements in Table 58). Body light yellow and elongated (Fig. 109–110), with round black eyes that do not disappear after mounting in Hoyer's medium. Pseudohemispherical cephalic papillae (secondary clavae) and minute (primary) clavae (Fig. 109A, 110, 112A); peribuccal cirri with poorly developed cirrophores. Cirrus *A* short, with cirrophore.

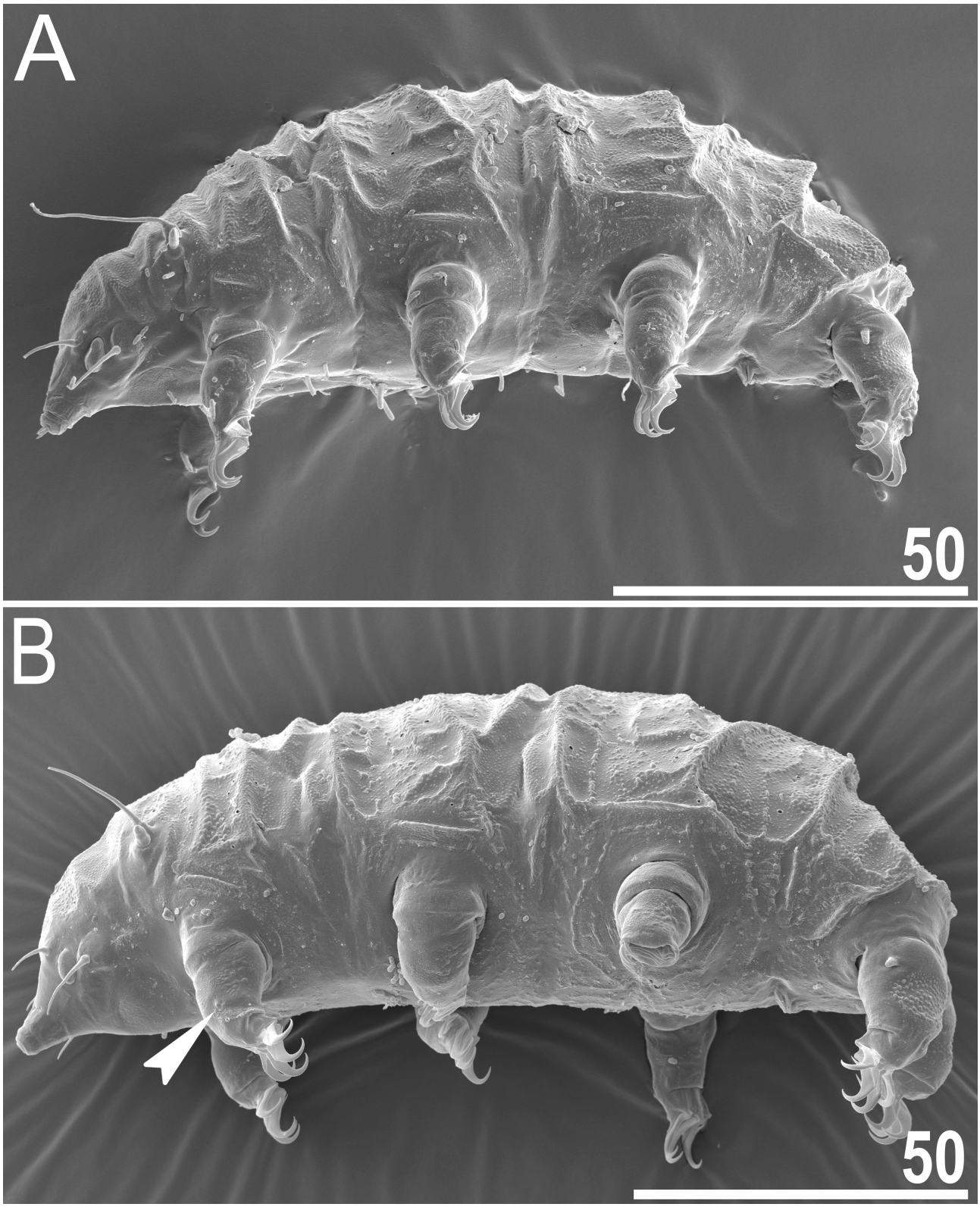

FIGURE 110. Habitus of *Pseudechiniscus* (*P.*) cf. *ehrenbergi* (SEM, females in lateral view; arrowhead indicates the rudimentary receptor on the leg I). Scale bars = 50 µm.

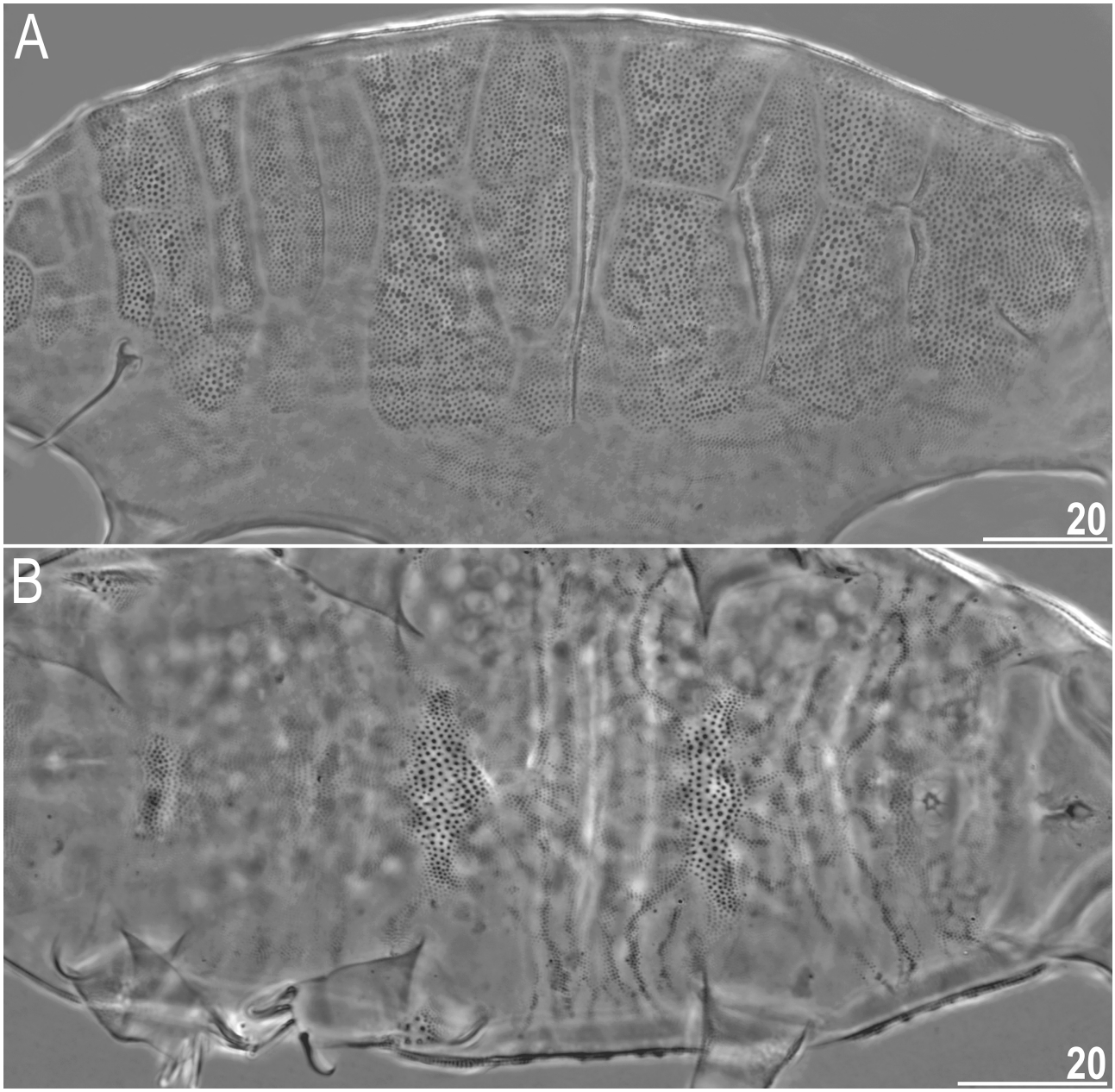

FIGURE 111. Sculpturing of *Pseudechiniscus* (*P.*) cf. *ehrenbergi* (PCM, female): A—dorsolateral view, B—ventral view. Scale bars = 20 μm.

Dorsal plates poorly sclerotised, but well-demarcated, with the *Pseudechiniscus*-type sculpturing, *i.e*. endocuticular pillars protruding under the epicuticle as granules, visible under PCM as dark dots (Fig. 109, 111A) and as granules under SEM (Fig. 110, 112A, C–E); additionally, irregularly distributed pores may be identifiable under SEM (Fig. 110, 112A, D–E). *Striae* absent (Fig. 111A), but epicuticular ornamentation present (Fig. 112C–E) and visible under PCM as a system of dark epicuticular ridges (Fig. 109A, 111A). The cephalic plate hexapartite, with the anteriormost oval portion, two median trapezoid portions, and three posterior, largest portions (Fig. 109A). The cervical (neck) plate absent. The scapular plate with sutures (Fig. 109A, 111A) dividing it into the largest anterior portion and four smaller posterior rectangular facets, with the lateral ones being smaller than internal parts (Fig. 109A, 111A, 112C). Three median plates: m1–2 bipartite, with much reduced posterior portions, m3 unipartite (Fig. 109A, 111A, 112C–E); two pairs of lateral intersegmental platelets flanking the borders of m1–2 (Fig. 110–111A). Two pairs of large segmental plates with a pronounced median longitudinal suture. The pseudosegmental plate IV' divided by a median suture; appendages on the posterior margin of the plate absent. The caudal (terminal) plate with short and weakly developed longitudinal crests (Fig. 109A, 111A, 112E).

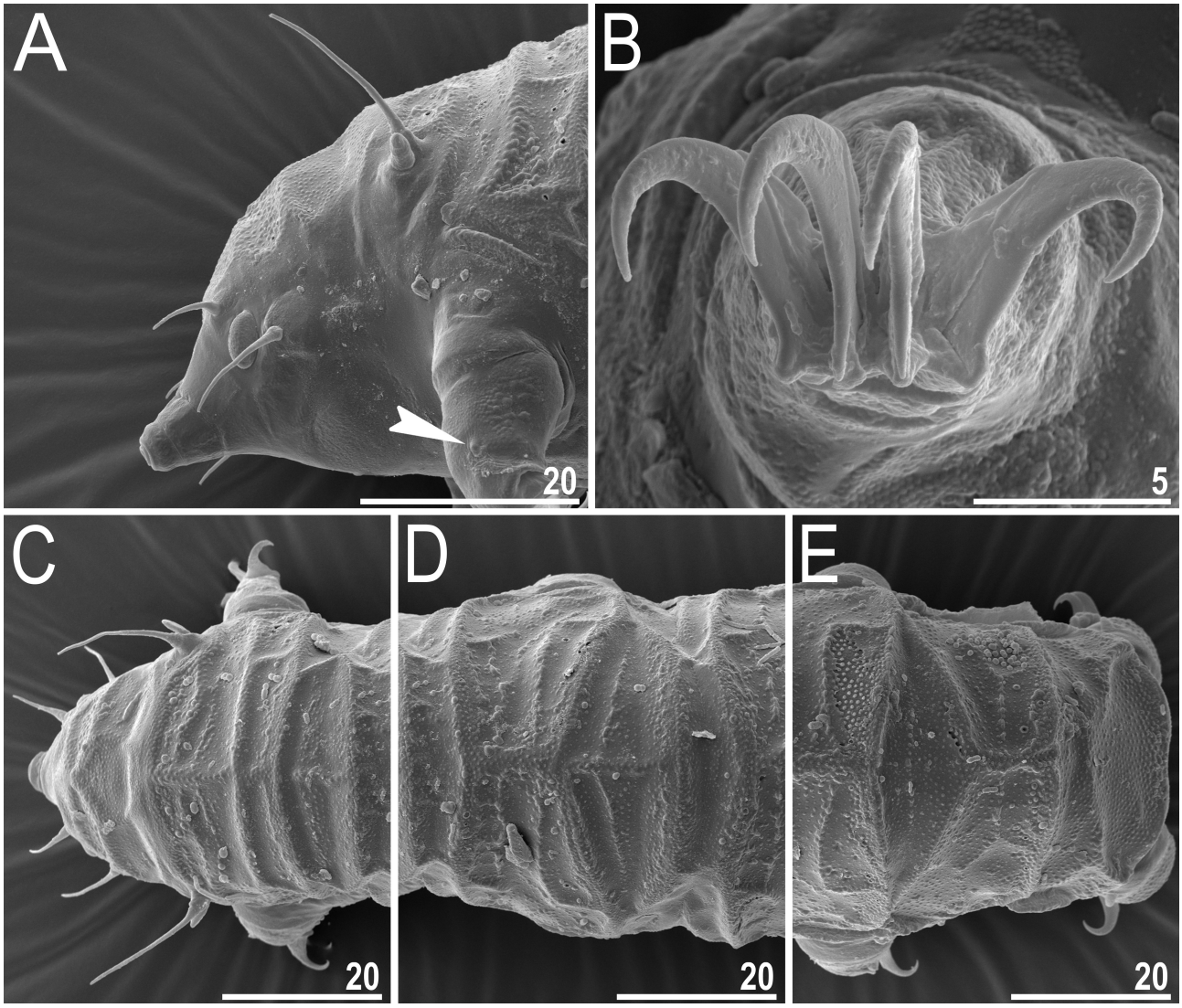

FIGURE 112. Morphology of *Pseudechiniscus* (*P.*) cf. *ehrenbergi* (SEM, females): A—cephalic appendages in lateral view (arrowhead indicates the rudimentary receptor on the leg I), B—claws II, C—anterior portion of the body, D—central portion of the body, E—posterior portion of the body. Scale bars in μm.

Ventral cuticle with a faint species-specific pattern reaching the lateroventral sides of the body (Fig. 110, 111B), but usually only the accumulations of pillars at the level of legs I–III and in the genital zone are visible, not reaching the anal zone (Fig. 113). Ventral epicuticular thickenings absent. Sexpartite gonopore located anteriorly of legs IV and a trilobed anus between legs IV.

Pedal plates and dentate collar IV absent, instead large patches of pillars are present centrally on each leg. Pulvini weakly developed. A minuscule papilla on leg I present and visible only under SEM (Fig. 112A), and a papilla on leg IV present (Fig. 110). Claws I–IV similar in size, short and delicate (Fig. 109A, insert, 112B). All external claws spurless. All internal claws with minute, thin spurs positioned at *ca.* 20–25% of the claw height.

Juveniles (*i.e*. from the second instar onwards; measurements in Table 59). The morphometric gap between juveniles and adult females does not exist, juveniles are similar to adults beside of the lack of the gonopore.

DNA markers and phylogenetic position. The species stays in polytomy with three Asian species (*P. asper* Abe *et al*., 1998, *P. shintai*, *P. totoro*) and two undescribed species from the Madagascan and Nearctic regions (*P*. sp. 12–13) (Fig. 119).

Geographic distribution. Originally described from Italy (Roszkowska *et al.* 2020), and with a genetically verified record from Mongolia (Cesari *et al*. 2020). Populations ascribed to *Pseudechiniscus* (*P.*) cf. *ehrenbergi* were found in numerous locations in South Africa (Fig. 120N), but also in East Asia (specifically in Burma, Indonesia, and Vietnam; see Gąsiorek *et al.* 2021a for details).

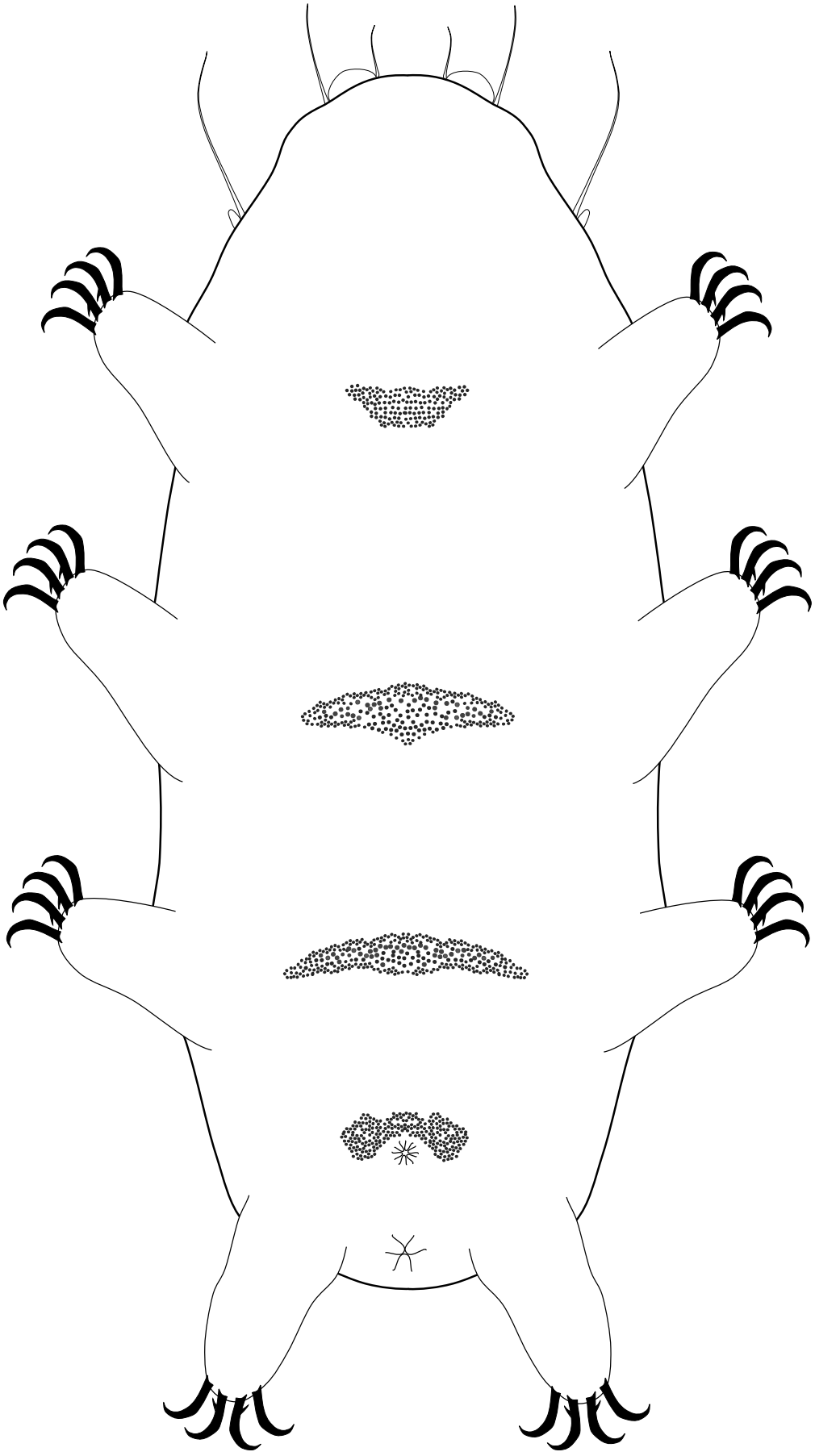

FIGURE 113. Schematic drawing of the venter of *Pseudechiniscus* (*P.*) cf. *ehrenbergi*.

Remarks. We noted that there is a considerable variability in the ventral sculpturing patterns between populations of otherwise genetically close populations of *P. ehrenbergi*. This requires further studies to ascertain whether these populations constitute indeed a single, widely distributed species or a complex of closely related taxa, each with a limited geographic range. Hence, we have provided a cautious identification for the South African records.

Raw measurements. Supplementary Materials (SM.03).

TABLE 58. Measurements [in µm] of selected morphological structures of the adult females of *Pseudechiniscus* cf. *ehrenbergi* mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Holotype	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	20	146	–	200	*626*	–	*889*	176	*733*	15	*66*	179	*747*
Scapular plate length	20	21.1	–	26.7		–		24.1	–	1.3	–	24.0	–
Head appendages lengths													
Cirrus *internus*	19	4.7	–	8.7	*19.8*	–	*34.6*	7.1	*29.4*	0.9	*3.7*	7.0	*29.2*
Cephalic papilla	20	2.6	–	5.0	*10.3*	–	*19.6*	3.9	*16.0*	0.6	*2.4*	4.7	*19.6*
Cirrus *externus*	20	8.9	–	13.7	*36.8*	–	*55.5*	10.9	*45.1*	1.4	*5.0*	11.2	*46.7*
Clava	20	4.0	–	5.4	*16.1*	–	*22.7*	4.7	*19.5*	0.5	*1.7*	4.0	*16.7*
Cirrus *A*	17	17.5	–	30.8	*73.8*	–	*125.7*	23.1	*95.1*	2.8	*11.1*	24.0	*100.0*
Cirrus *A*/Body length ratio	17	11%	–	16%		–		13%	–	2%	–	13%	–
Body appendages lengths													
Papilla on leg IV length	20	1.7	–	4.5	*7.1*	–	*17.8*	3.2	*13.3*	0.6	*2.2*	1.7	*7.1*
Claw I heights													
Branch	18	7.1	–	8.9	*29.3*	–	*37.1*	8.0	*33.2*	0.6	*1.8*	7.7	*32.1*
Spur	17	0.9	–	1.8	*3.7*	–	*7.1*	1.4	*5.7*	0.3	*1.1*	1.2	*5.0*
Spur/branch height ratio	17	9%	–	22%		–		17%	–	3%	–	16%	–
Claw II heights													
Branch	18	6.8	–	8.7	*29.2*	–	*36.3*	7.9	*32.7*	0.6	*2.0*	8.1	*33.8*
Spur	16	1.0	–	1.8	*3.9*	–	*7.3*	1.3	*5.5*	0.3	*1.2*	1.7	*7.1*
Spur/branch height ratio	16	11%	–	22%		–		17%	–	3%	–	21%	–
Claw III heights													
Branch	17	6.9	–	9.0	*28.5*	–	*39.1*	8.1	*33.2*	0.7	*2.7*	8.0	33.3
Spur	16	0.9	–	2.1	*3.5*	–	*8.6*	1.4	*5.9*	0.3	*1.3*	1.2	*5.0*
Spur/branch height ratio	16	11%	–	26%		–		18%	–	3%	–	15%	–
Claw IV heights													
Branch	12	7.4	–	9.8	*30.6*	–	*40.6*	8.9	*37.1*	0.8	*3.3*	?	*?*
Spur	12	1.2	–	2.1	*4.9*	–	*9.0*	1.6	*6.7*	0.3	*1.3*	?	*?*
Spur/branch height ratio	12	12%	–	22%		–		18%	–	3%	–	?	–

TABLE 59. Measurements [in µm] of selected morphological structures of the juveniles of *Pseudechiniscus* cf. *ehrenbergi* mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD	
		µm			*sp*			µm	*sp*	µm	*sp*
Body length	5	142	–	151	*715*	–	*771*	145	*743*	4	*21*
Scapular plate length	5	19.1	–	20.1		–		19.5	–	0.4	–
Head appendages lengths											
Cirrus *internus*	5	5.0	–	5.8	*26.2*	–	*29.2*	5.5	*28.1*	0.3	1.3
Cephalic papilla	5	2.3	–	3.2	*11.6*	–	*16.5*	2.6	*13.5*	0.4	*2.0*
Cirrus *externus*	5	7.6	–	10.3	*39.8*	–	*51.2*	9.0	*46.0*	1.1	*5.0*
Clava	5	3.0	–	4.0	*15.6*	–	*20.6*	3.7	*18.7*	0.4	*1.9*
Cirrus *A*	5	14.4	–	18.7	*74.2*	–	*97.9*	17.3	*88.6*	1.7	*8.9*
Cirrus *A*/Body length ratio	5	10%	–	13%		–		12%	–	1%	–
Body appendages lengths											
Papilla on leg IV length	5	2.0	–	3.1	*10.1*	–	*16.0*	2.6	*13.4*	0.5	2.4
Claw I heights											
Branch	5	6.3	–	7.9	*33.0*	–	*39.3*	7.0	*35.9*	0.6	2.8
Spur	4	1.0	–	1.3	*5.0*	–	*6.7*	1.1	*5.8*	0.2	*0.8*
Spur/branch height ratio	4	13%	–	19%		–		16%	–	2%	–
Claw II heights											
Branch	4	5.4	–	7.0	*27.1*	–	*36.5*	6.4	*32.8*	0.7	*4.1*
Spur	3	1.0	–	1.4	*5.2*	–	*7.2*	1.1	*5.9*	0.2	*1.2*
Spur/branch height ratio	3	14%	–	21%		–		17%	–	3%	–
Claw III heights											
Branch	4	5.7	–	7.6	*28.6*	–	*38.0*	6.9	*35.3*	0.8	*4.5*
Spur	2	1.0	–	1.1	*5.2*	–	*5.5*	1.1	*5.3*	0.1	0.2
Spur/branch height ratio	2	14%	–	14%		–		14%	–	1%	–
Claw IV heights											
Branch	4	8.0	–	8.5	*41.9*	–	*43.8*	8.3	*42.5*	0.3	*0.9*
Spur	4	1.0	–	1.6	*5.0*	–	*8.2*	1.3	*6.4*	0.3	*1.4*
Spur/branch height ratio	4	12%	–	19%		–		15%	–	3%	–

4. Pseudechiniscus (*Pseudechiniscus*) *linnaei* sp. nov. Vončina, Gąsiorek, Morek & Michalczyk

Pseudechiniscus sp. 10 in Gąsiorek *et al*. 2021a, d

urn:lsid:zoobank.org:act:C6549A50-8286-4E04-8517-F946C11FFCB5

Figures 114–116, Tables 60–61

Data source:

A total of 28 specimens (16 ♀♀, 6 ♂♂, 1 juvenile, 1 larva, and 4 specimens of unknown instar/sex):

- Sample ZA.364: 2 specimens (2 ♀♀ on a slide); found with *Echiniscus perarmatus*, *Pseudechiniscus* (*P.*) cf. *ehrenbergi*, and *P.* (*M.*) *wallacei* **sp. nov.**
- Sample ZA.366: 8 specimens (4 ♀♀ and 4 specimens used for DNA extraction); found with *Echiniscus scabrospinosus* and *E. virginicus*.
- Sample ZA.367: 18 specimens (10 ♀♀, 6 ♂♂, 1 juvenile and 1 larva on slides); found with *Echiniscus scabrospinosus*, and *Ramazzottius szeptycki*.

