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## Monograph

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# Proposal of new genera and species of the subfamily Diosaccinae (Copepoda: Harpacticoida: Miraciidae)

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**Abstract.** Representatives of several genera of the family Miraciidae (Copepoda: Harpacticoida) were found in sediment samples taken in the year 2019 from a coastal system in north-western Mexico. The subfamily Diosaccinae (Miraciidae) was by far the most diverse taxon followed by the subfamily Stenheleinae (Miraciidae). Here we report on a new miraciid species, *Typhlamphiascus medici* sp. nov., and provide a new amended diagnosis for *Typhlamphiascus* Lang, 1944 along with a key to its species. Additionally, *Typhlamphiascus lamellifer lamellifer* (Sars, 1911) and *T. l. capensis* Kunz, 1975 are considered as distinct species and the latter is given full species rank. Upon preliminary inspection, another diosaccin species was thought to be a derived form of *Bulbamphiascus* Lang, 1944. This promoted us to perform a more in-depth phylogenetic analysis. Our results showed that the new presumed derived form of *Bulbamphiascus* represents a new genus, *Spinodiosaccus* gen. nov. and that the genus *Bulbamphiascus*, which we propose a new amended diagnosis for, could be split into different genera. Also, the possible relationships amongst the different diosaccin clades found during our analyses are commented. Three new genera are proposed: *Spinopedia* gen. nov., *Pallarica* gen. nov. and *Dinetia* gen. nov. We give a brief ecological analysis on the distribution of *T. medici* sp. nov. and *S. primus* gen. et sp. nov. in the Uriás system.

**Keywords.** Taxonomy, meiofauna, key to species.

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## Introduction

With 53 genera and 479 species (WoRMS Editorial Board 2020), the family Miraciidae Dana, 1846 is one of the most diverse of Harpacticoida. The miraciid subfamilies Diosaccinae Sars, 1906a and Stenheliinae Brady, 1880 are the most species rich in the family. These two subfamilies were the most abundant and diverse harpacticoid taxa collected during a series of meiofauna samplings during the year 2019 along the Uriás system, a polluted estuary in north-western Mexico (see also Gómez 2020a). A report of the subfamily Stenheliinae from the Uriás system, with a record of *Pseudostenhelia wellsii* Coull & Fleeger, 1977, and the description of *Lonchoidestenhelia prote* Gómez, 2020 and *Willenstenhelia reducta* Gómez, 2020, were dealt with in Gómez (2020a). Besides the new taxa presented there, two species of *Robertgurneya* Apostolov & Marinov, 1988 (*R. rostrata* (Gurney, 1927) and *R. mexicana* Gómez, 2020; see Gómez 2020b), two species of *Amphiascoides* Nicholls, 1941 (*A. cf. breviararticulatus* Kunz, 1983 and *A. atopus* Lotufo & Fleeger, 1995), one species of *Sarsamphiascus* Huys, 2009 (*S. cf. minutus* (Claus, 1863)) and one species of *Haloschizopera* Lang, 1944 (*H. cf. ruthorum* Por, 1967) (S. Gómez, pers. obs.) have been found in this system. Here we present the full description of a new species of the problematic genus *Typhlamphiascus* Lang, 1944, *Typhlamphiascus medici* sp. nov., and a new species of the so far monotypic new genus *Spinodiosaccus* gen. nov., *S. primus* gen. et sp. nov., collected during a sampling campaign carried out in January 2019.

The last diagnosis of the genus *Typhlamphiascus* is that by Lang (1948: 705). Here we propose a new diagnosis for the genus. The taxonomic complexity of *Typhlamphiascus* resides on the lack of apomorphies to objectively define the genus, but also on the failure to detect (syn)apomorphies for the known species (see Tables 1–2; Discussion section). Some potential (syn)apomorphies were detected and are presented below. The new species proposed herein, *Typhlamphiascus medici* sp. nov., belongs to Por's group II (Por 1963), and seems to be related to *T. pectinifer* Lang, 1965 and *T. lutincola* Soyer, 1963. These three species share the bifurcated distal inner seta of the male P5 exopod, but the Mexican species seems to be more closely related to *T. pectinifer* from Monterey Bay. Additionally, we propose a key to the species of *Typhlamphiascus* based on original descriptions and records.

If the loss of armature on the first to fourth swimming legs observed in *Spinodiosaccus primus* gen. et sp. nov. is considered as a derived trait, the species could be allocated to *Bulbamphiascus* Lang, 1944 (see Lang 1944; see Lang 1948 for a diagnosis of that genus). However, we opted to split the different lineages within *Bulbamphiascus* into new genera. So, in addition to the proposal of *Spinodiosaccus* gen. nov. for *S. primus* gen. et sp. nov., we propose *Dinetia* gen. nov., *Pallarica* gen. nov. and *Spinopedia* gen. nov. for *B. minutus* Dinet, 1971, *B. cibimae* Pallares, 1982 and *B. spinulosus* Mu & Gee, 2000, respectively. Also, we offer a phylogenetic analysis based mostly on some character states displayed in the swimming legs revealing a close relationship between *Spinodiosaccus* gen. nov. and *Bulbamphiascus*.

Finally, we provide some ecological notes on *T. medici* sp. nov. and *S. primus* gen. et sp. nov. related to some environmental variables in the Uriás system, north-western Mexico.

## Material and methods

### Field work

Sediment samples were taken from a series of sampling stations along the Uriás system (a polluted estuary in southern Sinaloa State, north-western Mexico; see also Gómez 2020a: 43, fig. 1) on January 18, 2019, using an Eckman grab of 25 × 25 cm (sampling surface 625 cm<sup>2</sup>). Triplicate sediment cores were taken at each station using acrylic corers of 5.6 cm ID (sampling surface 24.6 cm<sup>2</sup>) and 20 cm in length, from which the upper 3 cm layer was retrieved and fixed in pure ethanol. An additional sediment core was taken for the analysis of organic matter content and grain size. Environmental variables (dissolved oxygen (mg l<sup>-1</sup>), salinity (ups), and temperature (°C)) were recorded in situ with a YSI Professional Plus hand-held multiparameter meter. Depth was also recorded at each sampling station.

**Table 1** (continued on next page). Main diagnostic characters (females) of the species of *Typhlamphiascus* considered in this study. Abbreviations: INC = inconclusive; NA = not available; 8(?) = 8 segments; segms = segments; P5 = 5 segments; P5 EXP = 5 segments; P5 ENP = 5 segments; P5 BENP = 5 segments; P5 BENP distal inner seta = 5 segments; P5 BENP distal outer seta = 5 segments.