Description. Mature females (*i.e*. from the third instar onwards; measurements in Table 60). Body orange and elongated (Fig. 114A), with ovoid black eyes that do not disappear after mounting in Hoyer's medium. Pseudohemispherical cephalic papillae (secondary clavae) and minute (primary) clavae (Fig. 114A, 115A); peribuccal cirri with poorly developed cirrophores. Cirrus *A* short, with cirrophore.

Dorsal plates poorly sclerotised, but well-demarcated, with the *Pseudechiniscus*-type sculpturing, *i.e*. endocuticular pillars protruding under the epicuticle, visible under PCM as dark dots (Fig. 115A). *Striae* and epicuticular ornamentation absent. The cephalic plate tetrapartite, with the anterior bi-halved portion and three posterior portions, all roughly equal in size (Fig. 114A). The cervical (neck) plate absent. The scapular plate with sutures, separating less (Fig. 114A) or more (Fig. 115A) delineated anterior facets, and more elongated rectangular posterior facets. Three median plates: m1–2 bipartite, with much reduced, narrow posterior portions, m3 unipartite (Fig. 114A, 115A); the anterior portion of m2 with an incomplete suture; two pairs of lateral intersegmental platelets flanking the boarders of m1–2. Two pairs of large segmental plates with well-delineated median longitudinal suture. Paired segmental plate II with sutures on both anterior and posterior margins (Fig. 115A). The pseudosegmental plate IV' divided by a median suture; the posterior margin of the plate with a broadened lobe overlapping with the caudal plate (Fig. 114A, 115A). The caudal (terminal) plate with long and evident longitudinal crests bifurcating in the proximity of the anterior margin of the plate (Fig. 114A, 115A).

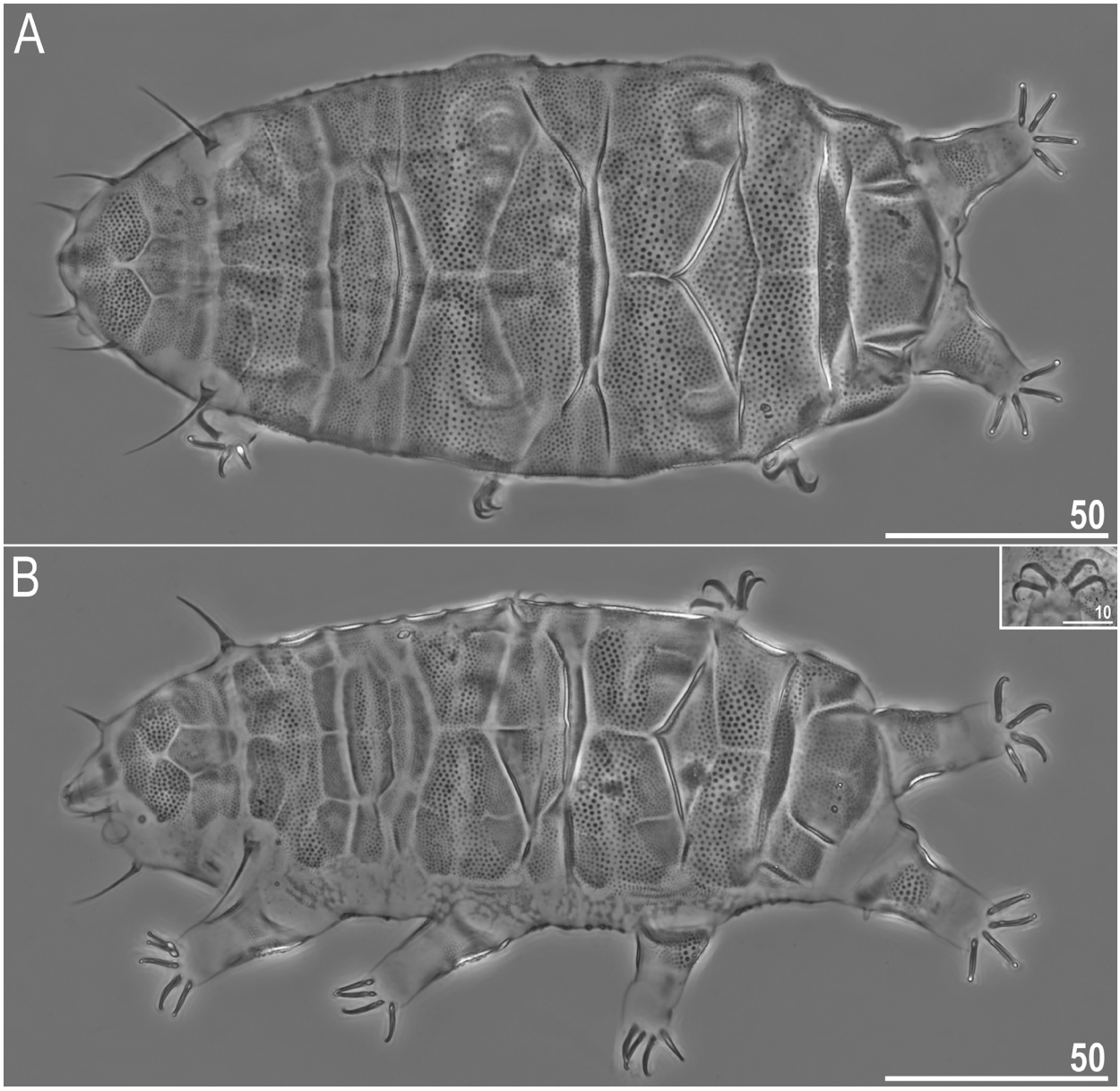

FIGURE 114. Habitus of *Pseudechiniscus* (*P.*) *linnaei* **sp. nov.** (PCM): A—holotype, female in dorsal view, B—allotype, male in dorsolateral view (insert shows claws II). Scale bars in µm.

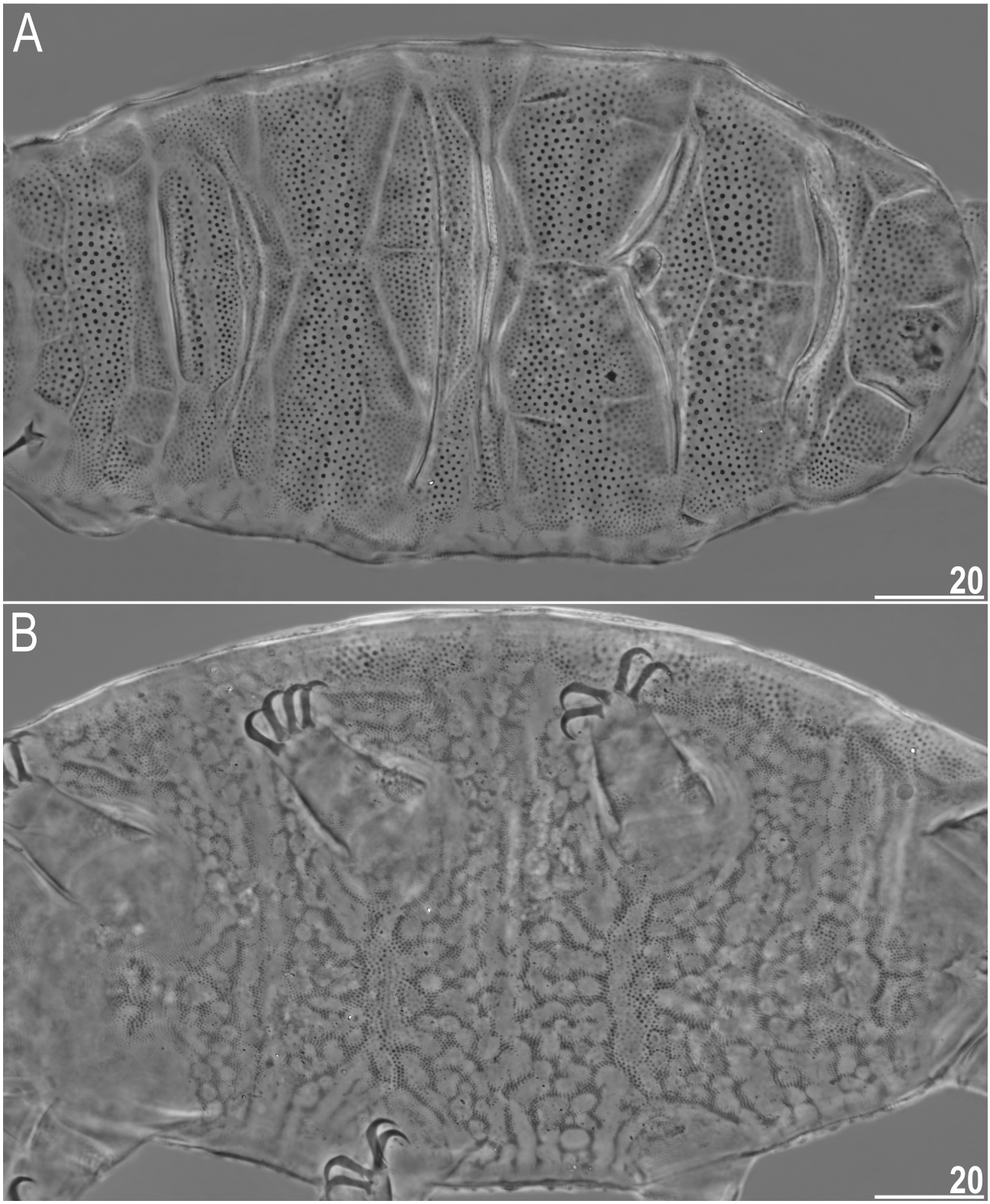

FIGURE 115. Sculpturing of *Pseudechiniscus* (*P.*) *linnaei* **sp. nov.** (PCM, paratype): A—dorsal view, B—ventral view. Scale bars = 20 μm.

Ventral cuticle with a pronounced species-specific pattern reaching the lateroventral sides of the body (Fig. 115B–116), being a typical *reticulum*; epicuticular thickenings absent. Sexpartite gonopore located anteriorly of legs IV and a trilobed anus between legs IV.

Pedal plates and dentate collar IV absent, but large patches of pillars are present centrally on each leg. Pulvini

weakly developed. A papilla on leg I absent and a papilla on leg IV present. Claws I–IV similar in size, short and delicate (Fig. 114B, insert). All external claws spurless. All internal claws with minute, thin spurs positioned at *ca.* 25% of the claw height.

Mature males (*i.e*. from the second instar onwards; measurements in Table 61). Dorsal plates more sclerotised than in females (Fig. 114B). Gonopore circular.

Juveniles (*i.e*. the second instar). Phenotypically like females, beside of the lacking gonopore. Morphometric data for the single found juvenile: body length 146 µm, the scapular plate length 18.1 µm; cephalic appendages: *cirrus internus* 5.8 µm, cephalic papilla 3.7 µm, *cirrus externus* 10.3 µm, (primary) clava 3.4 µm, cirrus *A* 17.8 µm; papilla IV length: 2.7 µm; claw heights 6.0–6.3 µm, claw spurs 1.0–1.2 µm.

Larvae (*i.e*. the first instar). The distinction between dorsal plates blurred. No gonopore and anus. Morphometric data for the single found larva: body length 126 µm, the scapular plate length 17.3 µm; cephalic appendages: *cirrus internus* 5.2 µm, cephalic papilla 2.7 µm, *cirrus externus* 7.2 µm, (primary) clava 2.8 µm, cirrus *A* 13.9 µm; papilla IV length: 2.0 µm; claw heights 6.1–6.8 µm, claw spurs 1.5–1.8 µm.

DNA markers and phylogenetic position. The species is the sister taxon to *P.* (*P.*) *aquatilis* **sp. nov.** (Fig. 119; p-distance = 2.9% in ITS-1).

Type material. 10 ♀♀, 6 ♂♂, 1 juvenile and 1 larva on slides ZA.367.01–4; holotype: mature ♀ on slide ZA.367.02, allotype: mature ♂ on slide ZA.367.03. Mounted together with 5 ♀♀ and 1 juvenile of *E. scabrospinosus*. 4 specimens used for DNA extraction.

Type locality. 33°20’0.06”S, 26°32’41.28”E, 690 m asl: Republic of South Africa, Eastern Cape, vicinity of Grahamstown; shrubland, lichen from tree branch (sample ZA.367).

Etymology. The name honours Carl von Linné, the inventor of modern biological systematics. A noun in the genitive singular.

Geographic distribution. Recorded only from two localities in South Africa (Fig. 120N).

Remarks. None.

Differential diagnosis. The species can be distinguished from other *Pseudechiniscus* spp. inhabiting South Africa based on the pattern of ventral sculpturing. See above for the distinction with other members of the subgenus *Pseudechiniscus*. Moreover, it differs from:

- *P. beasleyi*, by the wide lobe on the pseudosegmental plate IV’ (present in *P. linnaei* **sp. nov.** *vs* absent in *P. beasleyi*);
- *P. chengi*, by the wide lobe on the pseudosegmental plate IV’ (present in *P. linnaei* **sp. nov.** vs absent in *P. chengi*);
- *Pseudechinicus ehrenbergi*, by presence of the papillae on the leg I (absent in *P. linnaei* **sp. nov.** *vs* rudimentarily developed in *P. ehrenbergi*) and by the subdivision of the scapular plate (without the median longitudinal suture in *P. linnaei* **sp. nov**. *vs* with the median longitudinal suture in *P. ehrenbergi*);
- *P. formosus*, by the wide lobe on the pseudosegmental plate IV’ (present in *P. linnaei* **sp. nov.** *vs* absent in *P. formosus*);
- *P. lacyformis*, by the wide lobe on the pseudosegmental plate IV’ (present in *P. linnaei* **sp. nov.** *vs* absent in *P. lacyformis*);
- *P. lalitae*, by the wide lobe on the pseudosegmental plate IV’ (present in *P. linnaei* **sp. nov.** *vs* absent in *P. lalitae*), the cirrus *A*/body length ratio (12–15% in *P. linnaei* **sp. nov.** *vs* 13–20% in *P. lalitae*), and higher claws (8.1–12.4 µm in *P. linnaei* **sp. nov.** *vs* 5.4–8.8 µm in *P. lalitae*);
- *P. shintai*, by the presence of epicuticular ornamentation (absent in *P. linnaei* **sp. nov.** *vs* present in *P. shintai*);
- *P. suillus*, by the body length (181–235 µm in adult females of *P. linnaei* **sp. nov.** *vs* 142–186 µm in adult females in *P. suillus*), and by the claw lengths (8.1–12.4 µm in adult females of *P. linnaei* **sp. nov.** *vs* 5.8–8.7 µm in *P. suillus*);
- *P. totoro*, by the body length (181–235 µm in adult females of *P. linnaei* **sp. nov.** *vs* 141–170 µm in adult females in *P. totoro*), the cirrus *A*/body length ratio (12–15% in *P. linnaei* **sp. nov.** *vs* 14–20% in *P. totoro*), and higher claws (8.1–12.4 µm in *P. linnaei* **sp. nov.** *vs* 6.1–8.0 µm in *P. totoro*);
- *P. xiai*, by the wide lobe on the pseudosegmental plate IV’ (present in *P. linnaei* **sp. nov.** *vs* absent in *P. xiai*), and by the subdivision of the pseudosegmental plate IV’ (divided in *P. linnaei* **sp. nov.** *vs* undivided in *P. xiai*).

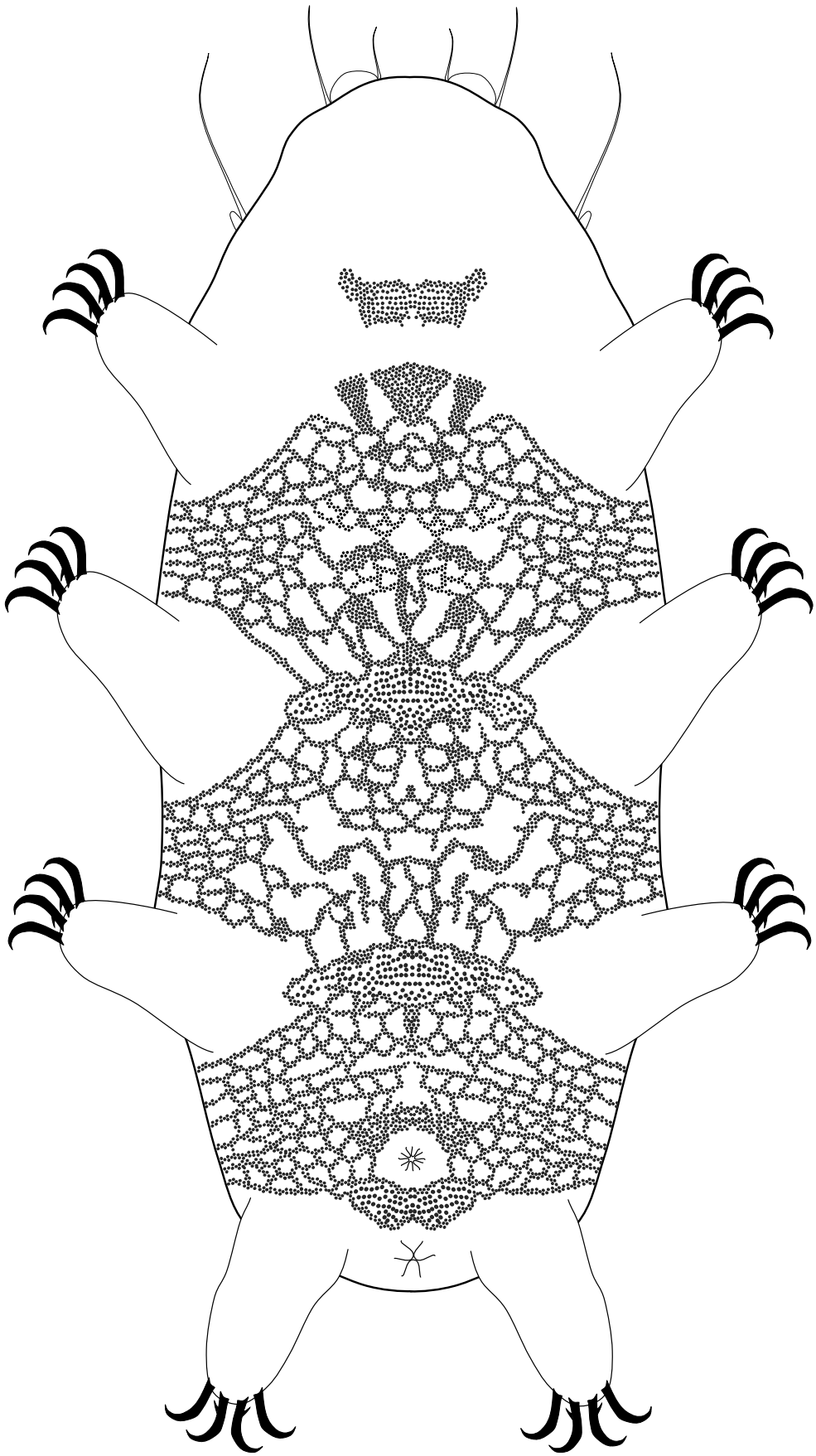

FIGURE 116. Schematic drawing of the venter of *Pseudechiniscus* (*P.*) *linnaei* **sp. nov.**

Raw measurements. Supplementary Materials (SM.03) and Tardigrada Register (www.tardigrada.net/register/0102.htm).

TABLE 60. Measurements [in µm] of selected morphological structures of the adult females of *Pseudechiniscus linnaei* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Holotype	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	10	181	–	235	*693*	–	*787*	207	*737*	17	*34*	203	*703*
Scapular plate length	10	23.1	–	32.8		–		28.1	–	2.7	–	28.8	–
Head appendages lengths													
Cirrus *internus*	9	8.2	–	12.0	*29.2*	–	*42.7*	10.7	*38.8*	1.4	*4.2*	11.8	*41.0*
Cephalic papilla	10	3.7	–	5.5	*11.3*	–	*20.3*	4.6	*16.6*	0.6	*3.1*	3.8	*13.2*
Cirrus *externus*	9	13.7	–	18.0	*47.6*	–	*63.7*	16.0	*56.7*	1.5	*4.6*	13.7	*47.6*
Clava	10	3.6	–	5.7	*12.4*	–	*17.7*	4.4	*15.5*	0.6	*1.9*	4.2	*14.6*
Cirrus *A*	8	23.7	–	29.2	*82.3*	–	*109.5*	26.6	*96.1*	1.9	*7.9*	23.7	*82.3*
Cirrus *A*/Body length ratio	8	12%	–	14%		–		13%	–	1%	–	12%	–
Body appendages lengths													
Papilla on leg IV length	10	3.2	–	4.4	*11.4*	–	*14.6*	3.7	*13.2*	0.4	*1.1*	3.5	*12.2*
Claw I heights													
Branch	8	9.0	–	11.2	*33.5*	–	*39.0*	10.3	*36.5*	0.7	*1.9*	?	*?*
Spur	8	2.2	–	2.8	*7.3*	–	*10.0*	2.5	*8.9*	0.2	*0.9*	?	*?*
Spur/branch height ratio	8	22%	–	101%		–		24%	–	2%	–	?	–
Claw II heights													
Branch	10	8.1	–	10.9	*30.5*	–	*36.6*	9.8	*34.8*	0.9	*2.0*	9.2	*31.9*
Spur	10	1.9	–	2.6	*6.7*	–	*11.3*	2.3	*8.1*	0.2	*1.3*	2.2	*7.6*
Spur/branch height ratio	10	20%	–	32%		–		23%	–	3%	–	24%	–
Claw III heights													
Branch	9	8.8	–	11.2	*30.9*	–	*39.0*	9.8	*35.0*	0.9	*2.5*	8.9	*30.9*
Spur	9	2.0	–	2.7	*6.9*	–	*11.7*	2.4	*8.7*	0.2	*1.4*	2.0	6.9
Spur/branch height ratio	9	21%	–	30%		–		25%	–	3%	–	22%	–
Claw IV heights													
Branch	4	9.8	–	12.4	*38.8*	–	*42.4*	11.2	*40.7*	1.1	*1.6*	?	*?*
Spur	4	2.3	–	3.2	*8.3*	–	*11.0*	2.7	*9.7*	0.4	*1.1*	?	*?*
Spur/branch height ratio	4	21%	–	28%		–		24%	–	3%	–	?	–

Incertae sedis

5. Pseudechiniscus (*Pseudechiniscus*) *bispinosus* (Murray, 1907)

Literature:

- Original description: Murray (1907a).

Geographic distribution. Recorded only in South Africa (Murray 1907a) and Brazil (Rahm 1931, 1932), although the South American record needs to be verified under modern taxonomic standards.

Remarks. *Pseudechiniscus* embraces two monophyletic subgenera: *Pseudechiniscus* (the former *suillus-facettalis* group) and *Meridioniscus* (the former *novaezeelandiae* group) (Cesari *et al*. 2020; Tumanov 2020b; Gąsiorek *et al*. 2021a). According to the current diagnosis of the genus (Gąsiorek *et al*. 2021a), only cephalic cirri are present, thus the two species with filamentous/long trunk appendages, *P. pulcher* from Australia and *P. bispinosus* from South Africa, should be transferred from *Pseudechiniscus* either to *Antechiniscus* (*P. pulcher*; see Claxton 2004; Tumanov 2020b) or to another (probably new) genus (*P. bispinosus*; see Gąsiorek *et al*. 2021a). The drawing from Murray (1907a) leaves no doubt that *P. bispinosus* has the pseudosegmental plate IV' between the paired segmental plate II and the caudal plate, *i.e*. it is a *Pseudechiniscus*-like echiniscid. Unfortunately, animals fitting the description were not found in our samples, confirming Murray's observation that *P. bispinosus* is rare.

TABLE 61. Measurements [in µm] of selected morphological structures of the adult males of *Pseudechiniscus linnaei* **sp. nov.** mounted in Hoyer's medium. N—number of specimens/structures measured, RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation; *sp*—the proportion between the length of a given structure and the length of the scapular plate.

CHARACTER	N	RANGE						MEAN		SD		Allotype	
		µm			*sp*			µm	*sp*	µm	*sp*	µm	*sp*
Body length	6	168	–	203	*677*	–	*789*	183	*734*	13	*43*	186	789
Scapular plate length	6	23.6	–	26.9		–		25.0	–	1.2	–	23.6	–
Head appendages lengths													
Cirrus *internus*	4	9.5	–	12.1	*38.3*	–	*46.2*	10.7	*42.9*	1.1	*3.5*	10.9	*46.2*
Cephalic papilla	6	5.3	–	6.6	*21.4*	–	*27.3*	5.9	*23.8*	0.6	*2.2*	5.6	*23.7*
Cirrus *externus*	4	16.1	–	17.0	*63.2*	–	*69.1*	16.4	*66.3*	0.4	*2.5*	16.3	*69.1*
Clava	6	5.0	–	5.9	*19.3*	–	*25.0*	5.3	*21.4*	0.3	*2.1*	5.9	*25.0*
Cirrus *A*	6	22.3	–	28.1	*89.6*	–	*109.3*	24.4	*97.7*	2.0	*6.6*	22.3	*94.5*
Cirrus *A*/Body length ratio	6	12%	–	15%		–		13%	–	1%	–	12%	–
Body appendages lengths													
Papilla on leg IV length	6	3.5	–	4.4	*14.5*	–	*17.1*	3.9	*15.5*	0.3	*1.0*	3.5	*14.8*
Claw I heights													
Branch	4	9.1	–	10.7	*36.7*	–	*45.3*	10.2	*40.9*	0.7	*3.8*	10.7	*45.3*
Spur	4	2.3	–	2.8	*9.3*	–	*10.4*	2.5	*9.8*	0.2	*0.5*	2.3	*9.7*
Spur/branch height ratio	4	21%	–	27%		–		24%	–	2%	–	21%	–
Claw II heights													
Branch	3	10.4	–	11.2	*41.6*	–	*44.1*	10.8	*43.2*	0.4	*1.4*	10.4	*44.1*
Spur	3	2.4	–	2.6	*9.3*	–	*10.5*	2.5	*10.0*	0.1	*0.6*	2.4	*10.2*
Spur/branch height ratio	3	22%	–	24%		–		23%	–	1%	–	23%	–
Claw III heights													
Branch	3	10.0	–	10.5	*39.0*	–	*43.0*	10.3	*40.8*	0.3	*2.0*	?	*?*
Spur	3	2.6	–	2.6	*9.7*	–	*10.7*	2.6	*10.3*	0.0	*0.6*	?	*?*
Spur/branch height ratio	3	25%	–	26%		–		25%	–	1%	–	?	–
Claw IV heights													
Branch	0		?			?		?	*?*	?	*?*	?	*?*
Spur	0		?			?		?	*?*	?	*?*	?	*?*
Spur/branch height ratio	0		?			–		?	–	?	–	?	–

Diagnostic key to the formally described Echiniscidae recorded to date in South Africa

The key refers to adults (females and males treated collectively). The majority of the representatives of the *Echiniscus spinulosus* complex are extremely similar to each other, thus we advise utmost caution when identifying these species (*i.e*. an observation of many individuals is needed).

1. Cirri *A* horn-shaped (Fig. 121B), cephalic papillae hemispherical (Fig. 123C) pseudosegmental plate IV' with posterior projections in the form of clearly delineated lobes (not a thickened posterior margin) or spines (Fig. 122D), found only in terrestrial moss samples with large amounts of soil. . . . . *Cornechiniscus madagascariensis* (Figs 6–8)
-. Cirri *A* filamentous (Fig. 121A), cephalic papillae dactyloid (Fig. 123A) or pseudohemispherical (Fig. 123B), pseudosegmental plate IV' absent (Fig. 122B) or only with a slightly broadened posterior edge (Fig. 122C), found mostly in moss and lichen samples without a significant admixture of soil 2
2(1). Pseudosegmental plate IV' present 3
-. Pseudosegmental plate IV' absent 7
3(2). Long flexible spine *C* present . . . . . *Pseudechiniscus bispinosus*
-. Trunk unappendaged 4
4(3). Dactyloid cephalic papillae (Fig. 123A) . . . . . *Pseudechiniscus* (*M.*) *wallacei* (Figs 101–105)
-. Pseudohemispherical cephalic papillae (Fig. 123B) 5
5(4). Epicuticular ornamentation in the form of dark belts visible under PCM (Fig. 124C) . . . . . *Pseudechiniscus* (*P.*) *ehrenbergi* (Figs 109–113)
-. Epicuticular ornamentation absent. 6
6(5). Posterior margin of the pseudosegmental plate IV' thickened/slightly lobate . . . *Pseudechiniscus* (*P.*) *linnaei* (Figs 114–116)
-. Posterior margin of the pseudosegmental plate IV' straight . . . . . *Pseudechiniscus* (*P.*) *aquatilis* (Figs 106–108)
7(2). Elongated body with the *Pseudechiniscus*-like dorsal sculpturing (only granules present, Fig. 124C), ventral sculpturing in the form of a complex ornamented pattern (Fig. 126B), cephalic plate composed of facets (Fig. 122A) . . . . . *Hypechiniscus africanus* (Figs 98–100)
-. Typically plump body with the dorsal sculpturing comprising at least pores/pseudopores (Fig. 124A–B, 125), ventral sculpturing in the form of uniform punctuation covering the entire venter (Fig. 126A), cephalic plate unipartite with an anterior incision or semicircular (Fig. 123A) 8
8(7). Dorsal plate margins with minute spines and spicules 9
-. Dorsal plate margins without supernumerary cuticular protrusions 10
9(8). Minute spines only on the posterior margin of the scapular plate, dorsal sculpturing of the mixed type (Fig. 125C): large pores of the *Echiniscus blumi-canadensis* type with polygonal edges present only in the scapular and the caudal plate, whereas the remaining plates with endocuticular pillars and epicuticular ornamentation, centrodorsal spines present. . . . . *Echiniscus africanus* (Fig. 9A)
-. Minute spines distributed along all plate margins and caudal incisions, dorsal sculpturing uniform, with the dominant dense epicuticular matrix visible as dark grey elements under PCM, centrodorsal spines absent . . . . . *Echiniscus dentatus* (Figs 20–25)
10(8). Dorsal plate sculpturing of the *Echiniscus spinulosus* type (only pores without thickened margins in the form of polygons present—only a dark circumporal ring may be present, Fig. 124A) 11
-. Dorsal plate sculpturing different (with epicuticular granules, endocuticular pillars and/or pores with thickened margins in the form of polygons, Fig. 124B, 125A–B). 19
11(10). Body appendage configuration *A*-C^d-D^d, pedal plates with large pores identical to pores present in the cephalic and the anterior portions of paired segmental plates I–II . . . . . *Echiniscus tetraspinosus* (Fig. 95)
-. Body appendage configuration different, pedal plates poreless or with minute pores developed differently to pores present in the dorsal plates 12
12(11). Body appendage configuration *A*-*E* . . . . . *Echiniscus baius* (Fig. 13)
-. Body appendage configuration different 13
13(12). Spines D^d much thicker than the remaining spines . . . . . *Echiniscus crassispinosus* (Fig. 19)
-. Spines D^d of a similar thickness to the remaining spines 14
14(13). Dark circumporal rings visible under PCM. . . . . *Echiniscus oreas* (Figs 63–65)
-. Dark circumporal rings absent. 15
15(14). Caudal plate typically with a pattern of faceting caused by dark epicuticular ridges 16
-. Caudal plate typically non-faceted 17
16(15). Body appendage configuration *A*-*(C)*-D^d-*E* . . . . . *Echiniscus tristis*
-. Body appendage configuration *A*-*C*-*D*-D^d-*E* . . . . . *Echiniscus scabrospinosus* (Figs 82–85)
17(15). Dark intraporal (endocuticular) rings absent . . . . . *Echiniscus regularis* (Figs 73–76)
-. Dark intraporal (endocuticular) rings present (e.g. Fig. 17A) 18
18(17). Body appendage configuration *A*-*(C)*-*(*D^d*)*-*(E)*, pedal plates IV typically porous . . . . . *Echiniscus cavagnaroi* (Figs 16–18)
-. Body appendage configuration *A*-*C*-*(D)*-D^d-*E*, pedal plates IV typically poreless . . . . . *Echiniscus marginatus*
19(10). Trunk unappendaged . . . . . *Echiniscus intricatus* (Figs 40–43D)
-. Trunk appendaged 20
20(19). Spines on legs II–III present, the posterior margin of the caudal plate with minuscule teeth. . . . . .

. . . . . *Echiniscus perarmatus* (Figs 68–72)

-. Spines on legs II–III absent, the posterior margin of the caudal plate smooth 21

21(20). At least the scapular and caudal plates with the *Echiniscus blumi-canadensis* type of sculpturing (large pores with polygonal edges, Fig. 125A). 22

-. Dorsal plates without the *Echiniscus blumi-canadensis* type of sculpturing. 23

22(21). Body appendage configuration *A-(B)-C-C^d-D-D^d*, all appendages but *D^d* in the form of long filamentous cirri, pores in all dorsal plates, typically secondary and tertiary spurs on external claws IV (Fig. 121C) . . . . . *Echiniscus blumi* (Fig. 14)

-. Body appendage configuration *A-(B)-C-C^d-D-D^d-E*, all appendages in the form of long stiff spines, pores in the scapular, posterior portions of paired segmental I–II and caudal plates, the remaining plates with endocuticular pillars and epicuticular ornamentation, external claws IV spurless . . . . . *Echiniscus pusae** (Fig. 125C)

23(21). Appendages *E* present 24

-. Appendages *E* absent 29

24(23). Appendage *C^d* in the form of a filamentous cirrus, much longer than the remaining appendages . . . . . *Echiniscus setaceus* (Figs 86–93)

-. Appendage *C^d* in the form of a filamentous cirrus or a short rigid spine, shorter or similar in length to the remaining appendages 25

25(24). Dorsal plate sculpturing of the *Echiniscus merokensis* type, with large polygonal granules joined by *striae* and pseudopores/pores between them (Fig. 124B) 26

-. Dorsal plate sculpturing different 28

26(25). Epicuticular granules on dorsal plates with a strong tendency towards merging and forming uniform smooth matrix, males present . . . . . *Echiniscus latruncularis* (Figs 49–52)

-. Epicuticular granules on dorsal plates always separated, males absent 27

27(26). Cirri *B–E* of similar lengths, anterior portions of paired segmental plates and median plate 2 with large pillars protruding as granules . . . . . *Echiniscus merokensis* (Fig. 62)

-. Cirri *E* usually much longer than cirri *B–E*, anterior portions of paired segmental plates and median plate 2 without pillars, or with pillars not joined by *striae* . . . . . *Echiniscus pellucidus* (Figs 66–67)

28(25). Dorsal plate sculpturing of the *Echiniscus virginicus* type, comprising prominent endocuticular pillars and ridge-like epicuticular ornamentation (Fig. 125B), males absent . . . . . *Echiniscus virginicus* (Fig. 97)

-. Dorsal plate sculpturing comprising epicuticular granules and scarce, minute pores, males present . . . . . *Echiniscus attenboroughi* (Figs 10–12)

29(23). All trunk appendages in the form of thick cirri with irregular (tufted) surface . . . . . *Echiniscus scabrocirrosus* (Figs 77–81)

-. All trunk appendages with smooth surface 30

30(29). Subcephalic and genital plates porous 31

-. Subcephalic and genital plates poreless or absent 32

31(30). Body appendage configuration *A-(B)-(B^d)-C-C^d-D-D^d*, appendages in the form of short cirri/long spines, pedal plate sculpturing evident under PCM . . . . . *Echiniscus longispinosus* (Figs 57–61)

-. Body appendage configuration *A-B-C-C^d-D-D^d*, appendages in the form of long filamentous cirri, pedal plate sculpturing (minute wrinkling) not visible under PCM . . . . . *Echiniscus imitans* (Figs 35–39)

32(30). Dorsal sculpturing dominated by clearly separated granules . . . . . *Echiniscus irroratus* (Figs 45–48)

-. Dorsal sculpturing comprises solid endocuticular matrix and, sometimes, *reticulum* 33

33(32). Spines *B* present 34

-. Spines *B* absent 35

34(33). Body length 226–315 µm, the scapular plate length 33.6–58.7 µm, the cephalic papilla length 5.5–8.2 µm, appendages *C^d* (12.7–27.2 µm long) and *D^d* (11.1–31.5 µm long) in the form of spines and shorter than lateral cirri. . . . . *Echiniscus lichenorum* (Figs 53–56)

-. Body length 306–395 µm, the scapular plate length 58.0–72.5 µm, the cephalic papilla length 7.9–10.2 µm, appendages *C^d* (34.1–59.1 µm long) and *D^d* (43.4–64.8 µm long) in the form of cirri and similar in length to lateral cirri. . . . . *Echiniscus similaris* (Fig. 94)

35(33). Dorsal appendages present. . . . . *Echiniscus draconis* (Figs 26–29)

-. Dorsal appendages absent 36

36(35). Claws short and robust, with robust spurs positioned at *ca.* 30–40% of the internal claw length . . . . . *Echiniscus capensis* (Fig. 15)

-. Claws slender, with delicate, acute spurs positioned at *ca.* 25% of the internal claw length . . . . . *Echiniscus gracilis* (Figs 30–34)

**Echiniscus pusae* is a very rare, potentially pantropical echiniscid species that requires a redescription. Marcus (1928) established it after observing individuals found in Lombok (Malay Archipelago) and comparing them to specimens from South Africa. We compared populations of that species originating from Tanzania (Gąsiorek & Kristensen 2018, Bochnak *et al.* 2020), Gunung Silam in northern Borneo and Gunung Kiematubu in Tidore, the Moluccas (unpublished data), and Australia (Claxton 2004 and Claxton pers. comm.), and saw no morphological disparities between them. However, genetic data are necessary to exclude crypsis.

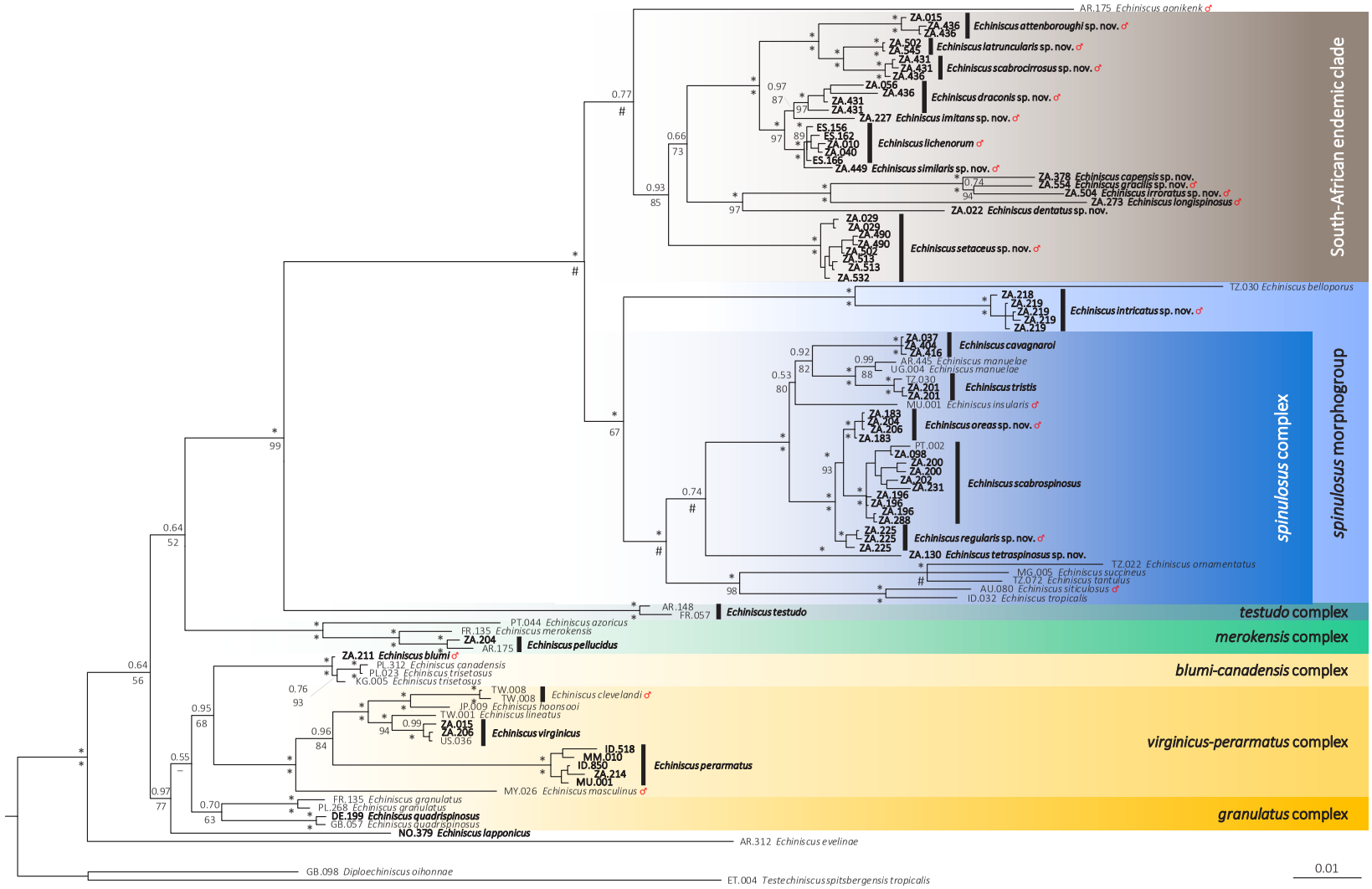

FIGURE 117. Phylogeny of *Echiniscus*, with *Diploechiniscus* and *Testechiniscus* used as the outgroup, based on concatenated 18S rRNA + 28S rRNA + ITS-1 + ITS-2 nucleotide sequences (2604 bp in total). Values above branches indicate Bayesian posterior probabilities, whereas those below branches show bootstrap supports; asterisks (*) indicate maximum values, whereas hashtags (#) signify a different topology in ML. BI evolution models: GTR+I+G (18S rRNA + 28S rRNA), GTR+I+G (ITS-1 + ITS-2); edge-unlinked partition models in ML: TIM3e+I+G4, TVMe+I+G4, TIM3+F+I+G4, TPM2+F+I+G4 (marker sequence as above). The scale refers to the Bayesian tree. Bolded names indicate newly sequenced species. Clade colouring correspond with Gąsiorek *et al*. (2021c). All new species were found only in South Africa.

Phylogeny

Both BI and ML *Echiniscus* phylogenies gave relatively well-supported and resolved trees of mostly congruent topologies (Fig. 117). The tree was subdivided into seven major clades: the *E. granulatus*, *E. virginicus-perarmatus*, *E. blumi-canadensis*, *E. merokensis*, and *E. testudo* complexes, the *E. spinulosus* morphogroup, and the "South-African endemic clade". There were three topological differences between the two analytical approaches that are not relevant from the perspective of the evolution of South African echiniscid fauna: (1) in ML, *Echiniscus aonikenk* Gąsiorek *et al*., 2021 constituted the sister lineage (with 100% bootstrap support) to the "South-African endemic clade" + the *E. spinulosus* morphogroup, instead being the sister lineage to the former as in BI; (2) in ML, *E. tetraspinosus* **sp. nov.** was the sister species to all other species from the *E. spinulosus* complex (with 100% bootstrap support); and (3) in ML, the relationships between three members of the *E. spinulosus* complex: *E. tantulus* Gąsiorek *et al*., 2020, *E. succineus* Gąsiorek & Vončina, 2019, and *E. ornamentatus* Gąsiorek & Kristensen, 2018, were resolved as follows: (*E. tantulus* (*E. succineus* + *E. ornamentatus*)).

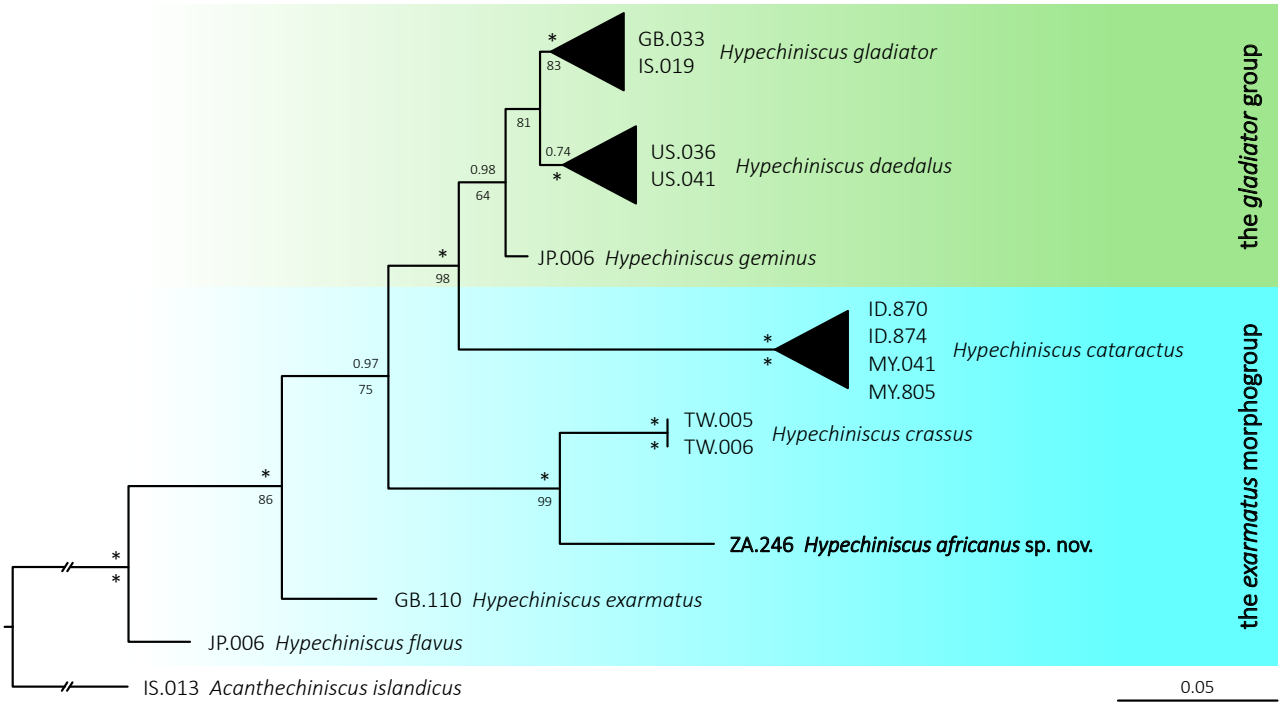

FIGURE 118. The concatenated 18S rRNA + 28S rRNA + ITS-1 (2363 bp in total) consensus Bayesian phylogenetic tree of *Hypechiniscus*, with *Acanthechiniscus islandicus* (Richters, 1904) as the outgroup. Branch support is given as BI posterior probability values above branches and ML bootstrap values below branches. Maximum supports, i.e. 1.00 for BI and 100 for ML, are indicated by asterisks (*). The ML and the BI tree had the same topology. BI evolution models: TRN+I+G, GTR+G, TVM+I; edge-unlinked partition models in ML: K2P+G4, TVMe+G4, K3Pu+F+I (marker sequence as above). Scale bar represents substitutions per site.

In the phylogenetic tree of *Hypechiniscus*, *H. africanus* **sp. nov.** was placed as the sister species of *H. crassus* Gąsiorek *et al*., 2021 within the *H. exarmatus* morphogroup (Fig. 118).

The *Pseudechiniscus* phylogeny showed the topology known from previous reconstructions (Gąsiorek *et al*. 2021a, d), with one South African species, *P. wallacei* **sp. nov.**, belonging to the subgenus *Meridioniscus*, and three species: *P.* cf. *ehrenbergi*, *P. aquatilis* **sp. nov.**, and *P. linnaei* **sp. nov.** (the latter two being closely related sister taxa), representing the nominal subgenus *Pseudechiniscus* (Fig. 119).

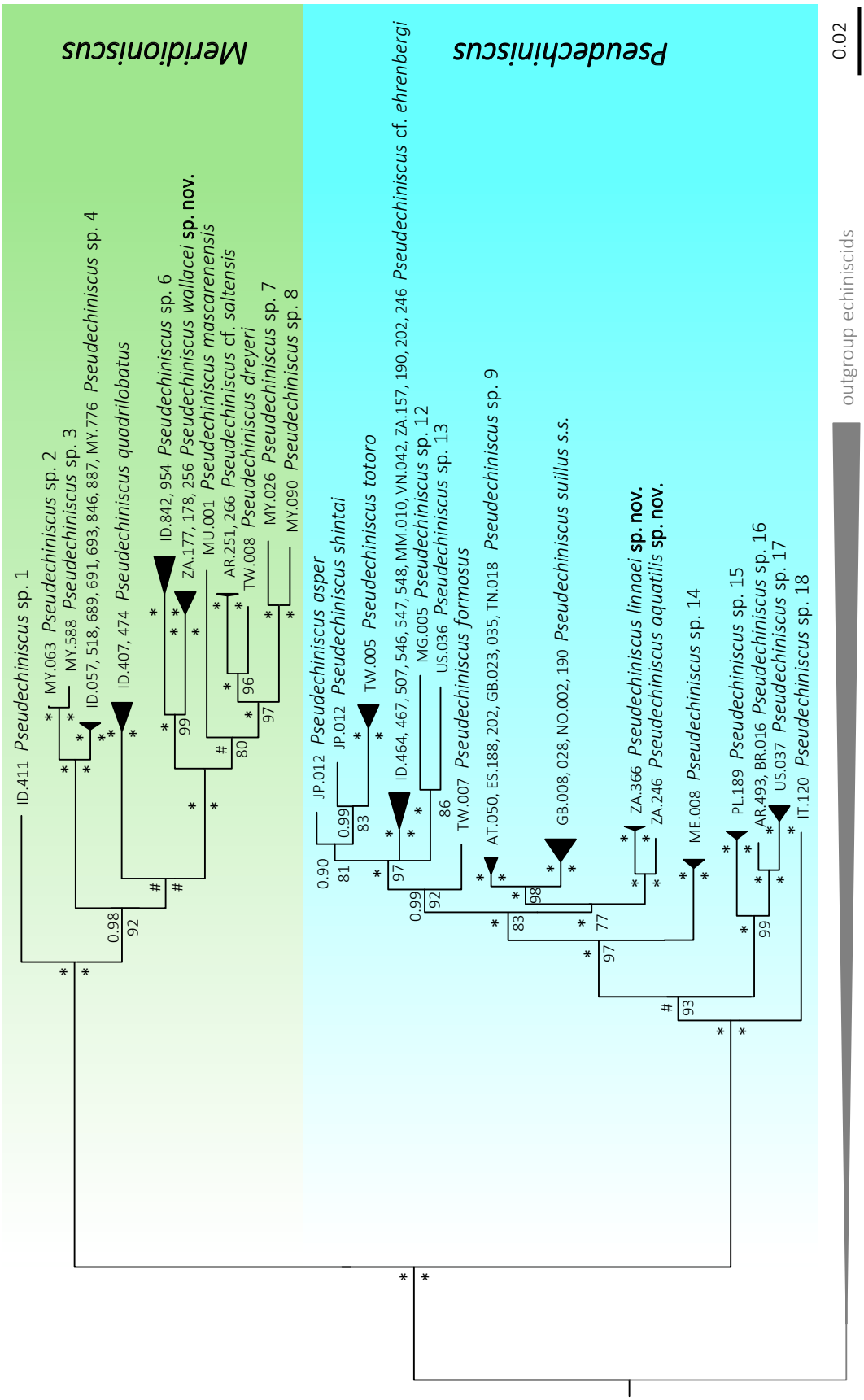

FIGURE 119. Position of the African species on the phylogenetic tree of *Pseudechiniscus* based on the concatenated matrix (18S rRNA + 28S rRNA + ITS-1, 2307 bp in total). Branch support is given as BI posterior probability values above branches and ML bootstrap values below branches. Maximum supports, i.e. 1.00 for BI and 100 for ML, are indicated by asterisks (*), whereas nodes unsupported in either analysis are marked by hashtags (#). BI evolution models: SYM+I+G4, SYM+G4, GTR+F+G4; edge-unlinked partition models in ML: SYM+I+G4, SYM+G4, GTR+F+G4 (marker sequence as above). The scale refers to the Bayesian consensus tree and represents substitutions per site. Species numbering preserved from Gąsiorek *et al.* (2021a).

Discussion

Composition of the South African fauna of Echiniscidae

Diverse echiniscid fauna of South Africa is unique in many aspects, which are discussed in the following paragraphs. A glaring observation is the overwhelming dominance of *Echiniscus* (30 out of total 38 species representing 5 genera, ~79%) against other echiniscid genera found in the South African samples (only 8 species belonging in 4 genera). Although *Echiniscus* is usually the most frequently found among heterotardigrade genera, this dominance is exceptionally high in contrast to other comprehensively studied tardigrade faunae of the world. Specifically, in the Swedish part of the Scandinavian Peninsula, characterised by a subarctic climate changing into humid continental climate in the southern provinces, *Echiniscus* comprises around a half of all echiniscids (8/17 spp., ~47%, 9 genera in total; Guidetti *et al*. 2015 with amendments from Degma *et al*. 2009–2021 applied also to the examples given below); in Poland, with a transitional humid continental climate, this ratio is similar (10/24 spp., ~42%, 9 genera in total; Dastych 1988 with amendments from Gąsiorek & Degma 2018); but the dominance is even less evident in Italy, mostly with a Mediterranean climate: 15/39 spp., ~38%, 12 genera in total (Maucci 1986), and in Costa Rica, characterised by a tropical rainforest climate: 6/16 spp., ~38%, 6 genera in total (Kaczmarek *et al*. 2014). Interestingly, within *Echiniscus*, the *E. spinulosus* group, a complex of species usually most speciose in the tropics (Bochnak *et al*. 2020), is in minority compared to other groups (8/30 spp.), although it is still frequently found.