		FEMALE															
References	Caudal rami length:width ratio	Division of genital double-somite	A1 # segms	P1		P2		P3		P4		P5		P5 EXP shape	P5 BENP distal inner seta	P5 BENP distal outer seta	
				EXP	ENP	EXP	ENP	EXP	ENP	EXP	ENP	EXP	ENP				
<i>T. accraensis</i> <sup>1</sup>	1.7	INC	9	0-1-0,2,3	1-0(?)1,1,1	9	9	9	9	9	1-1-0,2,3	1-1-2,2,1	6	5	normal	normal	normal
<i>T. gracilicaudatus</i>	3.3	INC															
Thompson & Scott (1903)																	
Por (1967)	2.1-2.8	NA	8	0-1-0,2,3	1-1-1,1,1	10	10	10	10	10	1-1-2,2,3	1-1-2,2,1	5	4	normal	normal	normal
Por (1963)	2.5	laterally															
Por (1963)	1.4	laterally	NA	0-1-0,2,3	1-1-1,1,1	1-1-1,2,3	1-2-1,2,1	1-1-1,2,3	1-1-2,2,1	1-1-2,2,3	1-1-2,2,1	5	5	normal	normal	normal	normal
Bodin (1968)	1.4	NA															
<i>T. capensis</i>	1.2	INC	8	0-1-0,2,3	1-1-1,1,1	1-1-1,2,3	1-2-1,2,1	1-1-1,2,3	1-1-2,2,1	1-1-2,2,3	1-0(?)1-2,2,1	6	5	normal	normal	normal	normal
Kunz (1975)																	
<i>T. laticola</i> <sup>2</sup>	2.5	dorsolaterally	8	0-1-0,2,3	1-1-1,1,1	1-1-1,2,3	1-2-1,2,1	1-1-1,2,3	1-1-2,2,1	1-1-2,2,3	1-1-2,2,1	6	5	normal	normal	normal	normal
Soyer (1963b)																	
Soyer (1963a)	NA	NA															
<i>T. blanchardi</i>	2.5	INC	8	0-1-0,2,3	1-1-1,1,1	NA	NA	NA	NA	NA	1-1-2,2,3	1-1-2,2,1	8(?)	5	hook-like	small, setiform	very small
Scott & Scott (1895)																	
<i>T. dentipes</i>	1.4	INC	7	0-1-0,2,2	1-1-1,1,1	10	10	10	10	10	1-1-3,2,3	1-1-2,2,1	5	5	hook-like	small, spiniform	very small
Thompson & Scott (1903)																	
<i>T. bouligandi</i>	3	laterally	8	0-1-0,2,3	1-1-1,1,1	1-1-1,2,3	1-2-1,2,1	1-1-1,2,3	1-1-2,2,1	1-1-2,2,3	1-1-2,2,1	6	5	normal	normal	normal	normal
Soyer (1971)																	
<i>T. dracht</i> <sup>3</sup>	1.3-1.8	laterally	8	0-1-0,2,3	1-1-1,1,1	1-1-1,2,3	1-2-1,2,1	1-1-1,2,3	1-1-2,2,1	1-1-2,2,3	1-1-2,2,1	5	5	normal	normal	normal	normal
Soyer (1963a)																	
<i>T. longifurcatus</i> <sup>3</sup>	3.5-4.5	INC	8	0-1-0,2,3	1-1-1,1,1	1-1-1,2,3	1-2-1,2,1	1-1-1,2,3	1-1-2,2,1	1-1-2,2,3	1-1-2,2,1	4	5	normal	normal	normal	normal
Rouch (1962)																	
<i>T. higginsi</i>	1.8	dorsolaterally	8	0-1-0,2,3	1-1-1,1,1	1-1-0,2,3	1-2-1,2,1	1-1-0,2,3	1-1-1,2,1	1-1-2,2,3	1-1-1,2,1	6	5	normal	normal	normal	normal
Chullasorn (2009)																	
<i>T. unibacatus</i>	2.3	dorsolaterally	8	0-1-0,2,3	1-1-1,1,1	1-1-1,2,3	1-2-1,2,1	1-1-1,2,3	1-1-1,2,1	1-1-2,2,3	1-1-1,2,1	6	5	normal	normal	normal	normal
Lang (1965)																	
<i>T. brevicornis</i> <sup>4</sup>	3	INC	8	0-1-0,2,2	1-1-1,1,1	11	11	11	11	11	1-1-2,2,3	1-1-1,2,1	6	5	normal	normal	normal
Thompson & Scott (1903)																	
<i>T. confusus confusus</i> <sup>5</sup>	as long as anal somite	INC															
Scott (1902)																	
<i>T. confusus erythraicus</i> <sup>6</sup>	1.7	dorsolaterally	8	0-1-0,2,3	1-1-1,1,1	1-1-1,2,3	1-2-1,2,1	1-1-1,2,3	1-1-2,2,1	1-1-2,2,3	1-1-1,2,1	6	5	normal	normal	normal	normal
Por (1963)																	
<i>T. confusus gullmaricus</i> <sup>7</sup>	2.0-3.2	dorsolaterally	8	0-1-0,2,3	1-1-1,1,1	1-1-1,2,3	1-2-1,2,1	1-1-1,2,3	1-1-2,2,1	1-1-2,2,3	1-1-1,2,1	6	5	normal	normal	normal	normal
Por (1963)																	
Bodin (1968)	2.0-3.2	NA	8	0-1-0,2,3	1-1-1,1,1	1-1-1,2,3	1-2-1,2,1	1-1-1,2,3	1-1-2,2,1	1-1-2,2,3	1-1-1,2,1	6	5	normal	normal	normal	normal
Por (1967)	2.0-3.2	dorsolaterally															
<i>T. lamelifer</i>	1.7	laterally	8	0-1-0,2,3	1-1-1,1,1	NA	NA	NA	NA	NA	NA	NA	6	5	normal	normal	normal
Saas (1911)																	
Klie (1941)	NA	NA															

**Table 1** (continued). Main diagnostic characters (females) of the species of *Typhlamphiascus* considered in this study. Abbreviations: INC = inconclusive; NA = not available; segms = segments.

	References	Caudal rami length:width ratio	Division of genital double-somite	A1 # segms	FEMALE													
					P1		P2		P3		P4		P5		P5 BENP distal inner seta	P5 BENP distal outer seta		
					EXP	ENP	EXP	ENP	EXP	ENP	EXP	ENP	EXP	ENP				
<i>T. latifurca</i>	Por (1968)	1.3-1.5	dorsally and ventrally	8	12	12	12	12	12	12	12	12	6	5	normal	normal		
<i>T. ovile</i>	Wells & Rao (1987)	1.1	dorsolaterally	8	0-1-0,2,3	1-1-1,1,1	1-1-1,2,3	1-2-1,2,1	1-1-1,2,3	1-1-1,2,3	1-1-1,2,3	1-1-2,2,1	1-1-2,2,3	1-1-1,2,1	6	5	normal	normal
<i>T. pectinifer</i>	Lang (1965) Pallares (1975)	2 2.2	dorsolaterally NA	8	0-1-0,2,3	1-1-1,1,1	1-1-1,2,3	1-2-1,2,1	1-1-1,2,3	1-1-1,2,3	1-1-1,2,3	1-1-2,2,1	1-1-2,2,3	1-1-1,2,1	6	5	normal	normal
<i>T. tuerkayi</i>	Ma & Li (2017)	3.2	dorsolaterally	8	0-1-0,2,3	1-1-1,1,1	1-1-1,2,3	1-2-1,2,1	1-1-1,2,3	1-1-1,2,3	1-1-2,2,1	1-1-2,2,3	1-1-1,2,1	6	4	normal	normal	
<i>T. typhloides</i> <sup>3</sup>	Sars (1911)	1.7	laterally	8	0-1-0,2,3	1-1-1,1,1	1-1-1,2,3	1-2-1,2,1	1-1-1,2,3	1-1-1,2,3	1-1-2,2,1	1-1-2,2,3	1-1-1,2,1	6	5	normal	normal	
<i>T. typhlops</i> <sup>8</sup>	Sars (1906b) <sup>15</sup> Klie (1941) Chislenko (1967) Por (1963)	1.7 2 2.2 1.6	laterally INC INC INC	8	0-1-0,2,3	1-1-1,1,1	1-1-1,2,3	1-2-1,2,1	1-1-1,2,3	1-1-1,2,3	1-1-2,2,1	1-1-2,2,3	1-1-1,2,1	6	5	normal	normal	
<i>T. medici</i> sp. nov.	Present contribution	1.7	dorsolaterally	8	0-1-0,2,3	1-1-1,1,1	1-1-1,2,3	1-2-1,2,1	1-1-1,2,3	1-1-1,2,3	1-1-2,2,1	1-1-2,2,3	1-1-1,2,1	6	5	normal	normal	

<sup>1</sup> Incertae sedis in Wells (2007); identical with *C. confusus* (Por 1963).  
<sup>2</sup> Bodin (1964) questioned the necessity of creating *T. latincola*. Incertae sedis in Wells (2007).  
<sup>3</sup> Incertae sedis in Wells (2007).  
<sup>4</sup> The only difference between *T. brevicornis* and *T. confusus* are the bifid inner setae on the female P5 BENP in *T. confusus*, normal in *T. brevicornis*; the latter species might not be valid (Por 1963). Other differences between *T. brevicornis* and *T. confusus* are probably due to erroneous interpretations (Lang 1948).  
<sup>5</sup> Highly variable. Described in Brady (1905) as *Stenhetia meeki* Brady 1905. Por (1967) was reluctant to split *T. confusus* into several subspecies. See also Lang (1965).  
<sup>6</sup> Por (1963) gave differences between *T. c. confusus*, *T. c. erythraeus* and *T. c. gulfmaricus*. Por (1967) was reluctant to split *T. confusus* into several subspecies.  
<sup>7</sup> Por (1967) was reluctant to split *T. confusus* into several subspecies.  
<sup>8</sup> Specimens in the Sars collection at the Zoological Museum in Oslo are actually *T. confusus* (Por 1963). Also, Sars' description of the male of *T. typhlops* (see Sars 1906b) is actually the male of *T. confusus* (Por 1963). Two samples of *T. typhlops* in Lang's collection at the Museum of Natural History in Stockholm possess an inner seta on P4ENP2 and were considered as representatives of that species by Por (1963).  
<sup>9</sup> Nearly as in *Stenhetia ina* (= *Bulbamphiascus imus*) (T. Scott 1894).  
<sup>10</sup> As in *Stenhetia brevicornis* (= *Typhlamphiascus brevicornis*) (L.C. Thompson & A. Scott 1903).  
<sup>11</sup> As in *Stenhetia ina* (= *Bulbamphiascus imus*) (L.C. Thompson & A. Scott 1903).  
<sup>12</sup> As in *T. confusus* (Por 1968).  
<sup>13</sup> Very little different from *Amphiascus confusus* (Sars 1911).  
<sup>14</sup> Probably with an inner seta on ENP2 (Kunz 1975).  
<sup>15</sup> The male of *T. typhlops* of Sars (1906b) is the male of *T. confusus* (Por 1963).