The second most speciose genus within Echiniscidae and also in South Africa is *Pseudechiniscus* (Cesari *et al*. 2020). The hitherto concealed species richness of *Pseudechiniscus* is currently being unravelled (Roszkowska *et al*. 2020; Gąsiorek *et al*. 2021a), and high genetic diversity disclosed within few samples (Cesari *et al*. 2020) implies that this taxon may eventually even surpass *Echiniscus* in the number of species, especially that new genera are being extracted from the polyphyletic *Echiniscus* (e.g. see Gąsiorek *et al*. 2018b, 2019a). However, with the exception of the relatively common *P.* cf. *ehrenbergi* and *P. wallacei* **sp. nov.**, the remaining three species reported from South Africa remain rare or extremely rare, further underlining *Echiniscus* predominance in this region of the continent.

The three remaining heterotardigrade genera found in South Africa, *i.e. Bryodelphax*, *Hypechiniscus*, and *Cornechiniscus*, are generally rare (Kristensen 1987). This is evidenced in the extremely small number of samples in which they were found (5 out of 558; ~1%). However, a risk of sampling bias should be considered when reporting this figure. For example, *Cornechiniscus* prefers xeric habitats with dispersed moss cushions containing high amounts of soil, which is usually avoided by other echiniscids (Kristensen 1987; Gąsiorek & Michalczyk 2020a). Given that we did not sample in such habitats, e.g. in the Northern Cape, we may have missed many *Cornechiniscus* populations. Consequently, e.g. *C. madagascariensis* may be more common in the semi-desertic and arid regions of South Africa, especially that it has already been reported from other regions harbouring such habitats (Gąsiorek & Michalczyk 2020a).

Interestingly, our survey revealed two geographic clusters of *Echiniscus* spp. in South Africa, south-western and south-eastern assemblages. Ten species are specific to the first subregion (*E. attenboroughi* **sp. nov.**, *E. capensis* **sp. nov.**, *E. dentatus* **sp. nov.**, *E. gracilis* **sp. nov.**, *E. irroratus* **sp. nov.**, *E. latruncularis* **sp. nov.**, *E. marginatus*, *E. merokensis*, *E. scabrocirrosus* **sp. nov.** and *E. similaris* **sp. nov.**), whereas six are found only in the second subregion (*E. baius*, *E. blumi*, *E. cavagnaroi*, *E. oreas* **sp. nov.**, *E. pellucidus*, *E. tristis*). However, the reason for this geographic division remains unknown.

Although the high species diversity observed in the South Africa is definitely striking, equally interesting is the absence of some otherwise widespread echiniscid genera from samples collected in the region. Cosmopolitan *Claxtonia* and *Nebularmis* seem to be absent in this part of the World, as habitats preferred by many representatives of both genera, such as high elevations and humid river banks, were sampled and returned negative results. Stenothermic *Testechiniscus*, known from the Holarctic and Arctic, but also from eastern parts of Central Africa (Gąsiorek *et al*. 2018a), also does not seem to inhabit South Africa. This is particularly interesting, because other species exhibiting similar thermic preferences and found in the Palaearctic and Arctic, e.g. *E. blumi*, has been found in the Drakensberg range in South Africa. Finally, tropical *Kristenseniscus* has not been found either, although it should be underlined that the northernmost Limpopo Province, which exhibits some habitats that could harbour populations of this genus, has not been sampled. Thus, its absence in South Africa requires further investigation.

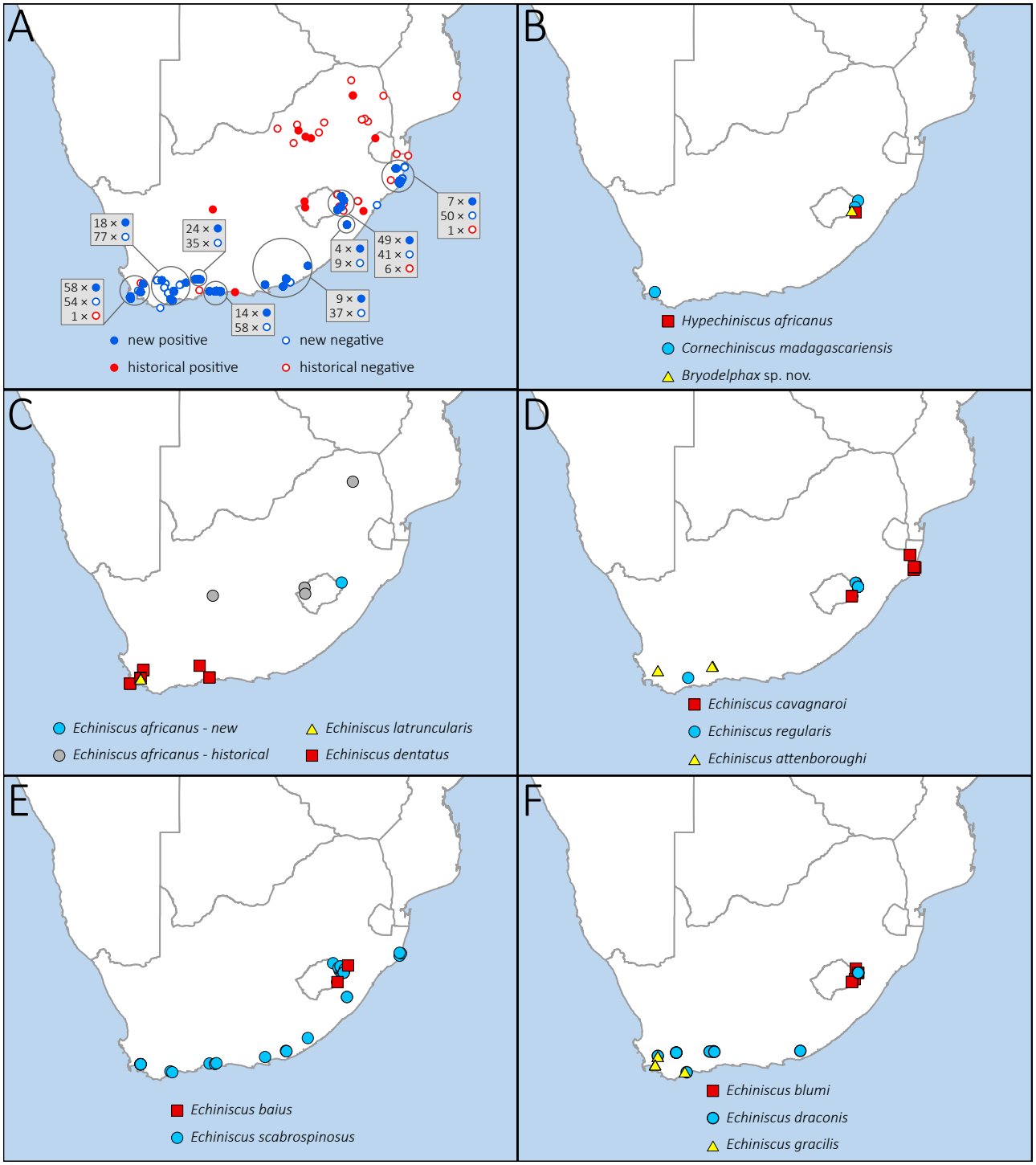

FIGURE 120. Distribution map for South African Echiniscidae: (A) sampling sites, (B–F) species.

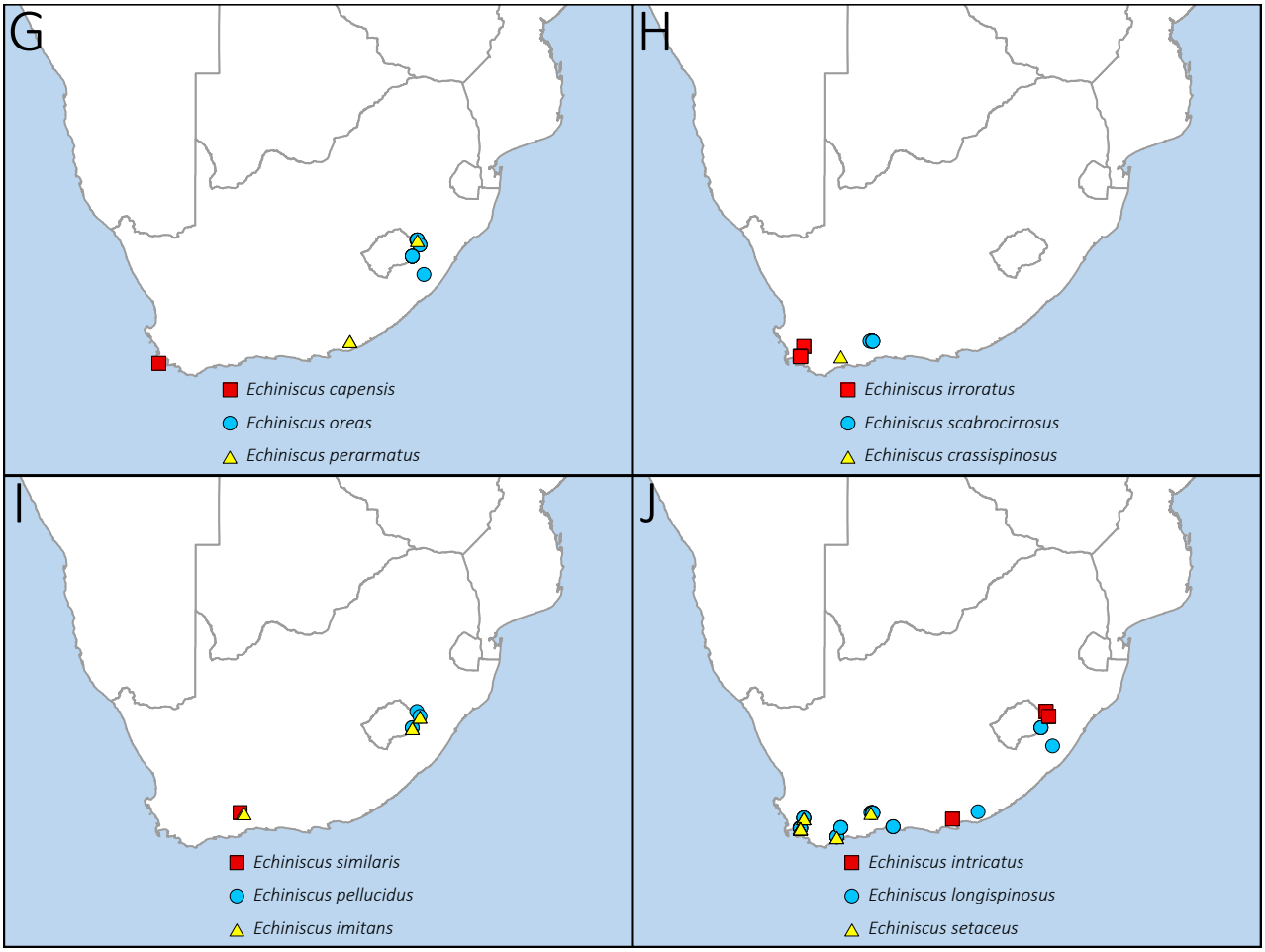

FIGURE 120. Distribution map for South African Echiniscidae: (G–J) species. *(continued)*.

Altitudinal zonation of South African Echiniscidae

Most typically, animal α-diversity is negatively correlated with an increasing elevational gradient (Peters *et al*. 2016). Interestingly, it was shown several times that tardigrades, as a phylum, deviate from this pattern and their species richness is usually higher in mountains than in adjacent lowlands, both in the temperate zone (Ramazzotti 1956; Dastych 1987, 1988) and in the tropics (Kaczmarek *et al*. 2011). However, in the Arctic, there seem to be no correlation between altitude and species richness (Zawierucha *et al*. 2015), suggesting that tardigrades, in general, prefer cold habitats. The specificity of mountain habitats is usually augmented by increasing local endemism due to insular speciation (Merckx *et al*. 2015) and relictual character of animal species inhabiting mountain peaks (Bertolani & Rebecchi 1996). Importantly, in tropical mountain forests, the elevational gradient is non-linear, with the largest numbers of species occurring at intermediate altitudes (i.e. between 500–2000 m asl) and much lower biodiversity being recorded outside this range (Kessler & Kluge 2008).

Altitudinal floral zones for Afrotropical mountains were distinguished by Boughey (1956). All four zones (Fig. 127) are found in South Africa only in the Drakensberg, which contains the highest peaks in this part of the continent, with the most prominent Thabana Ntlenyana (*ca*. 3500 m asl). The Cape Fold Mountains (potentially serving as the main place of echiniscid radiation in South Africa), which were also sampled for the purpose of this work (*i.a*. Swartberg, Hottentots-Holland Mts.) or in past contributions (Tsitsikamma), do not exhibit the highest zone; that is the montane zone above 2,300 m asl. Our extensive sampling in the fynbos formation, characteristic for the highland zone, and in the scrub dominated by *Greyia* and *Protea* or in Afromontane forests in the riverbanks of the highland zone, revealed that, in contrast to what was documented for the Western Palaearctic and Central America, South African echiniscid fauna shows limited signs of elevational zonation (Fig. 127). As many as 13 species are eurytopic, inhabiting the entire set of sampled altitudes, *i.e*. from the lowlands to mountain summits. Few species are specific to a particular zone, mostly those that were found only in one locality (10 spp.). However, some echiniscids seem

to have preferences regarding the elevation: widely distributed *E. setaceus* **sp. nov.** is distinctive for the lowlands (I), rare *E. perarmatus* is specific for the foothills (II), and *E. blumi* occurs only in the highlands (III). The highland zone is the most distinct compared to the remaining zones, as common eurytopic species mix with many stenotopic taxa that prefer colder habitats: *E. baius*, *E. imitans* **sp. nov.**, *E. oreas* **sp. nov.**, *E. tristis*. Overall, 24 species inhabit both zone I and II, and 22 species occur only in zone III. This means that the species distribution curve is not hump-shaped, as observed for many animals in tropical mountains (Kessler & Kluge 2008), but rather a constant number of echiniscid species dwell in South African lowlands and mountains.

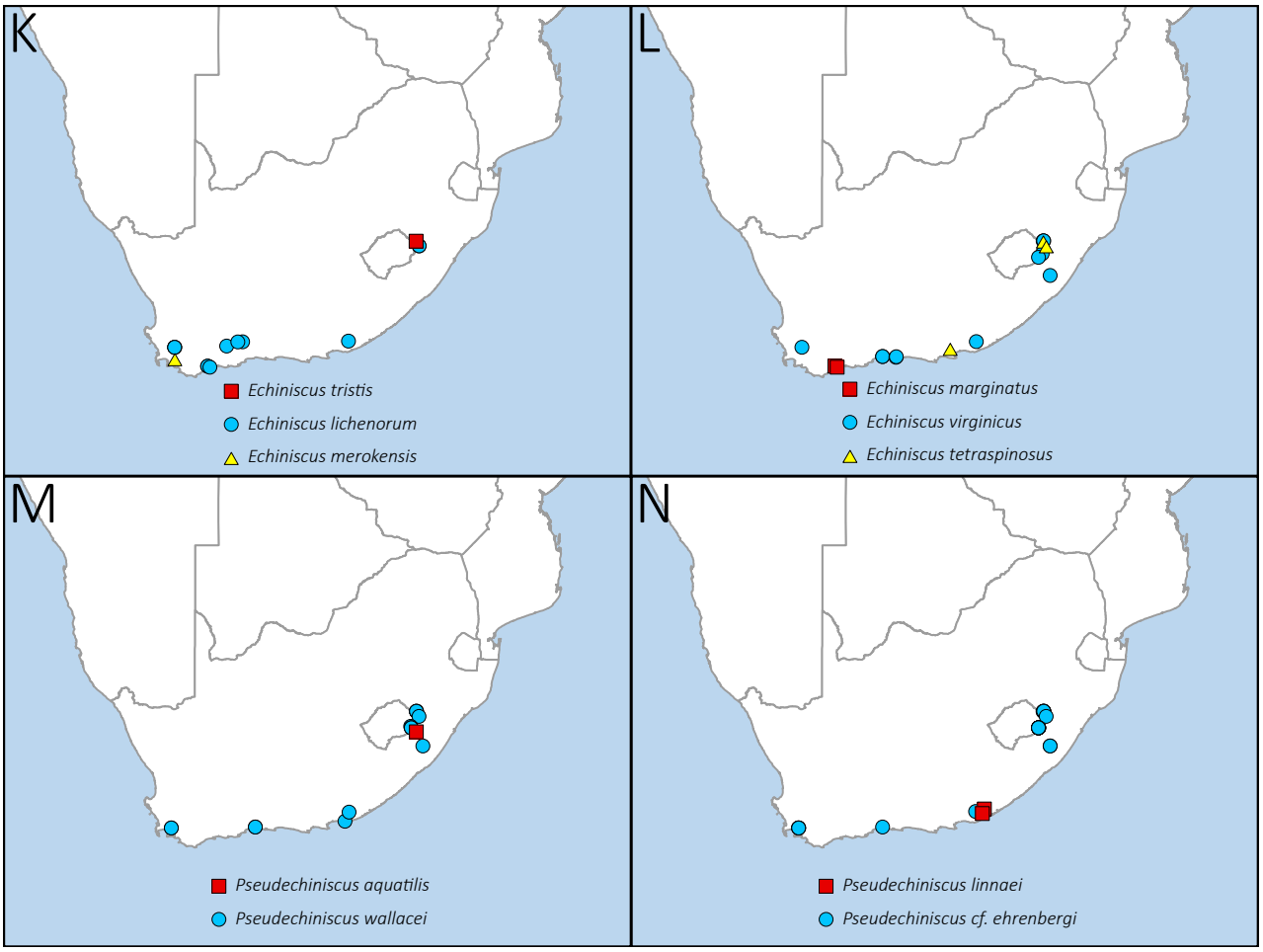

FIGURE 120. Distribution map for South African Echiniscidae: (K–N) species. *(continued)*.

Biogeographic and phylogenetic relationships of the South African Echiniscidae

The available data imply that the majority of originally Gondwanan South African echiniscid fauna was outcompeted by rivals dispersing from the Northern Hemisphere, as it was documented for the mite clade Hydrachnidia (Proctor *et al*. 2015). An analogous scenario, in which relictual Gondwanan descendants with restricted distributions survived only in some parts of the continent, was the case for several beetle (Toussaint *et al*. 2017), orthopteran (Allegrucci & Sbordoni 2019), and spider lineages (Labarque *et al*. 2018; Chousou-Polydouri *et al*. 2019). The post-Gondwanan lineages seem to be absent in the South African echiniscid fauna, since typical components of some post-Gondwanan lands, such as genera *Antechiniscus*, *Barbaria*, and *Mopsechiniscus*, or the family Oreellidae, closely related to Echiniscidae and of Gondwanan origin (McInnes & Pugh 2007), have not been found in Africa (Kristensen 1987; Guidetti *et al*. 2017; but see also the critique of the term "Gondwanan" in McGlone 2005; Goldberg *et al*. 2008). The only puzzling exception is the presence of the Neotropical *E. pellucidus* in Drakensberg (Fig. 120I), which might represent an example of a long-distance dispersal. A record by Heinis (1928) of another Neotropical species, *Barbaria bigranulata* (Richters, 1907), in South Africa is unreliable and should be considered erroneous (it likely represents *E. intricatus* **sp. nov.**, which is relatively common in the region). A recent revision of *Barbaria* showed that the genus inhabits the New World and Antarctica, and records from other parts of the world are wrong (Gąsiorek *et al*. 2022).

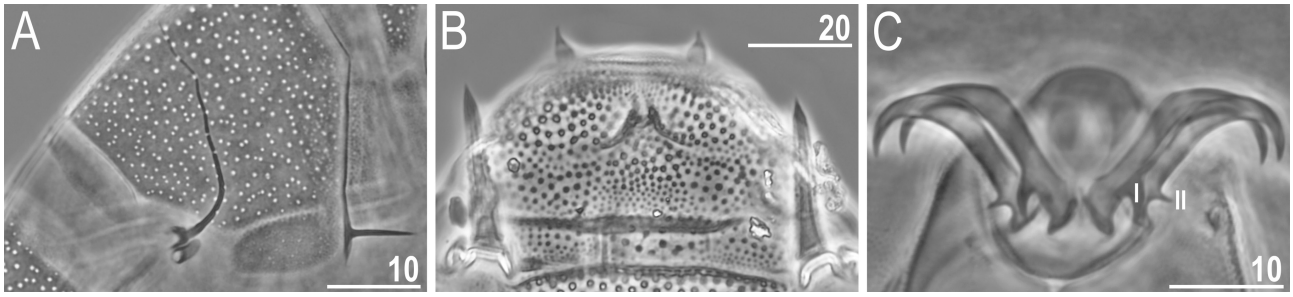

FIGURE 121. Taxonomic key aid I: A—flexible cirrus *A* (*E. setaceus* **sp. nov.**), B—horn-shaped appendage *A* (*C. madagascariensis*), C—primary (I) and secondary (II) claw spurs (*E. blumi*). Sometimes even tertiary spurs are present, above (II). Scale bars in μm.

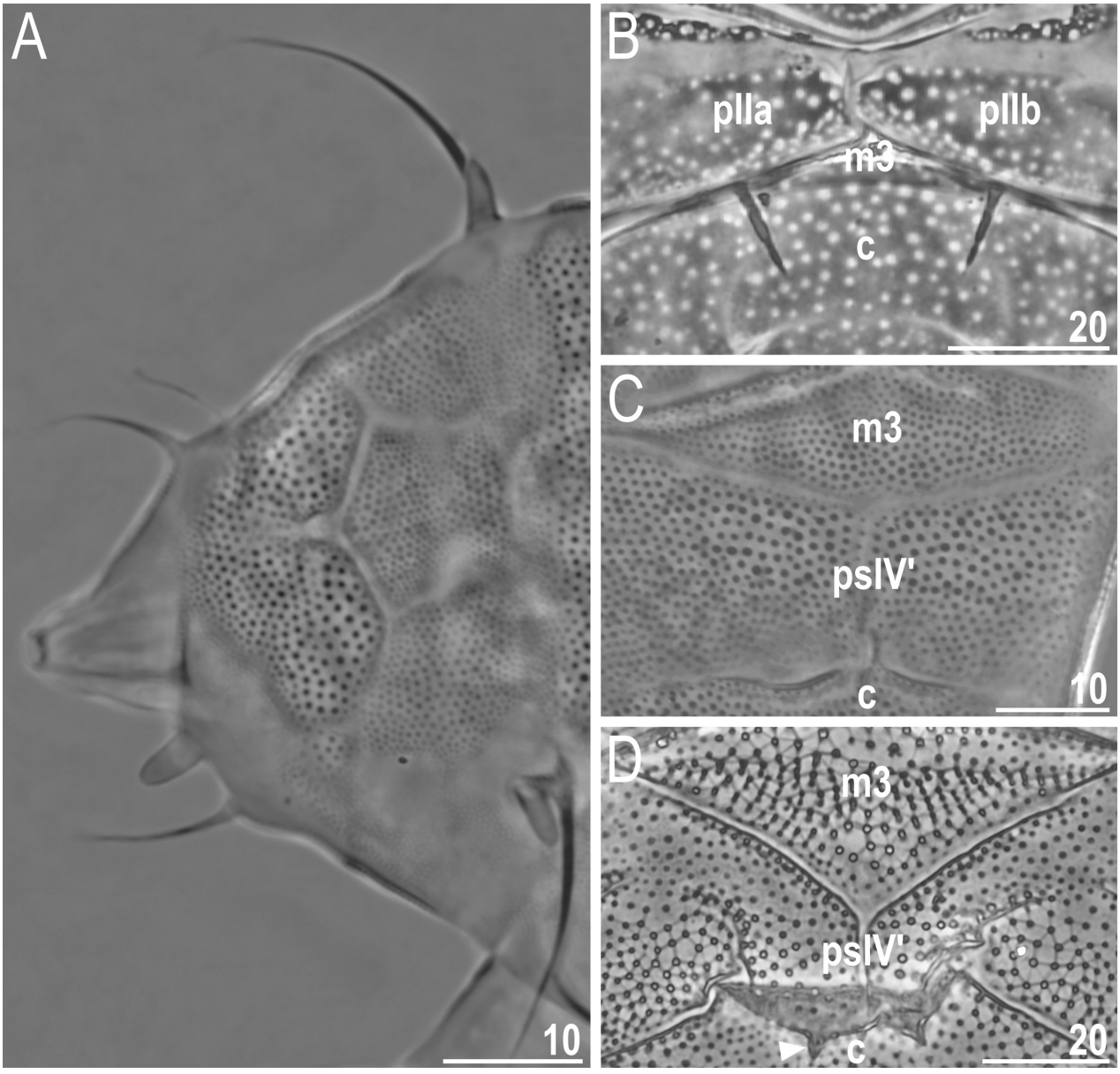

FIGURE 122. Taxonomic key aid II: A—cephalic plate composed of facets (*P.* (*M.*) *wallacei* **sp. nov.**), B—pseudosegmental plate IV' absent (*E. regularis* **sp. nov.**), C—pseudosegmental plate IV' straight (*P.* (*P.*) cf. *ehrenbergi*), D—pseudosegmental plate IV' lobated (*C. madagascariensis*). Abbreviations: pII—paired segmental plate II, m3—median plate 3, psIV'—pseudosegmental plate IV', c—caudal plate, arrowhead—projection on the pseudosegmental lobe. Scale bars in μm.