**Table 2.** Main diagnostic characters (males) of the species of *Typhlamphiascus* considered in this study. Abbreviations: INC = inconclusive; ME = modified, elongate; MU = male unknown; NA = not available; NM = not modified; segms = segments; WO = without.

	References	MALE					
		A1 # segms	P1 basis inner spine	P1 basis inner accessory spines	P5		P5 EXP inner seta
					EXP	ENP	
<i>T. accraensis</i> <sup>1</sup>	Scott (1894)	MU	MU	MU	MU	MU	normal
<i>T. gracilicaudatus</i>	Thompson & Scott (1903)						
	Por (1967) Por (1963)	NA	NM	3–5	4	2	normal
<i>T. gracilis</i>	Por (1963)	NA	NM	7–8	5	2	normal
	Bodin (1968)	x	x	x	x	x	x
<i>T. capensis</i>	Kunz (1975)	MU	MU	MU	MU	MU	normal
<i>T. lutincola</i> <sup>2</sup>	Soyer (1963b)						
	Soyer (1963a)	9	NM	3	6	2	bifurcated
<i>T. blanchardi</i>	Scott & Scott (1895)	MU	MU	MU	MU	MU	normal
<i>T. dentipes</i>	Thompson & Scott (1903)	MU	MU	MU	MU	MU	normal
<i>T. bouligandi</i>	Soyer (1971)	9	ME	WO	4	2	normal
<i>T. drachi</i> <sup>3</sup>	Soyer (1963a)	9	ME	3	5	2	normal
<i>T. longifurcatus</i> <sup>3</sup>	Rouch (1962)	NA	ME	NA	4	2	normal
<i>T. higginsii</i>	Chullasorn (2009)	8	NM	3	6	2	normal
<i>T. unisetosus</i>	Lang (1965)	MU	MU	MU	MU	MU	normal
<i>T. brevicornis</i> <sup>4</sup>	Thompson & Scott (1903)	MU	MU	MU	MU	MU	normal
<i>T. confusus confusus</i> <sup>5</sup>	Scott (1902)						
	Por (1963)						
	Sars (1911)	NA	NM	3–5	6	2	normal
	Brady (1905)						
<i>T. confusus erythraeicus</i> <sup>6</sup>	Por (1963)	NA	NM	4	NA	NA	normal
<i>T. confusus gullmaricus</i> <sup>7</sup>	Por (1963)						
	Bodin (1968)	NA	NM	5–7	NA	NA	normal
	Por (1967)						
<i>T. lamellifer</i>	Sars (1911)						
	Klie (1941)	NA	NM	2	6	2	normal
<i>T. latifurca</i>	Por (1968)	NA	NM	3	5	2	normal
<i>T. ovale</i>	Wells & Rao (1987)	9	NM	8	6	2	normal
<i>T. pectinifer</i>	Lang (1965)	9	NM	3	6	2	bifurcated
	Pallares (1975)						
<i>T. tuerkayi</i>	Ma & Li (2017)	9	NM	8	4	2	normal
<i>T. typhloides</i> <sup>3</sup>	Sars (1911)	NA	NA	NA	NA	NA	normal
<i>T. typhlops</i> <sup>8</sup>	Sars (1906b) <sup>11</sup>						
	Klie (1941)						
	Chislenko (1967)	INC	NM	4 <sup>9</sup> or 7–8 <sup>10</sup>	6	2	normal
	Por (1963)						
<i>T. medici</i> sp. nov.	Present contribution	10	NM	3	6	2	normal

<sup>1</sup> Incertae sedis in Wells (2007); identical with *C. confusus* (Por 1963).<sup>2</sup> Bodin (1964) questioned the necessity of creating *T. lutincola*. Incertae sedis in Wells (2007).<sup>3</sup> Incertae sedis in Wells (2007).<sup>4</sup> The only difference between *T. brevicornis* and *T. confusus* are the bifid inner setae on the female P5 BENP in *T. confusus*, normal in *T. brevicornis*; the latter species might not be valid (Por 1963). Other differences between *T. brevicornis* and *T. confusus* are probably due to erroneous interpretations (Lang 1948).<sup>5</sup> Highly variable. Described in Brady (1905) as *Stenhelia meeki*. Por (1967) was reluctant to split *T. confusus* into several subspecies. See also Lang (1965).<sup>6</sup> Por (1963) gave differences between *T. c. confusus*, *T. c. erythraeicus* and *T. c. gullmaricus*. Por (1967) was reluctant to split *T. confusus* into several subspecies.<sup>7</sup> Por (1967) was reluctant to split *T. confusus* into several subspecies.<sup>8</sup> Specimens in the Sars collection at the Zoological Museum in Oslo are actually *T. confusus* (Por 1963). Also, Sars' description of the male of *T. typhlops* (see Sars 1906b) is actually the male of *T. confusus* (Por 1963). Two samples of *T. typhlops* in Lang's collection at the Museum of Natural History in Stockholm possess an inner seta on P4ENP2 and were considered as representatives of that species by Por (1963).<sup>9</sup> After Sars (1906b).<sup>10</sup> After Por (1963) and Chislenko (1967).<sup>11</sup> The male of *T. typhlops* of Sars (1906b) is the male of *T. confusus* (Por 1963).

## Laboratory analyses

### Sample processing and taxonomy

Each sample was sieved through 500 and 38 µm sieves to separate macro- and meiofauna. Meiofauna was extracted through centrifugation with Ludox<sup>®</sup> HS-40 following Burgess (2001) and Rohal *et al.* (2016) and preserved in pure ethanol. Meiofauna was sorted at a magnification of 40× using an Olympus SZX12 stereo microscope equipped with a DF PLAPO 1× objective and WHS10× eyepieces, and harpacticoid copepods were stored separately in 1 ml vials with pure ethanol. Illustrations and figures were made from whole individuals and its dissected parts using a Leica DMLB microscope equipped with L PLAN 10× eyepieces, an N PLAN 100× oil immersion objective, and a drawing tube. The dissected parts were mounted on separate slides using lactophenol as mounting medium.

Huys & Boxshall (1991) was followed for general terminology.

### Abbreviations

acro	=	acrothek
ae	=	aesthetasc
BENP	=	baseoendopod
CI–CV	=	first to fifth copepodid
ENP	=	endopod
EXP	=	exopod
EXP(ENP)1(2,3)	=	first (second, third) exopodal (endopodal) segment
P1–P6	=	first to sixth legs
ICML	=	Instituto de Ciencias del Mar y Limnología, Mazatlán, Mexico

### Organic matter and grain size

Organic matter and organic carbon content were determined through the Walkley-Black titration and colorimetric method, and the grain size was assessed with a Malvern Mastersizer Hydro 2000MU laser diffraction particle size analyser.

## Statistical analyses

Spearman's correlation coefficient was calculated between the density of each species and the environmental variables using Minitab<sup>®</sup> Statistical Software ver. 19.2020.1 ([www.minitab.com](http://www.minitab.com)). Differences in density of *T. medici* sp. nov. and *S. primus* gen. et sp. nov. between sampling stations were assessed through a non-parametric one-way analysis of variance. Principal coordinates analysis (PCoA) between the Euclidean distance dissimilarity matrix for the environmental variables and the Bray-Curtis similarity matrix combined with a CLUSTER analysis for biological samples was used to assess the effects of the environmental variables that had major effects on the distribution of *T. medici* sp. nov. and *S. primus* gen. et sp. nov. Non-parametric one-way analysis of variance and PCoA were performed using PRIMER ver. 7 and PERMANOVA+ (Clarke & Gorley 2015).