Although the absence of evidence is not necessarily evidence of absence, and even though the majority of the taxa mentioned above are rare, the combined sampling of past studies and the current survey tend towards the rejection of the hypothesis about an ancient origin of South African Echiniscidae. The *Echiniscus* phylogeny (Fig. 117) indicates colonisation from other regions followed by isolation, but currently it is impossible to hypothesise about the geographic origin of the colonisers. The colonisation hypothesis is further supported by species composition and phylogeny of South African echiniscids. Specifically, as many as 20 of species found in this study (54%) are new to science and, together with further 4 species described earlier, are presumably endemic to Africa (65%); 2 species.: *E. lichenorum* and *E. scabrospinosus* (5%), are found both in the Afrotropic and Western Palaearctic; 8 species: *C. madagascariensis*, *E. africanus*, *E. baius*, *E. cavagnaroi* (Fig. 128A), *E. marginatus*, *E. perarmatus* (Fig. 128B), *E. pusae*, and *P. wallacei* **sp. nov.** (22%), have a pantropical distribution extending towards regions with the Mediterranean climate or they exhibit wide tropical and subtropical ranges, and finally 2 spp.: *E. blumi* and *E. merokensis* (5%), are cosmopolitan. It is of pivotal significance for the phylogenetic interpretation that the majority of endemic *Echiniscus* species cluster into young clades, and that the remaining *Echiniscus* spp. are mainly effective dispersalists (*i.e*. widely distributed or possibly even cosmopolitan taxa, *i.e*. effective dispersalists). Surprisingly, the ubiquitous *E. testudo* (Jørgensen *et al*. 2007) was not found, but this might be due to the omission of urban areas during sampling. The interpretation for this pattern in the framework of historical biogeography (Sanmartín 2012) is that the echiniscid fauna of South Africa is relatively young, which agrees with the estimates of a middle-aged origin (the duration of the Cape Orogeny: *ca*. 280–250 Mya; Hansma *et al*. 2016) of the mountains that harbour their largest diversity (Truswell 1977). The disjunct distribution of *E. lichenorum* (Portugal and South Africa) can be explained by two hypotheses: (a) anthropogenic dispersal (*e.g.* with Portuguese sailors in historical times), or (b) the species occurs also in Central Africa, presumably exhibiting a continuous range, but has yet to been found there. In our opinion, the second option is more probable because signs of continuous distribution has already been documented for *E. scabrospinosus* (see Fig. 128C). An interesting datum is the presence of *E. virginicus* in South Africa (Fig. 120L). We suppose that it constitutes an example of anthropogenic dispersal from the Nearctic (Gąsiorek *et al*. 2019b). A recent analysis of apochelan tardigrades extracted from the same South African samples as analysed in the present study indicated the presence of at least *ca.* 24 *Milnesium* species, including 18 potentially endemic (75%), in the region (Morek *et al.* 2021). Moreover, similar to echiniscids, the great majority of these endemic South African milnesiids are grouped in two clades that evolved *in situ* and are *ca.* 130 My old (Morek *et al.* 2021). This shows that South Africa is an important and valuable region in terms of limnoterrestrial tardigrade diversity.

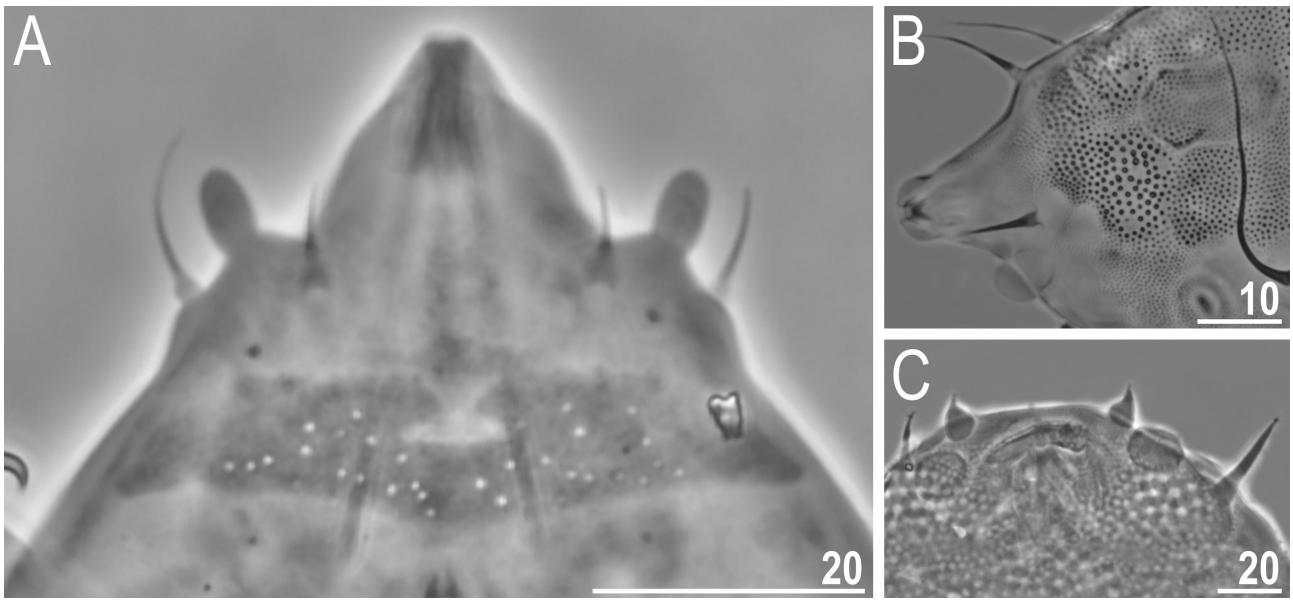

FIGURE 123. Taxonomic key aid III: A—dactyloid cephalic papillae and simple cephalic plate with an anterior incision (*E. regularis* **sp. nov.**), B—pseudohemispherical cephalic papillae (*P.* (*P.*) cf. *ehrenbergi*), C—hemispherical cephalic papillae (*C. madagascariensis*). Scale bars in μm.

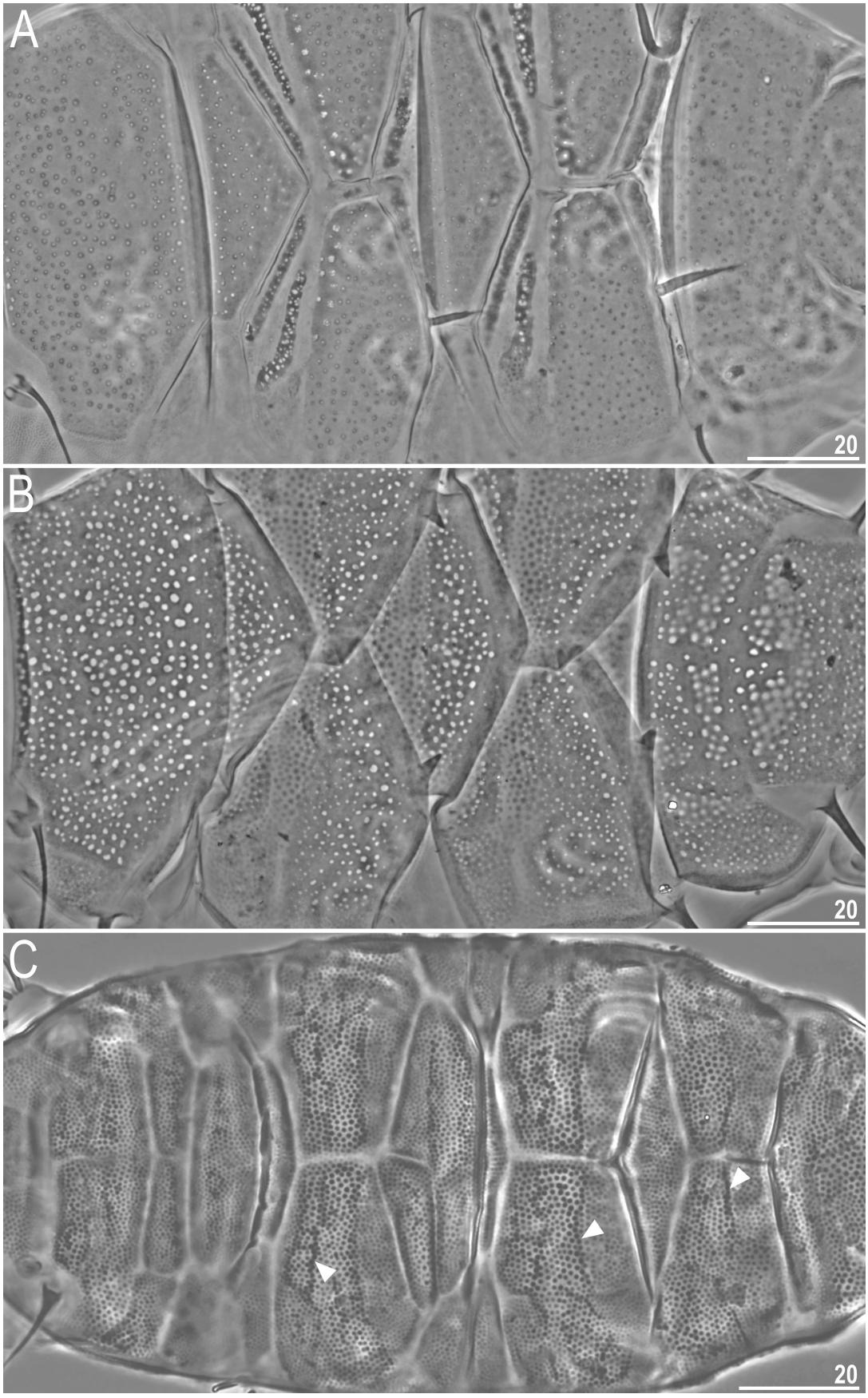

FIGURE 124. Taxonomic key aid IV—dorsal sculpturing: A—the *E. spinulosus* type (*E. oreas* **sp. nov.**), B—the *E. merokensis* type (*E. merokensis*), C—the *Pseudechiniscus* type (*P.* (*P.*) cf. *ehrenbergi*), arrowheads indicate epicuticular ornamentation. Scale bars = 20 μm.

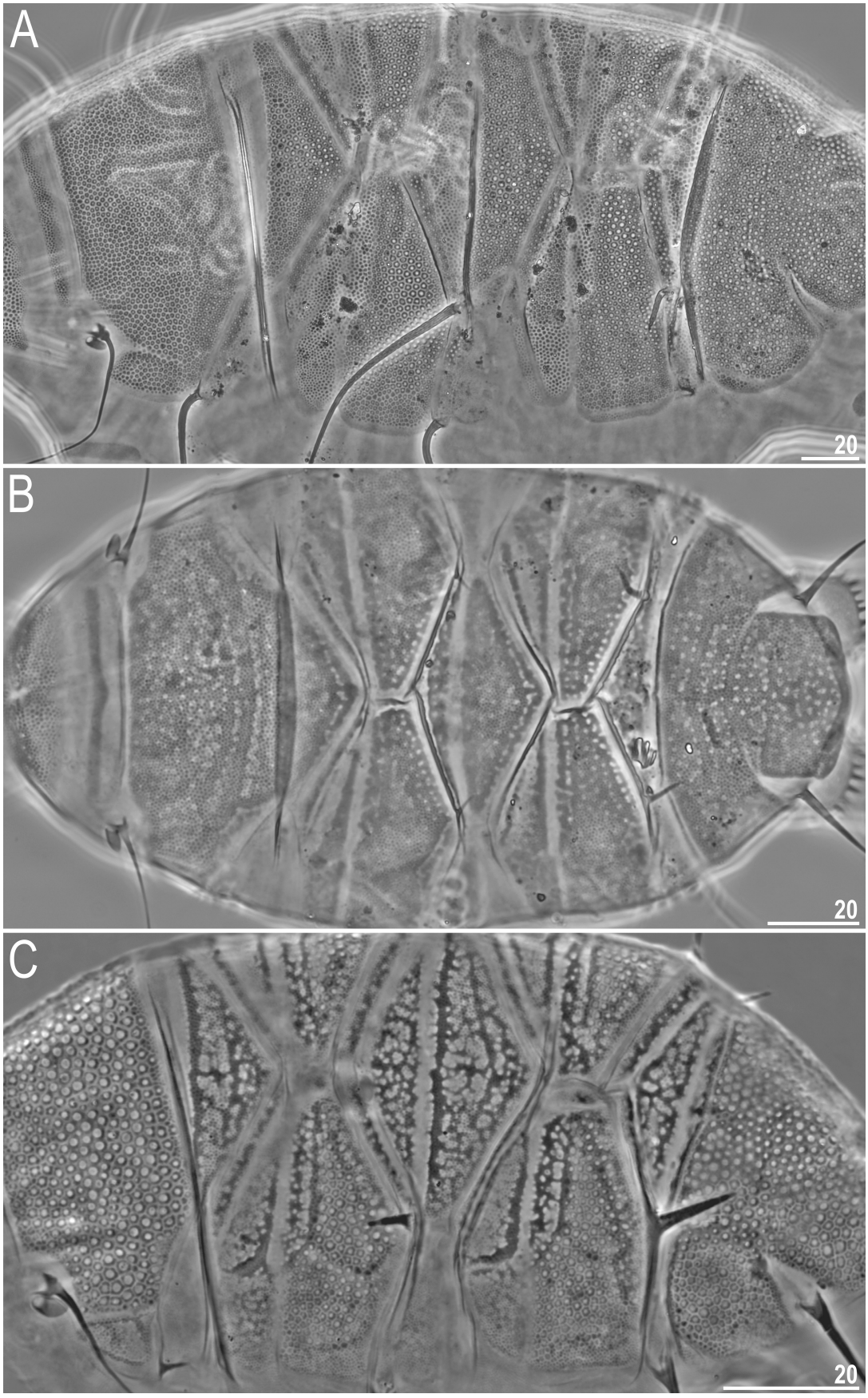

FIGURE 125. Taxonomic key aid V—dorsal sculpturing: A—the *E. blumi-canadensis* type (*E. blumi*), B—the *E. virginicus* type (*E. lineatus*), C—the mixed type (*E. pusae*). Scale bars = 20 μm.

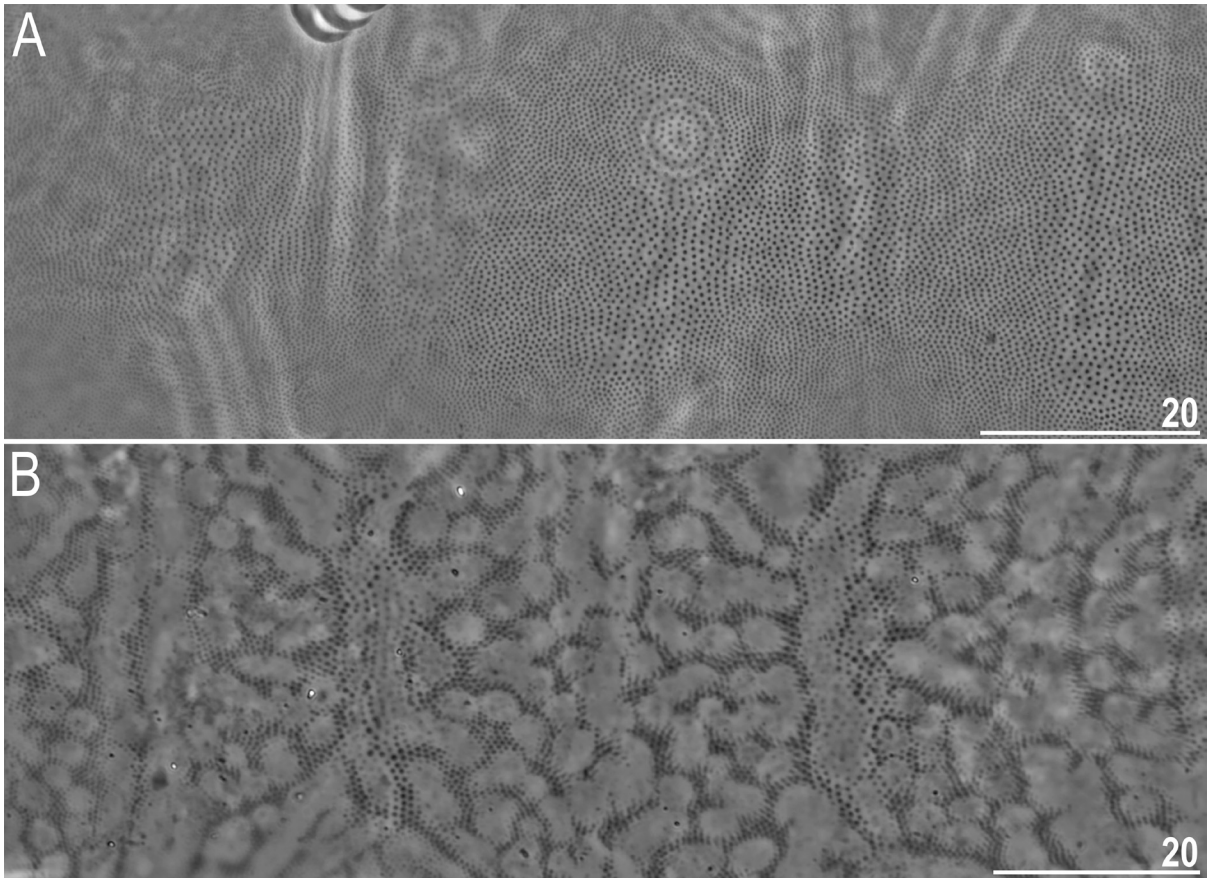

FIGURE 126. Taxonomic key aid VI—ventral sculpturing: A—simple, uniform, typical for *Echiniscus* (*E. imitans* **sp. nov.**), B—complex, typical for *Hypechiniscus* and *Pseudechiniscus* (*P.* (*P.*) *linnaei* **sp. nov.**). Scale bars = 20 μm.

The abundance of dioecious *Echiniscus* spp. in South Africa is a compelling peculiarity of its fauna since males were found only in small number of species in this genus in other parts of the world (*e.g.* see Gąsiorek *et al*. 2020). Over a half of all *Echiniscus* species recorded to date in South Africa by us (15/29 spp.) were represented by at least one population in which males were found (Figs 117 and 127), more than doubling the number of known amphigonic species in this genus (Gąsiorek *et al*. 2020). Most South African species of *Echiniscus* exhibited typically unbalanced sex ratios, with males constituting below 10% of the adults in a population (Table 62; see also Guil & Giribet 2009). Although in several species (*E. attenboroughi* **sp. nov.**, *E. scabrocirrosus* **sp. nov.**, *E. setaceus* **sp. nov.**, *E. similaris* **sp. nov.**) males were much more common, they were always the less frequent sex (10–44% of adults). In the Echiniscidae, dioecy is considered a plesiomorphic state, whereas parthenogenesis (both obligatory and facultative) is thought to be an advanced state (Kristensen 1987). Since until only recently echiniscid males were found almost exclusively in the Southern Hemisphere, Miller *et al*. (1999) hypothesised that *Echiniscus* evolved from a dioecious ancestor in Gondwana, and then spread to the Northern Hemisphere, where parthenogenesis became the predominant reproductive mode. Even though currently males are found in an increasing number of Northern Hemisphere *Echiniscus* species (Gąsiorek *et al*. 2020), dioecy seems to be more common in the Southern Hemisphere (Fig. 117), which is in line with the hypothesis by Miller *et al*. (1999). Importantly, however, the phylogeny of *Echiniscus* (Fig. 117) clearly shows that the basal clades of *Echiniscus* are either exclusively (the *E. granulatus* complex) or predominantly parthenogenetic (the *E. blumi-canadensis*, *E. virginicus-perarmatus* and *E. merokensis* complexes; when species representing these clades are dioecious, males are ultra-rare—see Miller *et al*. 1999 and Guil & Giribet 2009). Thus, there is a possibility is that South African species indeed exhibit dioecy more frequently than their congeners in other parts of the world. Notwithstanding this hypothesis, in light of the presented phylogeny (Fig. 117), the "Gondwanan" hypothesis (Miller *et al*. 1999) on the origin of the genus *Echiniscus* is falsified. We acknowledge the incomplete sampling in many lineages of the hyperdiverse *Echiniscus* (Gąsiorek *et al*. 2019a), especially in Australia (Claxton 2004), but current data infer cosmopolitan-cold/montane (*E. blumi*, *E. merokensis*), Palaearctic/Holarctic (*E. granulatus*, *E. quadrispinosus*), or pantropical (*E. lineatus*, *E. perarmatus*) taxa as

the oldest branches of the tree. It means that the place of origin of *Echiniscus* should be sought in the Northern rather than in the Southern Hemisphere. The hypothesis about the Laurasian origin of *Echiniscus* concurs with data for several other echiniscid genera that are found solely in the Holarctic, or are most speciose in the Northern Hemisphere, which suggests that they originated in the Northern Hemisphere: *Cornechiniscus* (see Gąsiorek & Michalczyk 2020a), *Diploechiniscus* (see Vicente *et al*. 2013), *Stellariscus* (see Gąsiorek *et al*. 2018b), *Testechiniscus* (see Gąsiorek *et al*. 2018a), or *Proechiniscus*, *Novechiniscus*, and *Parechiniscus* (see Kristensen 1987). Moreover, our phylogenetic analyses suggest that the evolution of reproductive modes (dioecy *vs* [facultative?] parthenogenesis) in *Echiniscus* is mosaic; as in *Milnesium* (Morek *et al*. 2021) and *Paramacrobiotus* (Guidetti *et al*. 2019), or other groups of microscopic invertebrates (*e.g*. oribatids, Domes *et al*. 2007).

TABLE 62. Approximate sex ratios in the populations of African dioecious *Echiniscus* species. Indices were calculated for populations consisting of above ten sexually mature specimens (adults). N—number of adults mounted on slides.

Species	Population	N	♂♂ : (♀♀+♂♂)	**Remarks**
Echiniscus attenboroughi **sp. nov.**	ZA.436	43	37.2%	♂♂ only in one of six examined populations
Echiniscus blumi	ZA.258	28	3.6%	see Guil & Giribet (2009)
Echiniscus gracilis **sp. nov.**	ZA.022	12	8.3%	–
	ZA.554	23	4.3%	
	ZA.555	18	5.6%	
Echiniscus imitans **sp. nov.**	ZA.227	59	22.0%	–
	ZA.247	15	20.0%	
	ZA.248	13	7.7%	
	ZA.480	13	7.7%	
Echiniscus intricatus **sp. nov.**	ZA.130	32	6.2%	–
	ZA.219	47	4.3%	
Echiniscus lichenorum	ZA.010	38	2.6%	♂♂ not recorded before
Echiniscus longispinosus	ZA.257	11	18.2%	♂♂ not recorded before
Echiniscus regularis **sp. nov.**	ZA.232	48	2.1%	–
	ZA.249	21	4.8%	
	ZA.252	22	31.8%	
Echiniscus scabrocirrosus **sp. nov.**	ZA.431	78	35.9%	the only species in which ♂♂ are almost always present in a population
	ZA.432	18	38.9%	
	ZA.480	18	27.8%	
Echiniscus setaceus **sp. nov.**	ZA.015	30	10.0%	–
	ZA.029	25	44.0%	
	ZA.490	11	18.2%	
	ZA.509	18	11.1%	
Echiniscus similaris **sp. nov.**	ZA.449	11	27.3%	secondary sexual dimorphism absent

We did not include five species in our list of South-African records that were reported from the region in the past: *B. bigranulata*, *E. crassispinosus fasciatus* Marcus, 1928, *E. duboisi* Richters, 1902, *P. jiroveci* Bartoš, 1963, and *P. suillus* (Ehrenberg, 1853). As discussed above, *B. bigranulata* is a valid species, but the South African record represents a different species. *Pseudechiniscus jiroveci* must be considered as a *nomen dubium* (Tumanov 2020b), and all former records of *P. suillus* were invalidated with the neotype redescription (Grobys *et al*. 2020). *Echiniscus duboisi* is certainly a *bona species*, but the details of its phenotype are unknown (Claxton 2004), as it has not yet been redescribed from the type locality in Java (Richters 1902). Considering that serration of trunk spines, once thought to be unique for *E. duboisi*, is a common trait among members of the *E. spinulosus* complex, the species is currently unidentfiable and designated herein as a *nomen inquirendum*. Finally, the subspecies of *E.*

crassispinosus recognised in the Marcus's monograph (1928) is highly dubious, because Marcus (1928) did not specify whether he examined Murray's specimens or erected a new taxon using only the description and illustration from Murray (1913). We stress that the description of *E. crassispinosus*, as provided by Murray (1913), is inconsistent (see remarks in the taxonomic part of this monograph), and so is the description of *E. crassispinosus fasciatus*, especially when these descriptions are confronted with the number of similar species of the *E. spinulosus* complex. Therefore, we designate *E. crassispinosus fasciatus* as a *nomen dubium*.

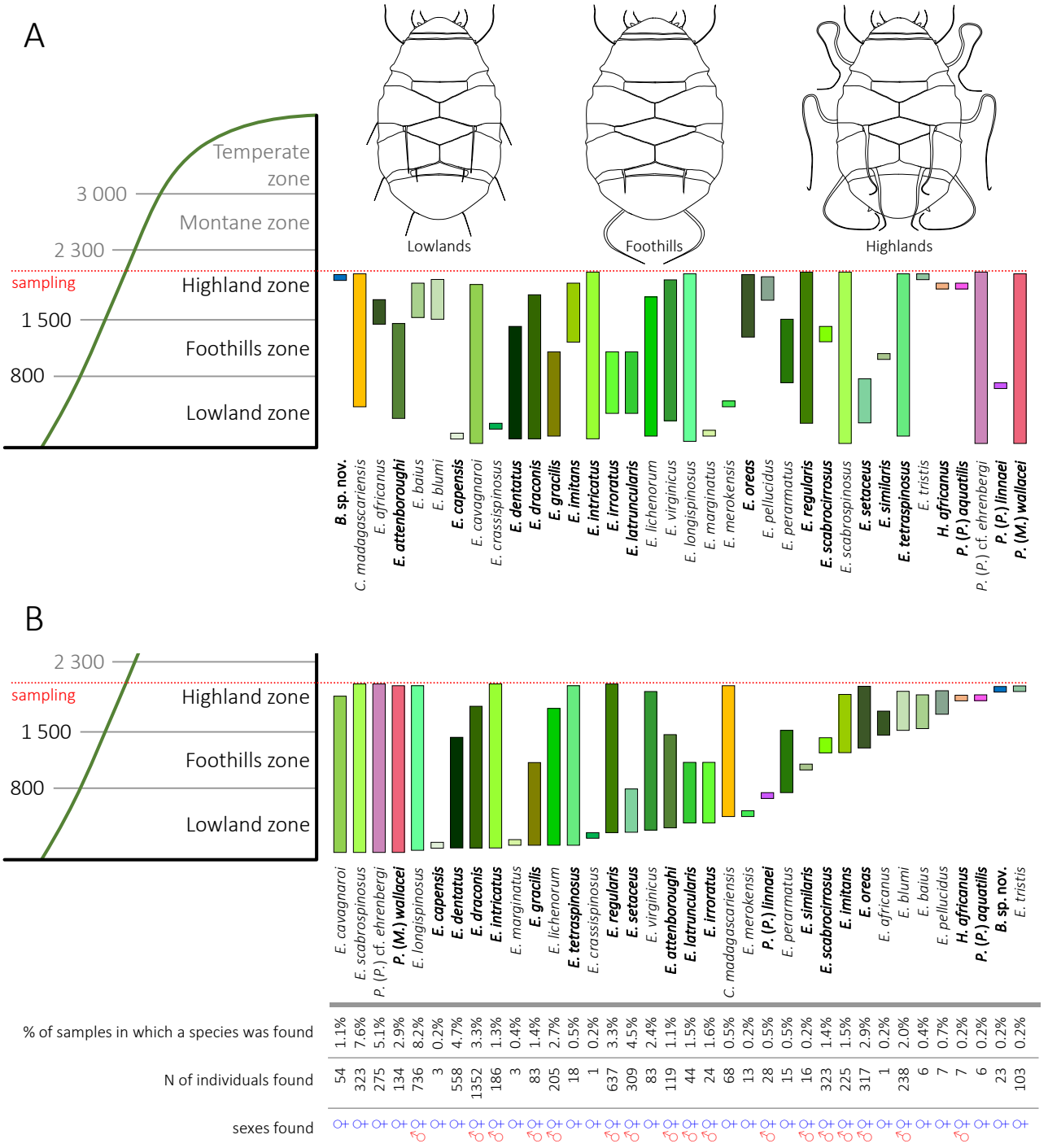

FIGURE 127. Altitudinal distribution of Echiniscidae in South Africa: (A) taxa arranged alphabetically, (B) taxa arranged with an increasing minimal elevation at which they occur. Floral zones follow Boughey (1956); the red line delimits the maximal elevation sampled during the expedition. Schematic drawings of three echiniscid species characteristic for the three lowest zones are depicted. New species are indicated by bold font.

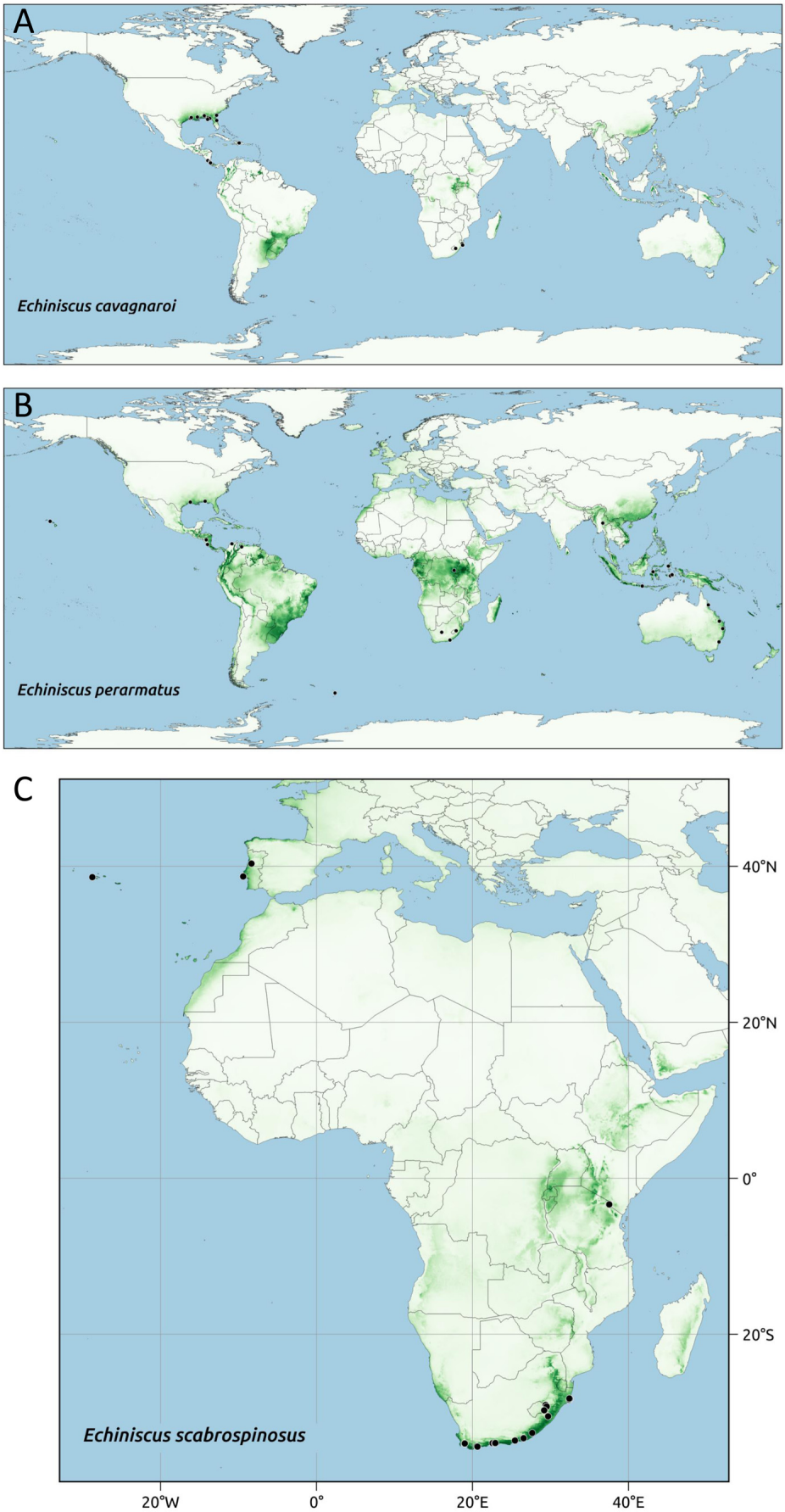

FIGURE 128. Modelled geographic distribution of: (A) *E. cavagnaroi*, (B) *E. perarmatus*, (C) *E. scabrospinosus*.

Untangling the Echiniscus Gordian knot: the diversity of sculpturing

The position of some *Echiniscus* spp. on the phylogenetic tree calls for a commentary with regard to their phenotype, especially to the dorsal sculpture. Specifically, *E. perarmatus* appeared as embedded within the *E. virginicus* complex (Fig. 117), which is in agreement with the supposition made by Gąsiorek *et al*. (2019a). The dominant endocuticular pillars in the dorsal plates are a distinctive characteristic of this clade. Consequently, we merge the *E. perarmatus* and *E. virginicus* complexes in a single *E. virginicus-perarmatus* complex of related species. The evolutionarily old character of the clade is corroborated by plesiomorphic characters of *E. perarmatus* (spines/receptors on all legs, cirri in the position *E*), whereas the evident epicuticular layer of ornamentation, specific for *E. lineatus* and its relatives, should be considered as an apomorphy.

In a recent step towards revising *Echiniscus* diversity (Gąsiorek *et al*. 2019a), a comparison of *E. granulatus* and the *E. blumi-canadensis* complex showed that a confident interpretation of the structure of cuticular sculpture can be performed only when LCM and SEM are used in tandem. In South Africa, the pair *E. imitans* **sp. nov.** + *E. quadrispinosus* is another example of a delusive convergence in the dorsal sculpturing. Large pores occur in the plates of both species, but *E. imitans* **sp. nov.** lacks endocuticular pillars typical for *E. quadrispinosus*. Another South African conundrum, whether *E. latruncularis* **sp. nov.** and *Claxtonia vincula* exhibit convergent sculpturing, cannot currently be solved since SEM photomicrographs are not available for *C. vincula*.

The monophyly of the *E. spinulosus* morphotype is challenged in the light of the presented diphyly (Fig. 117) and in accordance with our previous findings (Gąsiorek *et al*. 2021c): *E. belloporus* forms a clade of unappendaged species with *E. intricatus* **sp. nov.**, while all other species representing this complex belong to the second lineage. The important reason for such grouping may be highly aberrant barcodes for *E. belloporus*, that are much longer than for a typical *Echiniscus* species. Since the branch leading to *E. intricatus* **sp. nov.** is also very long, the clade *E. belloporus* + *E. intricatus* **sp. nov.** is potentially a long-branch attraction artefact (Bergsten 2005). From the morphological point of view, the sculpturing of *E. belloporus* is of a classic *spinulosus* type (Gąsiorek & Kristensen 2018) and having little in common with the complex sculpturing of *E. intricatus* **sp. nov.**

Conclusions

The diversity of echiniscids recovered from our large-scale survey, together with recently uncovered milnesiid lineages representing a number of potentially enedemic species (Morek *et al.* 2021), and the unusual species from other tardigrade families reported to date (McInnes *et al*. 2017), such as *Paradiphascon manningi* or *Ramazzottius szeptycki*, suggest that South Africa played an important role in the diversification of limno-terrestrial tardigrades. The two main mountain ranges of the Great Escarpment: Cape Fold Mountains and the Drakensberg, are of particular significance in this respect, as numerous endemic, stenotopic species inhabit the high elevations of these mountains. This is worrying from the nature conservation point of view, as it has been demonstrated that montane species with limited ranges are more vulnerable to extinction due to the climate changes (Ohlemüller *et al*. 2008). Tardigrades, together with nematodes and rotifers, are the main component of nival and glacier fauna (Zawierucha *et al*. 2018), thus the temperature raise will entail massive extinction of high-mountain biota.

Our analyses suggest that the South African echiniscid fauna is dominated by *Echiniscus*, with potential species complexes (*E. draconis* **sp. nov.**). More importantly, the regional *Echiniscus* community is largely specific, with a small fraction of species shared with Central Africa and other regions of the world. Premises leading to this biogeographic hypothesis are: (*i*) the mostly endemic South-African clade of *Echiniscus* uncovered in this study (Fig. 117); (*ii*) the absence of the genus *Kristenseniscus*, characterised by a tropical-subtropical distribution (Gąsiorek *et al*. 2019a); and (*iii*) the *Echiniscus spinulosus* group, which typically dominates *Echiniscus* communities in the tropics (Bochnak *et al*. 2020), not being a dominant component in South Africa. The topology of an updated phylogeny of *Echiniscus* (Fig. 117), in which the majority of South African species are grouped in mostly isolated clades (with no or few close African or extra-African relatives), indicates a derived and recent character of the South African fauna of Echiniscidae.

Acknowledgements

We are immensely grateful to Carol Simon (Stellenbosch University, Republic of South Africa) for her invaluable help in obtaining collecting and export permits and logistic support for WM and BS. Also, Thomas Pape and

Reinhardt M. Kristensen (University of Copenhagen, Denmark) are gratefully acknowledged for samples from the Waterval Nature Reserve. The samples were collected under permits No: CN35-285316 issued by CapeNature, OP 3570/2018 carried within iSimangaliso Wetland Park, a UNESCO World Heritage Site; both issued by Ezemvelo KZN Wildlife, all to WM. Sandra J. McInnes (British Antarctic Survey, United Kingdom), Reinhardt M. Kristensen and Denis V. Tumanov (Sankt Petersburg State University, Russia) are warmly acknowledged for spotting inconsistencies in the text and for their remarks that improved the manuscript. Roberto Guidetti (University of Modena and Reggio Emilia, Italy) and the Civic Museum of Natural History of Verona are thanked for making the Ramazzotti & Maucci collections available to us. Krzysztof Zając is thanked for performing the ecological modelling of species distributions. The study was supported by the *Preludium* programme (grant no. 2019/33/N/NZ8/02777 to PG) and the *Sonata Bis* programme (grant no. 2016/22/E/NZ8/00417 to ŁM) funded by the Polish National Science Centre, and a grant from the European Commission's Integrated Infrastructure Initiative programme SYNTHESYS (HU-TAF-2224 to ŁM).

References

Abe, W. & Takeda, M. (2000) A new record of *Cornechiniscus madagascariensis* Maucci, 1993 (Tardigrada: Echiniscidae) from India. *Proceedings of the Biological Society of Washington*, 113 (2), 480–485.

Abe, W., Utsugi, K. & Takeda, M. (1998) *Pseudechiniscus asper*, a new Tardigrada (Heterotardigrada: Echiniscidae) from Hokkaido, Northern Japan. *Proceedings of the Biological Society of Washington*, 111 (4), 843–848.

Allegrucci, G. & Sbordoni, V. (2019) Insights into the molecular phylogeny of Rhaphidophoridae, an ancient, worldwide lineage of Orthoptera. *Molecular Phylogenetics and Evolution*, 138, 126–138. https://doi.org/10.1016/j.ympev.2019.05.032

Anderson, R.P., Lew, D. & Peterson, A.T. (2003) Evaluating predictive models of species' distributions: criteria for selecting optimal models. *Ecological Modelling*, 162 (3), 211–232. https://doi.org/10.1016/S0304-3800(02)00349-6

Astrin, J.J. & Stüben, P.E. (2008) Phylogeny in cryptic weevils: molecules, morphology and new genera of western Palaearctic Cryptorhynchinae (Coleoptera: Curculionidae). *Invertebrate Systematics*, 22 (5), 503–522. https://doi.org/10.1071/IS07057

Barnard, K.H. (1932) South African may-flies (Ephemeroptera). *Transactions of the Royal Society of South Africa*, 21 (4), 201–259. https://doi.org/10.1080/00359193209518858

Barnard, K.H. (1934) South African caddis-flies (Trichoptera). *Transactions of the Royal Society of South Africa*, 21 (4), 291–394. https://doi.org/10.1080/00359193409518885

Bartoš, E. (1963) Die Tardigraden der chinesischen und javanischen Moosproben. *Acta Societatis Zoologicae Bohemoslovenicae*, 27 (2), 108–114.

Bartylak, T., Kulpa, A., Grobys, D., Kepel, M., Kepel, A., Kmita, H., Gawlak, M., Grabiński, W., Roszkowska, M. & Kaczmarek, Ł. (2019) Variability of *Echiniscus tristis* Gąsiorek & Kristensen, 2018—is morphology sufficient for taxonomic differentiation of Echiniscidae? *Zootaxa*, 4701 (1), 1–24. https://doi.org/10.11646/zootaxa.4701.1.1

Becker, R.A., Wilks, A.R., Brownrigg, R. & Minka, T.P. (2013) maps: Draw geographical maps. R package. Version 3.3.0. Available from: https://CRAN.R-project.org/package=maps (accessed 20 April 2021)

Bergsten, J. (2005) A review of long-branch attraction. *Cladistics*, 21 (2), 163–193. https://doi.org/10.1111/j.1096-0031.2005.00059.x

Bertolani, R. & Rebecchi, L. (1996) The tardigrades of Emilia (Italy). II. Monte Rondinaio. A multihabitat study on a high altitude valley of the northern Apennines. *Zoological Journal of the Linnean Society*, 116 (1–2), 3–12. https://doi.org/10.1111/j.1096-3642.1996.tb02329.x

Binda, M.G. (1984) Notizie sui Tardigradi dell'Africa Meridionale con descrizione di una nuove specie di *Apodibius* (Eutardigrada). *Animalia*, 11, 5–15.

Binda, M.G. & Pilato, G. (1987) Tardigrada dell'Africa. V. Notizie sui Tardigradi del Nord-Africa e descrizione della nuove specie *Macrobiotus diffusus*. *Animalia*, 14, 177–191.

Binda, M.G. & Pilato, G. (1994) Notizie sui Tardigradi delle Isole Hawaii con descrizione di due specie nuove. *Animalia*, 21 (1/3), 57–62.

Binda, M.G. & Pilato, G. (1995a) Some notes on African tardigrades with description of two new species. *Tropical Zoology*, 8 (2), 367–372. https://doi.org/10.1080/03946975.1995.10539294

Binda, M.G. & Pilato, G. (1995b) Remarks on tardigrades from the Seychelles, with a description of two new species. *Tropical Zoology*, 8 (1), 1–6. https://doi.org/10.1080/03946975.1995.10539269

Binda, M.G., Pilato, G., Moncada, E. & Napolitano, A. (2001) Some tardigrades from Central Africa with the description of two new species: *Macrobiotus ragonesei* and *M. priviterae* (Eutardigrada Macrobiotidae). *Tropical Zoology*, 14 (2), 233–242. https://doi.org/10.1080/03946975.2001.10531155

Bochnak, M., Vončina, K., Kristensen, R.M. & Gąsiorek, P. (2020) Continued exploration of Tanzanian rainforests reveals a new echiniscid species (Heterotardigrada). *Zoological Studies*, 59, 18. https://doi.org/10.6620/ZS.2020.59-18

Boughey, A.S. (1956) The nomenclature of the vegetation zones on the mountains of tropical Africa. *Webbia*, 11 (1), 413–423. https://doi.org/10.1080/00837792.1956.10669640

Bozhko, M.P. (1936) Tardigrada of the European parts of the U.S.S.R. *Proceedings of the Zoological and Biological Institute for Scientific Research in Kharkiv*, 1, 184–216.

Casquet, J., Thebaud, C. & Gillespie, R.G. (2012) Chelex without boiling, a rapid and easy technique to obtain stable amplifiable DNA from small amounts of ethanol-stored spiders. *Molecular Ecology Resources*, 12 (1), 136–141. https://doi.org/10.1111/j.1755-0998.2011.03073.x

Castresana, J. (2000) Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution*, 17 (4), 540–552. https://doi.org/10.1093/oxfordjournals.molbev.a026334

Cesari, M., Montanari, M., Kristensen, R.M., Bertolani, R., Guidetti, R. & Rebecchi, L. (2020) An integrated study of the biodiversity within the *Pseudechiniscus suillus–facettalis* group (Heterotardigrada: Echiniscidae). *Zoological Journal of the Linnean Society*, 188 (3), 717–732. https://doi.org/10.1093/zoolinnean/zlz045

Chernomor, O., von Haeseler, A. & Minh, B.Q. (2016) Terrace aware data structure for phylogenomic inference from supermatrices. *Systematic Biology*, 65 (6), 997–1008. https://doi.org/10.1093/sysbio/syw037

Chousou-Polydouri, N., Carmichael, A., Szűts, T., Saucedo, A., Gillespie, R., Griswold, C. & Wood, H.M. (2019) Giant goblins above the waves at the southern end of the world: The biogeography of the spider family Orsolobidae (Araneae, Dysderoidea). *Journal of Biogeography*, 46 (2), 332–342. https://doi.org/10.1111/jbi.13487

Claxton, S.K. (1996) Sexual dimorphism in Australian *Echiniscus* (Tardigrada, Echiniscidae) with descriptions of three new species. *Zoological Journal of the Linnean Society*, 116 (1–2), 13–33. https://doi.org/10.1111/j.1096-3642.1996.tb02330.x

Claxton, S.K. (2004) *The taxonomy and distribution of Australian terrestrial tardigrades*. Unpublished PhD thesis, Macquarie University, Sydney, 618 + 182 pp.

Cobos, M.E., Peterson, A.T., Barve, N. & Osorio-Olvera, L. (2019) *kuenm*: an R package for detailed development of ecological niche models using Maxent. *PeerJ*, 7, e6281. https://doi.org/10.7717/peerj.6281

Cowling, R.M., MacDonald, I.A.W. & Simmons, M.T. (1996) The Cape Peninsula, South Africa: physiographical, biological and historical background to an extraordinary hot-spot of biodiversity. *Biodiversity & Conservation*, 5, 527–550. https://doi.org/10.1007/BF00137608

Cowling, R.M., Pressey, R.L., Rouget, M. & Lombard, A.T. (2003) A conservation plan for a global biodiversity hotspot—the Cape Floristic Region, South Africa. *Biological Conservation*, 112 (1–2), 191–216. https://doi.org/10.1016/S0006-3207(02)00425-1

Cuénot, L. (1932) *Tardigrades*. *In*: Lechevalier, P. (Ed.), *Faune de France*, 24, pp. 1–96.

Dabert, J., Ehrnsberger, R. & Dabert, M. (2008) *Glaucalges tytonis* sp. nov. (Analgoidea: Xolalgidae) from the barn owl *Tyto alba* (Strigiformes: Tytonidae): compiling morphology with DNA barcode data for taxa descriptions in mites (Acari). *Zootaxa*, 1719 (1), 41–52. https://doi.org/10.11646/zootaxa.1719.1.2

da Cunha, A.X. & do Nascimento Ribeiro, F. (1962) A fauna de tardígrados da Ilha da Madeira. *Memórias e Estudos do Museu Zoológico da Universidade de Coimbra*, 279, 1–24.

da Cunha, A.X. & do Nascimento Ribeiro, F. (1964) Tardígrados de Angola. *Garcia de Orta, Lisboa*, 12, 397–406.

Daniels, S.R., Picker, M.D., Cowlin, R.M. & Hamer, M.L. (2009) Unravelling evolutionary lineages among South African velvet worms (Onychophora: *Peripatopsis*) provides evidence for widespread cryptic speciation. *Biological Journal of the Linnean Society*, 97 (1), 200–216. https://doi.org/10.1111/j.1095-8312.2009.01205.x

Daniels, S.R., Dambire, C., Klaus, S. & Sharma, P.P. (2016) Unmasking alpha diversity, cladogenesis and biogeographical patterning in an ancient panarthropod lineage (Onychophora: Peripatopsidae: *Opisthopatus cinctipes*) with the description of five novel species. *Cladistics*, 32 (5), 506–537. https://doi.org/10.1111/cla.12154

Dastych, H. (1980) *Hypsibius szeptycki* sp. nov., a new species of Tardigrada from South Africa. *Bulletin de l'Académie Polonaise des Sciences*, 27, 505–508.

Dastych, H. (1987) Altitudinal distribution of Tardigrada in Poland. *In*: Bertolani, R. (Ed.), *Biology of Tardigrades. Selected Symposia and Monographs, U.Z.I.*, 1, pp. 169–176.

Dastych, H. (1988) The Tardigrada of Poland. *Monografie Fauny Polski*, 16, 1–255.
Dastych, H. (1992) *Paradiphascon manningi* gen. n. sp. n., a new water-bear from South Africa, with the erecting of a new subfamily Diphasconinae (Tardigrada). *Mitteilungen aus dem Zoologischen Museum Hamburg*, 89, 125–139.
Dastych, H. (1993) A new genus and four new species of semiterrestrial water-bears from South Africa (Tardigrada). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 90, 175–186.
Dastych, H. (1999) A new species of the genus *Mopsechiniscus* Du Bois-Reymond Marcus, 1944 (Tardigrada) from the Venezuelan Andes. *Acta biologica Benrodis*, 10, 91–101.
Dastych, H. (2009) Notes on the African limno-terrestrial tardigrade *Ramazzottius szeptycki* (Dastych, 1980) (Tardigrada). *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, 15, 87–91.
de Barros, R. (1942) Tardígrados do Estado de São Paulo, Brasil. I. Introdução. Gêneros '*Echiniscus*' e '*Pseudechiniscus*'. *Revista Brasileira de Biologia*, 2 (3), 257–269.
Degma, P., Bertolani, R. & Guidetti, R. (2009–2021) Actual checklist of Tardigrada species. 40th Edition. Available from: https://iris.unimore.it/handle/11380/1178608#.Yl_7x9pByUk (accessed 20 October 2021)
https://doi.org/10.25431/11380_1178608
De Ridder, M. (1987) Distribution of rotifers in African fresh and inland saline waters. *In*: *Hydrobiologia*. Vol. 147. *In*: May, L., Wallace, R. & Herzig, A. (Eds.), *Rotifer Symposium IV. Developments in Hydrobiology*. *Vol. 42*. Springer, Dordrecht, pp. 9–14.
https://doi.org/10.1007/978-94-009-4059-8_3
Domes, K., Norton, R.A., Maraun, M. & Scheu, S. (2007) Reevolution of sexuality breaks Dollo's law. *PNAS*, 104 (17), 7139–7144.
https://doi.org/10.1073/pnas.0700034104
Doyère, P.L.N. (1840) Mémoire sur les Tardigrades. *Annales des Sciences Naturelles*, *Zoologie, Serie* 2, 14, 269–362.
Dumont, H.J. (1983) Biogeography of rotifers. *Hydrobiologia*, l04, 19–30.
https://doi.org/10.1007/BF00045948
Durante Pasa, M.V. & Maucci, W. (1979) Tardigradi muscicoli della Grecia. *Zeszyty Naukowe Uniwersytetu Jagiellońskiego*, 529 (25), 19–45.
Ehrenberg, C.G. (1853) Diagnoses novarum formarum. *Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin*, 8, 526–533.
Escobar, L.E., Lira-Noriega, A., Medina-Vogel, G. & Peterson, A.T. (2014) Potential for spread of the white-nose fungus (*Pseudogymnoascus destructans*) in the Americas: use of Maxent and NicheA to assure strict model transference. *Geospatial Health*, 9 (1), 221–229.
https://doi.org/10.4081/gh.2014.19
Fick, S.E. & Hijmans, R.J. (2017) WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37 (12), 4302–4315.
https://doi.org/10.1002/joc.5086
Fontoura, A.P. (1982) Deux nouvelles espèces de tardigrades muscicoles du Portugal. *Publicações do Instituto de Zoologia "Dr. Augusto Nobre" Faculdade de Ciências do Porto*, 165, 5–19.
Fontoura, P., Lisi, O. & Pilato, G. (2013) A new tardigrade *Doryphoribius maasaimarensis* sp. nov. (Eutardigrada: Hypsibiidae) from Kenya. *Zootaxa*, 3630 (2), 359–368.
https://doi.org/10.11646/zootaxa.3630.2.10
Fontoura, P., Pilato, G. & Lisi, O. (2008) Echiniscidae (Tardigrada, Heterotardigrada) from Faial and Pico Islands, the Azores, with the description of two new species. *Zootaxa*, 1693 (1), 49–61.
https://doi.org/10.11646/zootaxa.1693.1.4
Fontoura, P., Pilato, G. & Lisi, O. (2010) First record of Tardigrada from São Tomé (Gulf of Guinea, Western Equatorial Africa) and description of *Pseudechiniscus santomensis* sp. nov. (Heterotardigrada: Echiniscidae). *Zootaxa*, 2564 (1), 31–42.
https://doi.org/10.11646/zootaxa.2564.1.2
Foord, S.F., Dippenaar-Schoeman, A.S., Haddad, C.R., Lotz, L.N. & Lyle, R. (2011) The faunistic diversity of spiders (Arachnida: Araneae) of the Savanna Biome in South Africa. *Transactions of the Royal Society of South Africa*, 66 (3), 170–201.
https://doi.org/10.1080/0035919X.2011.639406
Gąsiorek, P. & Degma, P. (2018) Three Echiniscidae species (Tardigrada: Heterotardigrada) new to the Polish fauna, with the description of a new gonochoristic *Bryodelphax* Thulin, 1928. *Zootaxa*, 4410 (1), 77–96.
https://doi.org/10.11646/zootaxa.4410.1.4
Gąsiorek, P. & Kristensen, R.M. (2018) Echiniscidae (Heterotardigrada) of Tanzania and Uganda. *Tropical Zoology*, 31 (3), 131–160.
https://doi.org/10.1080/03946975.2018.1477350
Gąsiorek, P. & Michalczyk, Ł. (2020a) Revised *Cornechiniscus* (Heterotardigrada) denies recently hypothesised echiniscid subfamilies and tribes. *Royal Society Open Science*, 7, 200581.
https://doi.org/10.1098/rsos.200581
Gąsiorek, P. & Michalczyk, Ł. (2020b) *Echiniscus siticulosus* (Echiniscidae: *spinulosus* group), a new tardigrade from Western Australian scrub. *New Zealand Journal of Zoology*, 47 (2), 87–105.
https://doi.org/10.1080/03014223.2019.1603166

Gąsiorek, P. & Vončina, K. (2019) New Echiniscidae (Heterotardigrada) from Amber Mountain (Northern Madagascar). *Evolutionary Systematics*, 3, 29–39.
https://doi.org/10.3897/evolsyst.3.33580

Gąsiorek, P., Vončina, K. & Michalczyk, Ł. (2020) An overview of the sexual dimorphism in *Echiniscus* (Heterotardigrada, Echiniscoidea), with the description of *Echiniscus masculinus* sp. nov. (the *virginicus* complex) from Borneo. *Zoosystematics and Evolution*, 96 (1), 103–113.
https://doi.org/10.3897/zse.96.49989

Gąsiorek, P., Bochnak, M., Vončina, K. & Michalczyk, Ł. (2021c) Phenotypically exceptional *Echiniscus* species (Heterotardigrada: Echiniscidae) from Argentina (Neotropics). *Zoologischer Anzeiger*, 294, 210–228.
https://doi.org/10.1016/j.jcz.2021.08.003

Gąsiorek, P., Morek, W., Stec, D. & Michalczyk, Ł. (2019a) Untangling the *Echiniscus* Gordian knot: paraphyly of the "*arctomys* group" (Heterotardigrada: Echiniscidae). *Cladistics*, 35 (6), 633–653.
https://doi.org/10.1111/cla.12377

Gąsiorek, P., Stec, D., Morek, W. & Michalczyk, Ł. (2017) An integrative redescription of *Echiniscus testudo* (Doyère, 1840), the nominal taxon for the class Heterotardigrada (Ecdysozoa: Panarthropoda: Tardigrada). *Zoologischer Anzeiger*, 270, 107–122.
https://doi.org/10.1016/j.jcz.2017.09.006

Gąsiorek, P., Vončina, K., Kristensen, R.M. & Michalczyk, Ł. (2021d) High mountain echiniscid (Heterotardigrada) fauna of Taiwan. *Zoological Studies*, 60, 70.
https://doi.org/10.6620/ZS.2021.60-70

Gąsiorek, P., Vončina, K., Zając, K. & Michalczyk, Ł. (2021a) Phylogeography and morphological evolution of *Pseudechiniscus* (Heterotardigrada: Echiniscidae). *Scientific Reports*, 11, 7606.
https://doi.org/10.1038/s41598-021-84910-6

Gąsiorek, P. Wilamowski, A., Vončina, K. & Michalczyk, Ł. (2022) Neotropical jewels in the moss: biodiversity, distribution and evolution of the genus *Barbaria* (Heterotardigrada: Echiniscidae). *Zoological Journal of the Linnean Society*. [in press]
https://doi.org/10.1093/zoolinnean/zlab087

Gąsiorek, P., Stec, D., Zawierucha, K. Kristensen, R.M. & Michalczyk, Ł. (2018a) Revision of *Testechiniscus* Kristensen, 1987 (Heterotardigrada: Echiniscidae) refutes the polar-temperate distribution of the genus. *Zootaxa*, 4472 (2), 261–297.
https://doi.org/10.11646/zootaxa.4472.2.3

Gąsiorek, P., Suzuki, A.C., Kristensen, R.M., Lachowska-Cierlik, D. & Michalczyk, Ł. (2018b) Untangling the *Echiniscus* Gordian knot: *Stellariscus* gen. nov. (Heterotardigrada: Echiniscidae) from Far East Asia. *Invertebrate Systematics*, 32 (5), 1234–1247.
https://doi.org/10.1071/IS18023

Gąsiorek, P., Jackson, K.J., Meyer, H.A., Zając, K., Nelson, D.R., Kristensen, R.M. & Michalczyk, Ł. (2019b) *Echiniscus virginicus* complex: the first case of pseudocryptic allopatry and pantropical distribution in tardigrades. *Biological Journal of the Linnean Society*, 128 (4), 789–805.
https://doi.org/10.1093/biolinnean/blz147

Gąsiorek, P., Oczkowski, A., Blagden, B., Kristensen, R.M., Bartels, P.J., Nelson, D.R., Suzuki, A.C. & Michalczyk, Ł. (2021b) New Asian and Nearctic *Hypechiniscus* species (Heterotardigrada: Echiniscidae) indicate a pseudocryptic horn of plenty. *Zoological Journal of the Linnean Society*, 192 (3), 794–852.
https://doi.org/10.1093/zoolinnean/zlaa110

Gheerbrant, E. & Rage, J.-C. (2006) Paleobiogeography of Africa: How distinct from Gondwana and Laurasia? *Palaeogeography, Palaeoclimatology, Palaeoecology*, 241 (2), 224–246.
https://doi.org/10.1016/j.palaeo.2006.03.016

Goldberg, J., Trewick, S.A. & Paterson, A.M. (2008) Evolution of New Zealand's terrestrial fauna: a review of molecular evidence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363 (1508), 3319–3334.
https://doi.org/10.1098/rstb.2008.0114

Grigarick, A.A., Schuster, R.O. & Nelson, D.R. (1983) Heterotardigrada of Venezuela (Tardigrada). *Pan-Pacific Entomologist*, 59 (1–4), 64–77.

Grobys, D., Roszkowska, M., Gawlak, M., Kmita, H., Kepel, A., Kepel, M., Parnikoza, I., Bartylak, T. & Kaczmarek, Ł. (2020) High diversity in the *Pseudechiniscus suillus–facettalis* complex (Heterotardigrada: Echiniscidae) with remarks on the morphology of the genus *Pseudechiniscus*. *Zoological Journal of the Linnean Society*, 188 (3), 733–752.
https://doi.org/10.1093/zoolinnean/zlz171

Guidetti, R., Jönsson, K.I. & Kristensen, R.M. (2015) Tardigrades of Sweden; an updated check-list. *Zootaxa*, 3981 (4), 491–507.
https://doi.org/10.11646/zootaxa.3981.4.2

Guidetti, R., Cesari, M., Bertolani, R., Altiero, T. & Rebecchi, L. (2019) High diversity in species, reproductive modes and distribution within the *Paramacrobiotus richtersi* complex (Eutardigrada, Macrobiotidae). *Zoological Letters*, 5, 1.
https://doi.org/10.1186/s40851-018-0113-z

Guidetti, R., McInnes, S.J., Cesari, M., Rebecchi, L. & Rota-Stabelli, O. (2017) Evolutionary scenarios for the origin of an Antarctic tardigrade species based on molecular clock analyses and biogeographic data. *Contributions to Zoology*, 86 (2),

97–110.
https://doi.org/10.1163/18759866-08602001
Guil, N. & Giribet, G. (2009) Fine scale population structure in the *Echiniscus blumi-canadensis* series (Heterotardigrada, Tardigrada) in an Iberian mountain range—When morphology fails to explain genetic structure. *Molecular Phylogenetics and Evolution*, 51 (3), 606–613.
https://doi.org/10.1016/j.ympev.2009.02.019
Hansma, J., Tohver, E., Schrank, C., Jourdan, F. & Adams, D. (2016) The timing of the Cape Orogeny: New $^{40}Ar/^{39}Ar$ age constraints on deformation and cooling of the Cape Fold Belt, South Africa. *Gondwana Research*, 32, 122–137.
https://doi.org/10.1016/j.gr.2015.02.005
Heinis, F. (1928) Die Moosfauna des Krakatau. *Treubia,* 10, 231–244.
Helme, N.A. & Trinder-Smith, T.H. (2006) The endemic flora of the Cape Peninsula, South Africa. *South African Journal of Botany*, 72, 205–210.
https://doi.org/10.1016/j.sajb.2005.07.004
Hoang, D.T., Chernomor, O., von Haeseler, A., Minh, B.Q. & Vinh, L.S. (2018) UFBoot2: Improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution*, 35 (2), 518–522.
https://doi.org/10.1093/molbev/msx281
Horning, D.S., Schuster, R.O. & Grigarick, A.A. (1978) Tardigrada of New Zealand. *New Zealand Journal of Zoology*, 5 (2), 185–280.
https://doi.org/10.1080/03014223.1978.10428316
Iharos, G. (1967) Beitrage zur Kenntnis der Tardigradenfauna von Neuguinea. *Opuscula Zoologica*, 7 (1), 113–135.
Iharos, G. (1968) Ergebnisse der zoologischen Forschungen von Dr Z. Kaszab in der Mongolei. 162. Tardigrada, II. *Opuscula Zoologica*, 8 (1), 31–35.
Iharos, G. (1969) The scientific results of the Hungarian soil zoological expeditions to South America. 15. Tardigraden aus den Sammlungen der ersten und zweiten Expedition. *Opuscula Zoologica*, 9 (2), 279–289.
Iharos, G. (1973) Neuere Daten zur Kenntnis der Tardigraden-Fauna von Neuguinea. *Opuscula Zoologica*, 11 (1–2), 65–73.
Ito, M. (1993) Taxonomic study on the class Heterotardigrada (Tardigrada) from the northern slope of Mt. Fuji, Central Japan. *Edaphologia*, 50, 1–13.
Janion-Scheepers, C., Deharveng, L., Bedos, A. & Chown, S.L. (2015) Updated list of Collembola species currently recorded from South Africa. *ZooKeys*, 503, 55–88.
https://doi.org/10.3897/zookeys.503.8966
Janion-Scheepers, C., Measey, J., Braschler, B., Chown, S.L., Coetzee, L., Colville, J.F., Dames, J., Davies, A.B., Davies, S.J., Dais, A.L.V., Dippenaar-Schoemank, A.S., Duffy, G.A., Fourie, D., Griffiths, C., Haddad, C.R., Hamer, M., Herbert, D.G., Hugo-Coetzee, E.A., Jacobs, A., Jacobs, K., van Rensburg, C.J., Lamani, S., Lotz, L.N., Louw, S.M., Lyle, R., Malan, A.P., Marais, M., Neethling, J.A., Nxele, T.C., Plisko, D.J., Prendini, L., Rink, A.N., Swart, A., Theron, P., Truter, M., Ueckermann, E., Uys, V.M., Villet, M.H., Willows-Munro, S. & Wilson, J.R.U. (2016) Soil biota in a megadiverse country: Current knowledge and future research directions in South Africa. *Pedobiologia*, 59 (3), 129–174.
https://doi.org/10.1016/j.pedobi.2016.03.004
Jørgensen, A. (2001) Graphical presentation of the African tardigrade fauna using GIS with the description of *Isohypsibius malawiensis* sp. n. (Eutardigrada: Hypsibiidae) from Lake Malawi. *Zoologischer Anzeiger*, 240, 441–449.
https://doi.org/10.1078/0044-5231-00052
Jørgensen, A., Møbjerg, N. & Kristensen, R.M. (2007) A molecular study of the tardigrade *Echiniscus testudo* (Echiniscidae) reveals low DNA sequence diversity over a large geographical area. *Journal of Limnology*, 66 (Supplement 1), 77–83.
https://doi.org/10.4081/jlimnol.2007.s1.77
Kaczmarek, Ł. & Michalczyk, Ł. (2004) Notes on some tardigrades from South Africa, with the description of *Diphascon* (*Diphascon*) *zaniewi* sp. nov. (Eutardigrada: Hypsibiidae). *Zootaxa*, 576 (1), 1–6.
https://doi.org/10.11646/zootaxa.576.1.1
Kaczmarek, Ł. & Michalczyk, Ł. (2010) The genus *Echiniscus* Schultze 1840 (Tardigrada) in Costa Rican (Central America) rain forests with descriptions of two new species. *Tropical Zoology*, 23 (1), 91–106.
Kaczmarek, Ł., Beasley, C.W. & Michalczyk, Ł. (2006) The first record of the genus *Haplohexapodibius* Pilato & Beasley, 1987 in Africa, with notes on synonymy of *Hexapodibius beasleyi* Maucci, 1988, with *Haplohexapodibius seductor* Pilato & Beasley, 1987. *African Zoology*, 41 (2), 290–293.
https://doi.org/10.1080/15627020.2006.11407364
Kaczmarek, Ł., Michalczyk, Ł. & McInnes, S.J. (2014) Annotated zoogeography of non-marine Tardigrada. Part I: Central America. *Zootaxa*, 3763 (1), 1–62.
https://doi.org/10.11646/zootaxa.3763.1.1
Kaczmarek, Ł., Gołdyn, B., Wełnicz, W. & Michalczyk, Ł. (2011) Ecological factors determining Tardigrada distribution in Costa Rica. *Journal of Zoological Systematics and Evolutionary Research*, 49 (Supplement 1), 78–83.
https://doi.org/10.1111/j.1439-0469.2010.00603.x
Kalyaanamoorthy, S., Minh, B.Q., Wong, T.K.F., von Haeseler, A. & Jermiin, L.S. (2017) ModelFinder: Fast model selection for accurate phylogenetic estimates. *Nature Methods*, 14, 587–589.
https://doi.org/10.1038/nmeth.4285

Katoh, K. & Toh, H. (2008) Recent developments in the MAFFT multiple sequence alignment program. *Briefings in Bioinformatics*, 9 (4), 286–298.
https://doi.org/10.1093/bib/bbn013
Katoh, K., Misawa, K., Kuma, K. & Miyata, T. (2002) MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research*, 30 (14), 3059–3066.
https://doi.org/10.1093/nar/gkf436
Kayastha, P., Bartylak, T., Gawlak, M. & Kaczmarek, Ł. (2020) Integrative description of *Pseudechiniscus lalitae* sp. nov. (Tardigrada: Heterotardigrada: Echiniscidae) from the Azores Archipelago (Portugal). *Annales Zoologici*, 70 (4), 487–505.
https://doi.org/10.3161/00034541ANZ2020.70.4.002
Kessler, M. & Kluge, J. (2008) Diversity and endemism in tropical montane forests—from patterns to processes. *In*: Gradstein, S.R., Homeier, J. & Gansert, D. (Eds.), *The Tropical Mountain Forest—Patterns and Processes in a Biodiversity Hotspot. Biodiversity and Ecology Series*, 2, pp. 35–50.
Kiosya, Y., Vončina, K. & Gąsiorek, P. (2021) Echiniscidae in the Mascarenes: the wonders of Mauritius. *Evolutionary Systematics*, 5, 93–120.
https://doi.org/10.3897/evolsyst.5.59997
Kristensen, R.M. (1987) Generic revision of the Echiniscidae (Heterotardigrada), with a discussion of the origin of the family. *In*: Bertolani, R. (Ed.), *Biology of Tardigrades. Selected Symposia and Monographs U.Z.I.*, 1, pp. 261–335.
Kumar, S., Stecher, G. & Tamura, K. (2016) MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution*, 33 (7), 1870–1874.
https://doi.org/10.1093/molbev/msw054
Labarque, F.M., Pérez-González, A. & Griswold, C.E. (2018) Molecular phylogeny and revision of the false violin spiders (Araneae: Drymusidae) of Africa. *Zoological Journal of the Linnean Society*, 183 (2), 390–430.
https://doi.org/10.1093/zoolinnean/zlx088
Lanfear, R., Frandsen, P.B., Wright, A.M., Senfeld, T. & Calcott, B. (2017) PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution*, 34 (3), 772–773.
https://doi.org/10.1093/molbev/msw260
Li, X., Wang, L. & Yu, D. (2007) The Tardigrada fauna of China with descriptions of three new species of Echiniscidae. *Zoological Studies*, 46 (2), 135–147.
Linder, H.P. (2003) The radiation of the Cape flora, southern Africa. *Biological Reviews*, 78 (4), 597–638.
https://doi.org/10.1017/S1464793103006171
Linder, H.P., de Klerk, H.M., Born, J., Burgess, N.D., Fjeldså, J. & Rahbek, C. (2012) The partitioning of Africa: statistically defined biogeographical regions in sub-Saharan Africa. *Journal of Biogeography*, 39 (7), 1189–1205.
https://doi.org/10.1111/j.1365-2699.2012.02728.x
Lisi, O. (2011) Remarks on *Doryphoribius flavus* (Iharos, 1966), and description of three new species (Tardigrada, Hypsibiidae). *Zootaxa*, 2834 (1), 17–32.
https://doi.org/10.11646/zootaxa.2834.1.2
Lisi, O., Daza, A., Londoño, R. & Quiroga, S. (2017) Echiniscidae from the Sierra Nevada de Santa Marta, Colombia, new records and a new species of *Bryodelphax* Thulin, 1928 (Tardigrada). *ZooKeys*, 703, 1–14.
https://doi.org/10.3897/zookeys.703.12537
Marcus, E. (1927) Zur Anatomie und Ökologie mariner Tardigraden. *Zoologische Jahrbücher Abteilung für Systematik*, 53, 487–558.
Marcus, E. (1928) Spinnentiere oder Arachnoidea. IV. Bärtierchen (Tardigrada). *Tierwelt Deutschlands und der angrenzenden Meeresteile Jena*, 12, 1–230.
Marcus, E. (1936) Tardigrada. *Das Tierreich*, 66, 1–340.
Matenaar, D., Fingerle, M., Heym, E., Wirtz, S. & Hochkirch, A. (2018) Phylogeography of the endemic grasshopper genus *Betiscoides* (Lentulidae) in the South African Cape Floristic Region. *Molecular Phylogenetics and Evolution*, 118, 318–329.
https://doi.org/10.1016/j.ympev.2017.09.024
Maucci, W. (1972) Tardigradi muscicoli della Turchia. *Memorie del Museo Civico di Storia Naturale di Verona*, 20, 169–221.
Maucci, W. (1978) Una nuova specie di *Echiniscus* dall'Afganistan (Tardigrada, Echiniscoidea). *Memorie dell'Istituto Italiano di Idrobiologia*, 36, 117–120.
Maucci, W. (1983) *Echiniscus bisculptus* sp. nov., del Marocco, ed *E. lichenorum* sp. nov., del Portogallo. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale in Milano*, 124 (3–4), 257–261.
Maucci, W. (1986) Tardigrada. *Fauna d`Italia, Bologna, Calderini*, 24, 1–388.
Maucci, W. (1993) Prime notizie su Tardigradi 'terrestri' del Madagascar con descrizione di tre specie nuove. *Bollettino del Museo Civico di Storia Naturale di Verona*, 17, 381–392.
Maucci, W. & Ramazzotti, G. (1981) *Cornechiniscus* gen. nov.: Nuova posizione sistematica per i cosiddetti «*Pseudechiniscus* gruppo *cornutus*», con descrizione di una nuova specie (Tardigrada, Echiniscidae). *Memorie dell'Istituto Italiano di Idrobiologia*, 39, 147–151.
McDonald, D.E. & Daniels, S.R. (2012) Phylogeography of the Cape velvet worm (Onychophora: *Peripatopsis capensis*) reveals the impact of Pliocene/Pleistocene climatic oscillations on Afromontane forest in the Western Cape, South Africa. *Journal of Evolutionary Biology*, 25 (5), 824–835.
https://doi.org/10.1111/j.1420-9101.2012.02482.x

McGlone, M.T. (2005) Goodbye Gondwana. *Journal of Biogeography*, 32 (5), 739–740.
https://doi.org/10.1111/j.1365-2699.2005.01278.x

McInnes, S.J. (1994) Zoogeographic distribution of terrestrial/freshwater tardigrades from current literature. *Journal of Natural History*, 28 (2), 257–352.
https://doi.org/10.1080/00222939400770131

McInnes, S.J. (1995) Tardigrades from Signy Island, South Orkney Islands, with particular reference to freshwater species. *Journal of Natural History*, 29 (6), 1419–1445.
https://doi.org/10.1080/00222939500770601

McInnes, S.J. & Pugh, P.J.A. (2007) An attempt to revisit the global biogeography of limno-terrestrial Tardigrada. *Journal of Limnology*, 66 (Supplement 1), 90–96.
https://doi.org/10.4081/jlimnol.2007.s1.90

McInnes, S.J., Michalczyk, Ł. & Kaczmarek, Ł. (2017) Annotated zoogeography of non-marine Tardigrada. Part IV: Africa. *Zootaxa*, 4284 (1), 1–74.
https://doi.org/10.11646/zootaxa.4284.1.1

Merckx, V.S.F.T., Hendriks, K.P., Beentjes, K.K., Mennes, C.B., Becking, L.E., Peijnenburg, K.T.C.A., Afendy, A., de Boer, A.N.H., Biun, A., Buang, M.M., Chen, P., Chung, A.Y.C., Dow, R., Feijen, F.A.A., Feijen, H., Feijen-van Soest, C., Geml, J., Geurts, R., Gravendeel, B., Hovenkamp, P., Imbun, P., Ipor, I., Janssens, S.B., Jocqué, M., Kappes, H., Khoo, E., Koomen, P., Lens, F., Majapun, R.J., Morgado, L.N., Neupane, S., Nieser, N., Pereira, J.T., Rahman, H., Sabran, S., Sawang, A., Schwallier, R.M., Shim, P., Smit, H., Sol, N., Spait, M., Stech, M., Stokvis, F., Sugau, J.B., Suleiman, M., Sumail, S., Thomas, D.C., van Tol, J., Tuh, F.Y.Y., Yahya, B.E., Nais, J., Repin, R., Lakim, M. & Schilthhuizen, M. (2015) Evolution of endemism on a young tropical mountain. *Nature*, 524, 347–350.
https://doi.org/10.1038/nature14949

Meyer, H.A. (2016) Re-description of *Echiniscus cavagnaroi* Schuster & Grigarick, 1966 (Tardigrada: Heterotardigrada: Echiniscoidea: Echiniscidae) from type material, with new records from Hawaii and Bermuda. *Zootaxa*, 4121 (5), 575–582.
https://doi.org/10.11646/zootaxa.4121.5.7

Meyer, H.A. & Hinton, J.G. (2009) The Tardigrada of southern Africa, with the description of *Minibiotus harrylewisi*, a new species from KwaZulu-Natal, South Africa (Eutardigrada: Macrobiotidae). *African Invertebrates*, 50 (2), 255–268.
https://doi.org/10.5733/afin.050.0203

Meyer, H.A., Hinton, J.G. & Samletzka, C.A. (2013) Water bears in the anthropocene: a comparison of urban and woodland tardigrade (Phylum Tardigrada) communities in Southwestern Louisiana, USA. *Journal of Limnology*, 72 (Supplement 1), 123–127.
https://doi.org/10.4081/jlimnol.2013.s1.e15

Meyer, H.A., Tsaliki, M. & Hinton, J.G. (2018) First records of water bears (Phylum Tardigrada) from Swaziland. *African Invertebrates*, 59 (1), 47–53.
https://doi.org/10.3897/afrinvertebr.59.23191

Michalczyk, Ł. & Kaczmarek, Ł. (2013) The Tardigrada Register: a comprehensive online data repository for tardigrade taxonomy. *Journal of Limnology*, 72 (Supplement 1), 175–181.
https://doi.org/10.4081/jlimnol.2013.s1.e22

Michalczyk, Ł., Wełnicz, W., Frohme, M. & Kaczmarek, Ł. (2012) Redescriptions of three *Milnesium* Doyère, 1840 taxa (Tardigrada: Eutardigrada: Milnesiidae), including the nominal species for the genus. *Zootaxa*, 3154 (1), 1–20.
https://doi.org/10.11646/zootaxa.3154.1.1

Middleton, R.C. (2003) Tardigrades in southern Africa. *African Journal of Ecology*, 41 (3), 280–282.
https://doi.org/10.1046/j.1365-2028.2003.00439.x

Miller, W.R., Claxton, S.K., Heatwole, H.F. (1999) Tardigrades of the Australian Antarctic Territories: Males in the genus *Echiniscus* (Tardigrada: Heterotardigrada). *Zoologischer Anzeiger*, 238 (3–4), 303–309.

Mironov, S.V., Dabert, J. & Dabert, M. (2012) A new feather mite species of the genus *Proctophyllodes* Robin, 1877 (Astigmata: Proctophyllodidae) from the Long-tailed Tit *Aegithalos caudatus* (Passeriformes: Aegithalidae): morphological description with DNA barcode data. *Zootaxa*, 3253 (1), 54–61.
https://doi.org/10.11646/zootaxa.3253.1.2

Moon, S.Y. & Kim, W. (1994) New species of *Echiniscus* (Heterotardigrada: Echiniscoidea: Echiniscidae) from Korea. *Proceedings of the Biological Society of Washington*, 107, 511–513.

Morek, W., Surmacz, B., López-López, A. & Michalczyk, Ł. (2021) "Everything is *not* everywhere": Time-calibrated phylogeography of the genus *Milnesium* (Tardigrada). *Molecular Ecology*, 30 (14), 3590–3609.
https://doi.org/10.1111/mec.15951

Morgan, C.I. (1977) An annotated catalogue of Tardigrada in the collections of the Royal Scottish Museum, Edinburgh. *Natural History*, 5, 1–29.

Moussalli, A., Herbert, D.G. & Stuart-Fox, D. (2009) A phylogeny of the cannibal snails of southern Africa, genus *Natalina sensu lato* (Pulmonata: Rhytididae): Assessing concordance between morphology and molecular data. *Molecular Phylogenetics and Evolution*, 52 (1), 167–182.
https://doi.org/10.1016/j.ympev.2009.02.018

Murray, J. (1907a) Some South African Tardigrada. *Journal of the Royal Microscopical Society*, 27 (5), 515–524. https://doi.org/10.1111/j.1365-2818.1907.tb01665.x
Murray, J. (1907b) Scottish Tardigrada, collected by the lake survey. *Transactions of the Royal Society Edinburgh*, 45 (3), 641–668. https://doi.org/10.1017/S0080456800011777
Murray, J. (1910) Tardigrada. British Antarctic Expedition 1907–1909. *Reports on the Scientific Investigations*, *Biology (Part V)*, 1, 83–187. https://doi.org/10.5962/bhl.title.22427
Murray, J. (1913) African Tardigrada. *Journal of the Royal Microscopical Society*, 33 (2), 136–144. https://doi.org/10.1111/j.1365-2818.1913.tb01014.x
Nguyen, L.-T., Schmidt, H.A., von Haeseler, A. & Minh, B.Q. (2015) IQ-TREE: A fast and effective stochastic algorithm for estimating maximum likelihood phylogenies. *Molecular Biology and Evolution*, 32 (1), 268–274. https://doi.org/10.1093/molbev/msu300
Niedbała, W. (2006) Ptyctimous mites (Acari: Oribatida) of South Africa. *Annales Zoologici*, 56 (Supplement 1), 1–97. https://doi.org/10.3161/000345406778553355
Ohlemüller, R., Anderson, B.J., Araújo, M.B., Butchart, S.H.M., Kudrna, O., Ridgely, R.S. & Thomas, C.D. (2008) The coincidence of climatic and species rarity: high risk to small-range species from climate change. *Biology Letters*, 4 (5), 568–572. https://doi.org/10.1098/rsbl.2008.0097
Peters, M.K., Hemp, A., Appelhans, T., Behler, C., Classen, A., Detsch, F., Ensslin, A., Ferger, S.W., Frederiksen, S.B., Gebert, F., Haas, M., Helbig-Bonitz, M., Hemp, C., Kindeketa, W.J., Mwangomo, E., Ngereza, C., Otte, I., Röder, J., Rutten, G., Schellenberger Costa, D., Tardanico, J., Zancolli, G., Deckert, J., Eardley, C.D., Peters, R.S., Rödel, M.O., Schleuning, M., Ssymank, A., Kakengi, V., Zhang, J., Böhning-Gaese, K., Brandl, R., Kalko, E.K.V., Kleyer, M., Nauss, T., Tschapka, M., Fischer, M. & Steffan-Dewenter, I. (2016) Predictors of elevational biodiversity gradients change from single taxa to the multi-taxa community level. *Nature Communications*, 7, 13736. https://doi.org/10.1038/ncomms13736
Peterson, A.T., Papeş, M. & Soberón, J. (2008) Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecological Modelling*, 213 (1), 63–72. https://doi.org/10.1016/j.ecolmodel.2007.11.008
Phillips, S.J., Anderson, R.P., Dudík, M., Schapire, R.E. & Blair, M.E. (2017) Opening the black box: an open-source release of Maxent. *Ecography*, 40 (7), 887–893. https://doi.org/10.1111/ecog.03049
Picker, M.D. & Samways, M.J. (1996) Faunal diversity and endemicity of the Cape Peninsula, South Africa—a first assessment. *Biodiversity and Conservation*, 5 (5), 591–606. https://doi.org/10.1007/BF00137611
Pilato, G. & Binda, M.G. (1990) Notizie sui Tardigradi muscicoli di Bali (Indonesia). *Animalia*, 17, 209–218.
Pilato, G., Binda, M.G. & Catanzaro, R. (1991) Remarks on some tardigrades of the African fauna with the description of three new species of *Macrobiotus* Schultze 1834. *Tropical Zoology*, 4 (2), 167–178. https://doi.org/10.1080/03946975.1991.10539487
Pilato, G., Binda, M.G. & Lisi, O. (2003) Notes on some tardigrades from Central Africa, with the description of a new species of Hypsibiidae. *Zootaxa*, 241 (1), 1–7. https://doi.org/10.11646/zootaxa.241.1.1
Pilato, G., Binda, M.G. & Lisi, O. (2005) Remarks on some Echiniscidae (Heterotardigrada) from New Zealand with the description of two new species. *Zootaxa*, 1027 (1), 27–45. https://doi.org/10.11646/zootaxa.1027.1.2
Pilato, G., Claxton, S. & Binda, M.G. (1989) Tardigrades from Australia. III. *Echiniscus marcusi* and *Macrobiotus peteri*, new species of tardigrades from New South Wales. *Animalia*, 16, 43–48.
Pilato, G., Fontoura, P., Lisi, O. & Beasley, C. (2008) New description of *Echiniscus scabrospinosus* Fontoura, 1982, and description of a new species of *Echiniscus* (Heterotardigrada) from China. *Zootaxa*, 1856 (1), 41–54. https://doi.org/10.11646/zootaxa.1856.1.4
Pleijel, F., Jondelius, U., Norlinder, E., Nygren, A., Oxelman, B., Schander, C., Sundberg, P. & Thollesson, M. (2008) Phylogenies without roots? A plea for the use of vouchers in molecular studies. *Molecular Phylogenetics and Evolution*, 48 (1), 369–371. https://doi.org/ 10.1016/j.ympev.2008.03.024
Plisko, J.D. (2012) Notes on the status of the family Microchaetidae. *Zoology in the Middle East*, 58 (Supplement 4), 47–58. https://doi.org/10.1080/09397140.2012.10648984
Proctor, H.C., Smith, I.M., Cook, D.R. & Smith, B.P. (2015) Chapter 25. Subphylum Chelicerata, Class Arachnida. *In*: Thorp, J.H. & Rogers, D.C. (Eds.), *Thorp and Covich's Freshwater Invertebrates*. *4th Edition*. Academic Press, Cambridge, pp. 599–660. https://doi.org/10.1016/B978-0-12-385026-3.00025-5
QGIS Development Team (2020) QGIS Geographic Information System. Open Source Geospatial Foundation Project. Available form: https://www.qgis.org/en/site/ (accessed 20 April 2022)

Rahm, G. (1931) Tardigrada of the South of America. *Revista Chilena de Historia Natural*, 35, 118–141.
Rahm, G. (1932) Freilebende Nematoden, Rotatorien und Tardigraden aus Südamerika (besonders aus Chile). *Zoologisher Anzeiger*, 98, 94–128.
Ramazzotti, G. (1943) Nuova varieta del tardigrado *Pseudechiniscus cornutus*. *Rivista di Scienze Naturali 'Natura'*, 34, 89–90.
Ramazzotti, G. (1956) I Tardigradi delle Alpi. *Memorie dell'Istituto Italiano di Idrobiologia*, 9, 273–290.
Ramazzotti, G. & Maucci, W. (1983) Il Phylum Tardigrada. III edizione riveduta e aggiornata. *Memorie dell'Istituto Italiano di Idrobiologia*, 41, 1–1012.
Rambaut, A., Suchard, M.A., Xie, D. & Drummond, A.J. (2014) Tracer. Version 1.6. Available from: https://beast.bio.ed.ac.uk/Tracer (accessed 15 March 2020)
R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available from: https://www.R-project.org/ (accessed 20 April 2022)
Richters, F. (1902) Neue Moosbewohner. *Bericht über die Senckenbergische Naturforschende Gesselschaft in Frankfurt am Main*, 1902, 23–26.
Richters, F. (1903) Nordische Tardigraden. *Zoologisher Anzeiger*, 27, 168–172.
Richters, F. (1904) Arktische Tardigraden. *Fauna Arctica*, 3, 495–508.
Richters, F. (1907) Antarktische Tardigraden. *Zoologischer Anzeiger*, 31, 915–916.
Richters, F. (1926) Tardigrada. In: Kükenthal, W. & Krumbach, T. (Eds.), *Handbuch der Zoologie*. *Vol. 3*. Walter de Gruyter & Co., Berlin and Leipzig, pp. 58–61.
Riggin, G.T. (1962) Tardigrada of Southwest Virginia: with the addition of a description of a new marine species from Florida. *Virginia Agricultural Experimental Station, Technical Bulletin*, 152, 1–145.
Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19 (12), 1572–1574.
https://doi.org/10.1093/bioinformatics/btg180
Roszkowska, M., Grobys, D., Bartylak, T., Gawlak, M., Kmita, H., Kepel, A., Kepel, M., Parnikoza, I. & Kaczmarek, Ł. (2020) Integrative description of five *Pseudechiniscus* species (Heterotardigrada; Echiniscidae; the *suillus-facettalis* complex). *Zootaxa*, 4763 (4), 451–484.
https://doi.org/10.11646/zootaxa.4763.4.1
Roszkowska, M., Grobys, D., Zawierucha, K., Kmita, H. & Kaczmarek, Ł. (2018) Clarification of taxonomic status and geographic distribution of *Echiniscus merokensis* Richters, 1904 *sensu lato* in the light of integrative taxonomy. *Abstract Book of the 14th International Symposium on Tardigrada, Copenhagen*, 30 July–3 August, pp. 79.
Sanmartín, I. (2012) Historical biogeography: Evolution in time and space. *Evolution: Education and Outreach*, 5, 555–568.
https://doi.org/10.1007/s12052-012-0421-2
Sartory, D.P. (1981) Some planktonic brachionid rotifers from South African impoundments. *Journal of the Limnological Society of Southern Africa*, 7 (1), 29–36.
https://doi.org/10.1080/03779688.1981.9632935
Schultze, C.A.S. (1840) *Echiniscus Bellermanni, animal crustaceum, Macrobioto Hufelandii affine*. Apud G. Reimer, Berlin, 8 pp.
Schuster, R.O. & Grigarick, A.A. (1966a) New Tardigrada from Western North America: II, *Echiniscus*. *Proceedings of the Entomological Society of Washington*, 79, 127–130.
Schuster, R.O. & Grigarick, A.A. (1966b) Tardigrada from the Galápagos and Cocos Islands. *Proceedings of the California Academy of Sciences*, 34, 315–328.
Schuster, R.O. & Grigarick, A.A. (1971) Two new species of *Echiniscus* from the Pacific Northwest. *Proceedings of the Entomological Society of Washington*, 73 (2), 105–110.
Séméria, Y. (1985) Deux nouvelles formes de tardigrades du Nicaragua: *Echiniscus maesi* n. sp. (Heterotardigrada, Echiniscoidea, Echiniscidae) et *Macrobiotus islandicus nicaraguensis* n. ssp. (Eutardigrada, Macrobiotidae). *Comptes rendus de l'Academie de Sciences, Paris*, *Serie III*, 300 (1), 9–11.
Séméria, Y. (2003) Une espèce nouvelle de tardigrade pour l'Ile de la Reunion: *Cornechiniscus madagascariensis* Maucci. *Bulletin mensuel de la Société linnéenne de Lyon*, 72 (7), 233–234.
https://doi.org/10.3406/linly.2003.13476
Smirnov, N.N. (2008) Check-List of the South-African Cladocera (Crustacea: Branchiopoda). *Zootaxa*, 1788 (1), 47–56.
https://doi.org/10.11646/zootaxa.1788.1.4
Stec, D., Zawierucha, K. & Michalczyk, Ł. (2017) An integrative description of *Ramazzottius subanomalus* (Biserov, 1985) (Tardigrada) from Poland. *Zootaxa*, 4300 (3), 403–420.
https://doi.org/10.11646/zootaxa.4300.3.4
Stec, D., Smolak, R., Kaczmarek, Ł. & Michalczyk, Ł. (2015) An integrative description of *Macrobiotus paulinae* sp. nov. (Tardigrada: Eutardigrada: Macrobiotidae: *hufelandi* group) from Kenya. *Zootaxa*, 4052 (5), 501–526.
https://doi.org/10.11646/zootaxa.4052.5.1
Teunissen, R.J.H. (1938) Tardigraden. *Exploration du Parc National Albert. Mission G. F. de Witte (1933–1935)*, 16, 1–21.
Thulin, G. (1911) Beiträge zur Kenntnis der Tardigradenfauna Schwedens. *Arkiv för zoologi*, 7, 1–60.
https://doi.org/10.5962/bhl.part.1270

Thulin, G. (1928) Über die Phylogenie und das System der Tardigraden. *Heriditas*, 11 (2–3), 207–266. https://doi.org/10.1111/j.1601-5223.1928.tb02488.x
Tolley, K.A., Tilbury, C.R., Branch, W.R. & Matthee, C.A. (2004) Phylogenetics of the southern African dwarf chameleons, *Bradypodion* (Squamata: Chamaeleonidae). *Molecular Phylogenetics and Evolution*, 30 (2), 354–365. https://doi.org/10.1016/S1055-7903(03)00211-2
Toussaint, E.F.A., Bloom, D. & Short, A.E.Z. (2017) Cretaceous West Gondwana vicariance shaped giant water scavenger beetle biogeography. *Journal of Biogeography*, 44 (9), 1952–1965. https://doi.org/10.1111/jbi.12977
Trifinopoulos, J., Nguyen, L.T., von Haeseler, A. & Minh, B.Q. (2016) W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Research*, 44 (W1), 232–235. https://doi.org/10.1093/nar/gkw256
Truswell, J.F. (1977) *Geological evolution of South Africa*. Purnell, Cape Town, vi + 218 pp.
Tumanov, D.V. (2020a) Integrative description of *Mesobiotus anastasiae* sp. Eutardigrada, Macrobiotoidea) and first record of *Lobohalacarus* (Chelicerata, Trombidiformes) from the Republic of South Africa. *European Journal of Taxonomy*, 726, 102–131. https://doi.org/10.5852/ejt.2020.726.1179
Tumanov, D.V. (2020b) Analysis of non-morphometric morphological characters used in the taxonomy of the genus *Pseudechiniscus* (Tardigrada: Echiniscidae). *Zoological Journal of the Linnean Society*, 188 (3), 753–775. https://doi.org/10.1093/zoolinnean/zlz097
Vaidya, G., Lohman, D.J. & Meier, R. (2011) SequenceMatrix: concatenation software for the fast assembly of multi-gene datasets with character set and codon information. *Cladistics*, 27 (2), 171–180. https://doi.org/10.1111/j.1096-0031.2010.00329.x
Vecchi, M., Cesari, M., Bertolani, R., Jönsson, K.I., Rebecchi, L. & Guidetti, R. (2016) Integrative systematic studies on tardigrades from Antarctica identify new genera and new species within Macrobiotoidea and Echiniscoidea. *Invertebrate Systematics*, 30 (4), 303–322. https://doi.org/10.1071/IS15033
Vicente, F., Fontoura, P., Cesari, M., Rebecchi, L., Guidetti, R., Serrano, A. & Bertolani, R. (2013) Integrative taxonomy allows the identification of synonymous species and the erection of a new genus of Echiniscidae (Tardigrada, Heterotardigrada). *Zootaxa*, 3613 (6), 557–572. https://doi.org/10.11646/zootaxa.3613.6.3
Vončina, K., Kristensen, R.M. & Gąsiorek, P. (2020) *Pseudechiniscus* in Japan: re-description of *Pseudechiniscus asper* Abe *et al.*, 1998 and description of *Pseudechiniscus shintai* sp. nov. *Zoosystematics and Evolution*, 96 (2), 527–536. https://doi.org/10.3897/zse.96.53324
Vorster, M. & Roux, P.W. (1983) Veld of the karoo areas. *Proceedings of the Annual Congresses of the Grassland Society of Southern Africa*, 18 (1), 18–24. https://doi.org/10.1080/00725560.1983.9648975
Wang, L., Xue, J. & Li, X. (2018) A description of *Pseudechiniscus xiai* sp. nov., with a key to genus *Pseudechiniscus* in China. *Zootaxa*, 4388 (2), 255–264. https://doi.org/10.11646/zootaxa.4388.2.7
Wełnicz, W., Grohme, M.A., Kaczmarek, Ł., Schill, R.O. & Frohme, M. (2011) ITS-2 and 18S rRNA data from *Macrobiotus polonicus* and *Milnesium tardigradum* (Eutardigrada, Tardigrada). *Journal of Zoological Systematics and Evolutionary Research*, 49 (Supplement 1), 34–39. https://doi.org/10.1111/j.1439-0469.2010.00595.x
White, T.J., Bruns, T., Lee, S. & Taylor, J. (1990) *PCR protocols: a guide to methods and application*. Academic Press, San Diego, California, pp. 315–322.
Xue, J., Li, X., Wang, L., Xian, P. & Chen, H. (2017) *Bryochoerus liupanensis* sp. nov. and *Pseudechiniscus chengi* sp. nov. (Tardigrada: Heterotardigrada: Echiniscidae) from China. *Zootaxa*, 4291 (2), 324–334. https://doi.org/10.11646/zootaxa.4291.2.5
Zawierucha, K., Smykla, J., Michalczyk, Ł., Gołdyn, B. & Kaczmarek, Ł. (2015) Distribution and diversity of Tardigrada along altitudinal gradients in the Hornsund, Spitsbergen (Arctic). *Polar Research*, 34, 24168. https://doi.org/10.3402/polar.v34.24168
Zawierucha, K., Gąsiorek, P., Buda, J., Uetake, J., Janko, K. & Fontaneto, D. (2018) Tardigrada and Rotifera from moss microhabitats on a disappearing Ugandan glacier, with the description of a new species of water bear. *Zootaxa*, 4392 (2), 311–328. https://doi.org/10.11646/zootaxa.4392.2.5
Zeller, C. (2010) *Untersuchung der Phylogenie von Tardigraden anhand der Genabschnitte 18S rDNA und Cytochrom c Oxidase Untereinheit 1* (*COX I*). Unpublished MSc Thesis, Technische Hochschule Wildau, Wildau, 105 pp.

APPENDIX 1. Alphabetic index of the 95 echiniscid species mentioned in this work.

Species	Authority	Reference
Barbaria bigranulata	(Richters, 1907)	Richters (1907)
Bryodelphax parvulus	Thulin, 1928	Thulin (1928)
Claxtonia vincula	Horning, Schuster & Grigarick, 1978	Horning *et al*. (1978)
Cornechiniscus lobatus	(Ramazzotti, 1943)	Ramazzotti (1943)
Cornechiniscus madagascariensis	Maucci, 1993	Maucci (1993)
Diploechiniscus oihonnae	(Richters, 1903)	Richters (1903)
Echiniscus africanus	Murray, 1907	Murray (1907a)
Echiniscus angolensis	da Cunha & do Nascimento Ribeiro, 1964	da Cunha & do Nascimento Ribeiro (1964)
Echiniscus attenboroughi	Gąsiorek, Vončina, Morek & Michalczyk, 2022	This study
Echiniscus baius	Marcus, 1928	Marcus (1928)
Echiniscus baloghi	Iharos, 1973	Iharos (1973)
Echiniscus belloporus	Gąsiorek & Kristensen, 2018	Gąsiorek & Kristensen (2018)
Echiniscus bisculptus	Maucci, 1983	Maucci (1983)
Echiniscus becki	Schuster & Grigarick, 1966	Schuster & Grigarick (1966a)
Echiniscus blumi	Richters, 1903	Richters (1903)
Echiniscus canadensis	Murray, 1910	Murray (1910)
Echiniscus capensis	Gąsiorek, Vončina, Morek & Michalczyk, 2022	This study
Echiniscus cavagnaroi	Schuster & Grigarick, 1966	Schuster & Grigarick (1966b)
Echiniscus crassispinosus	Murray, 1907	Murray (1907a)
Echiniscus dentatus	Vončina, Gąsiorek, Morek & Michalczyk, 2022	This study
Echiniscus dikenli	Maucci, 1973	Maucci (1973)
Echiniscus draconis	Vončina, Gąsiorek, Morek & Michalczyk, 2022	This study
Echiniscus dreyfusi	de Barros, 1942	de Barros (1942)
Echiniscus duboisi	Richters, 1902	Richters (1902)
Echiniscus egnatiae	Durante Pasa & Maucci, 1979	Durante Pasa & Maucci (1979)
Echiniscus elaeinae	Pilato, Binda & Lisi, 2005	Pilato *et al*. (2005)
Echiniscus gracilis	Gąsiorek, Vončina, Morek & Michalczyk, 2022	This study
Echiniscus hoonsooi	Moon & Kim, 1990	Moon & Kim (1990)
Echiniscus imitans	Gąsiorek, Vončina, Morek & Michalczyk, 2022	This study
Echiniscus insularis	Gąsiorek, Vončina & Kiosya, 2021	Kiosya *et al*. (2021)
Echiniscus intricatus	Gąsiorek, Vončina, Morek & Michalczyk, 2022	This study
Echiniscus irroratus	Gąsiorek, Vončina, Morek & Michalczyk, 2022	This study
Echiniscus knowltoni	Schuster & Grigarick, 1971	Schuster & Grigarick (1971)
Echiniscus lapponicus	Thulin, 1911	Thulin (1911)
Echiniscus laterosetosus	Ito, 1993	Ito (1993)
Echiniscus latruncularis	Gąsiorek, Vončina, Morek & Michalczyk, 2022	This study
Echiniscus lichenorum	Maucci, 1983	Maucci (1983)
Echiniscus lineatus	Pilato, Fontoura, Lisi & Beasley, 2008	Pilato *et al*. (2008)
Echiniscus longispinosus	Murray, 1907	Murray (1907a)
Echiniscus manuelae	da Cunha & do Nascimento Ribeiro, 1962	da Cunha & do Nascimento Ribeiro (1962)
Echiniscus marcusi	Pilato, Claxton & Binda, 1989	Pilato *et al*. (1989)
Echiniscus marginatus	Binda & Pilato, 1994	Binda & Pilato (1994)

.....conitnued on the next page

APPENDIX 1. (Continued)

Species	Authority	Reference
Echiniscus merokensis	Richters, 1904	Richters (1904)
Echiniscus murrayi	Iharos, 1969	Iharos (1969)
Echiniscus oreas	Gąsiorek, Morek & Michalczyk, 2022	This study
Echiniscus ornamentatus	Gąsiorek & Kristensen, 2018	Gąsiorek & Kristensen (2018)
Echiniscus pellucidus	Gąsiorek, Bochnak, Vončina & Michalczyk, 2021	Gąsiorek *et al*. (2021c)
Echiniscus perarmatus	Murray, 1907	Murray (1907a)
Echiniscus polygonalis	Ito, 1993	Ito (1993)
Echiniscus punctus	McInnes, 1995	McInnes (1995)
Echiniscus pusae	Marcus, 1928	Marcus (1928)
Echiniscus quadrispinosus	Richters, 1902	Richters (1902)
Echiniscus regularis	Gąsiorek, Morek & Michalczyk, 2022	This study
Echiniscus scabrocirrosus	Gąsiorek, Vončina, Morek & Michalczyk, 2022	This study
Echiniscus scabrospinosus	Fontoura, 1982	Fontoura (1982)
Echiniscus setaceus	Gąsiorek, Vončina, Morek & Michalczyk, 2022	This study
Echiniscus similaris	Gąsiorek, Vončina, Morek & Michalczyk, 2022	This study
Echiniscus siticulosus	Gąsiorek & Michalczyk, 2020	Gąsiorek & Michalczyk (2020b)
Echiniscus succineus	Gąsiorek & Vončina, 2019	Gąsiorek & Vončina (2019)
Echiniscus tantulus	Gąsiorek, Bochnak, Vončina & Kristensen, 2020	Bochnak *et al*. (2020)
Echiniscus tetraspinosus	Gąsiorek, Vončina, Morek & Michalczyk, 2022	This study
Echiniscus trisetosus	Cuénot, 1932	Cuénot (1932)
Echiniscus tristis	Gąsiorek & Kristensen, 2018	Gąsiorek & Kristensen (2018)
Echiniscus tropicalis	Binda & Pilato, 1995	Binda & Pilato (1995)
Echiniscus virginicus	Riggin, 1962	Riggin (1962)
Echiniscus weisseri	Maucci, 1978	Maucci (1978)
Echiniscus zetotrymus	Horning, Schuster & Grigarick, 1978	Horning *et al*. (1978)
Hypechiniscus africanus	Gąsiorek, Morek & Michalczyk, 2022	This study
Hypechiniscus cataractus	Gąsiorek, Oczkowski, Kristensen & Michalczyk, 2021	Gąsiorek *et al*. (2021b)
Hypechiniscus crassus	Gąsiorek, Vončina, Kristensen & Michalczyk, 2021	Gąsiorek *et al*. (2021d)
Hypechiniscus exarmatus	(Murray, 1907)	Murray (1907b)
Hypechiniscus flavus	Gąsiorek, Oczkowski, Suzuki, Kristensen & Michalczyk, 2021	Gąsiorek *et al*. (2021b)
Pseudechiniscus (Meridioniscus) angelusalas	Roszkowska, Grobys, Bartylak & Kaczmarek, 2020	Roszkowska *et al*. (2020)
Pseudechiniscus (Meridioniscus) dastychi	Roszkowska, Grobys, Bartylak & Kaczmarek, 2020	Roszkowska *et al*. (2020)
Pseudechiniscus (*Meridioniscus*) *dreyeri*	Gąsiorek, Vončina, Kristensen & Michalczyk, 2021	Gąsiorek *et al*. (2021d)
Pseudechiniscus (Meridioniscus) indistinctus	Roszkowska, Grobys, Bartylak & Kaczmarek, 2020	Roszkowska *et al*. (2020)
Pseudechiniscus (*Meridioniscus*) *mascarenensis*	Kiosya, Vončina & Gąsiorek, 2021	Kiosya *et al*. (2021)

.....conitnued on the next page

APPENDIX 1. (Continued)

Species	Authority	Reference
Pseudechiniscus (*Meridioniscus*) *santomensis*	Fontoura, Pilato & Lisi, 2010	Fontoura *et al*. (2010)
Pseudechiniscus (Meridioniscus) wallacei	Vončina, Gąsiorek, Morek & Michalczyk, 2022	This study
Pseudechiniscus (Pseudechiniscus) aquatilis	Vončina, Gąsiorek, Morek & Michalczyk, 2022	This study
Pseudechiniscus (*Pseudechiniscus*) *asper*	Abe, Utsugi & Takeda, 1998	Abe *et al*. (1998)
Pseudechiniscus (*Pseudechiniscus*) *beasleyi*	X. Li, L. Wang & Yu, 2007	Li *et al*. (2007)
Pseudechiniscus (*Pseudechiniscus*) *chengi*	Xue, X. Li, L. Wang, Xian, Chen, 2017	Xue *et al*. (2017)
Pseudechiniscus (Pseudechiniscus) ehrenbergi	Roszkowska, Grobys, Bartylak & Kaczmarek, 2020	Roszkowska *et al*. (2020)
Pseudechiniscus (*Pseudechiniscus*) *formosus*	Gąsiorek, Vončina, Kristensen & Michalczyk, 2021	Gąsiorek *et al*. (2021d)
Pseudechiniscus (*Pseudechiniscus*) *lacyformis*	Roszkowska, Grobys, Bartylak & Kaczmarek, 2020	Roszkowska *et al*. (2020)
Pseudechiniscus (*Pseudechiniscus*) *lalitae*	Kayastha, Bartylak, Gawlak & Kaczmarek, 2020	Kayastha *et al*. (2020)
Pseudechiniscus (Pseudechiniscus) linnaei	Vončina, Gąsiorek, Morek & Michalczyk, 2022	This study
Pseudechiniscus (*Pseudechiniscus*) *shintai*	Vončina, Kristensen & Gąsiorek, 2020	Vončina *et al*. (2020)
Pseudechiniscus (*Pseudechiniscus*) *suillus*	(Ehrenberg, 1853)	Ehrenberg (1853)
Pseudechiniscus (*Pseudechiniscus*) *totoro*	Gąsiorek, Vončina, Kristensen & Michalczyk, 2021	Gąsiorek *et al*. (2021d)
Pseudechiniscus (*Pseudechiniscus*) *xiai*	L. Wang, Xue & X. Li, 2018	Wang *et al*. (2018)
Pseudechiniscus bispinosus	(Murray, 1907)	Murray (1907a)
Pseudechiniscus pulcher	(Murray, 1910)	Murray (1910)
Testechiniscus spitsbergensis tropicalis	Gąsiorek, Stec, Zawierucha, Kristensen & Michalczyk, 2018	Gąsiorek *et al*. (2018a)