## Phylogenetic analyses

The position of the new genus within the Diosaccinae was assessed following Hennig (1966). The corresponding cladogram was generated using the program NONA (Goloboff 1999) for cladistic parsimony in interface with WINCLADA (Nixon 2002). This program uses a heuristic algorithm with unconstrained search and multiple TBR + TBR (searches for trees using the tree bisection-reconnection method of branch-swapping, then repeats this process the number of times as indicated in the number of replications box) as search strategy for the best topology, and a Fitch algorithm that supports character reversal (allows 0 → n and n → 0 character changes) as a 'similarity' algorithm, but characters are nonadditive; hence 0 ↔ 1 ↔ 2 = 2 steps; 0 ↔ 2 = 1 step. Character states are coded as binary (0–1)



**Table 3** (continued on next page). List of characters used for the phylogenetic analysis.

Character	Description
1	Mxp: miraciid type, prehensile, but not heavily transformed into a grasping limb (0); transformed into a grasping limb (1)
2	Male A1: haplocer, 11-segmented (0); haplocer, 10-segmented (1); haplocer, nine-segmented (2); haplocer, eight-segmented (3)
3	A2 EXP3, number of setae: 3 distal setae (0); one distal seta, one spine and a longer spiniform seta (1)
4	Male P1, dimorphic ornamentation of basis: without dimorphic ornamentation (0); with chitinous ornamentation proximal to inner spine (1)
5	P1 ENP: issuing from an attenuated roundish process of basis (0); issuing from a long inner process, reaching middle of EXP1 and from which issues the ENP (1)
6	P1 EXP2, inner seta: present (0); absent (1)
7	P1 exopodal segments, relative length: subequal (0); P1 EXP2 longer than remaining exopodal segments or as long as EXP1 and EXP3 combined (1); P1 EXP2 much longer than EXP1 and EXP3 combined (2)
8	P1 EXP3, outer armature: with three outer spines and two distal setae, distal outer element may be transformed into a spiniform seta (0); with two outer spines and two distal setae (1); with two outer spines, one distal spiniform seta, and one inner thin seta (2); only with distal elements (3)
9	P1 EXP3, shape of proximal element: spiniform (0); transformed into a small seta (1)
10	P1 ENP, number of segments: three-segmented (0); two-segmented, with proximal seta of ENP2 indicating place of original division between second and third original segments (1); two segmented without proximal seta (2)
11	P1 ENP3, relative length: as long as ENP2 or ENP2 absent (0); elongate, at least 1.5 times as long as ENP2 (1)
12	P1 ENP1, relative length: shorter or slightly longer than EXP (0); ENP1 reaching far beyond EXP3 (1)
13	P1 distal endopodal segment, setae: with inner seta, distal (geniculate) seta and outer spiniform seta (0); with inner seta (maybe lost or not illustrated in some descriptions), distal long spine and distal shorter outer spine (1)
14	P2 EXP1, inner seta: present (0); absent (1)
15	P3 EXP1, inner seta: present (0); absent (1)
16	P4 EXP1, inner seta: present (0); absent (1)
17	P2 EXP2, inner seta: present (0); absent (1)
18	P3 EXP2, inner seta: present (0); absent (1)
19	P4 EXP2, inner seta: present (0); absent (1)
20	P2 ENP1, inner seta: present (0); absent (1)
21	P2 ENP2, number of inner setae: two (0); one (1)
22	P3 ENP2, number of inner setae: two (0); one (1)
23	P2 EXP3, inner seta(e): present (0); absent (1)
24	P2 EXP3, short distal seta inserted on inner margin: absent (0); present (1)
25	P3 EXP3, inner seta(e): present (0); absent (1)
26	P3 EXP3, short distal seta inserted on inner margin: absent (0); present (1)
27	P4 EXP3, inner seta(e): present (0); absent (1)
28	P4 EXP3, short distal seta inserted on inner margin: absent (0); present (1)
29	Male P2 ENP1, spinular ornamentation: bare or weakly spinulose (0); with a patch of spinules on the distal outer margin (1)
30	Male P2 ENP2, spinular ornamentation: bare or weakly spinulose (0); heavily spinulose (1)
31	Male P3 EXP3, anterior dimorphic tube pore: absent (0); present (1)

**Table 3** (continued). List of characters used for the phylogenetic analysis.

Character	Description
32	Female P5 BENP, number of setae: six (0); five (1); four (2); three (3)
33	Female P5 EXP, number of setae: six (0); five (1)
34	Male P5 EXP, number of setae/spines: six or seven (0); five (1); four (2); three (3)
35	Male P5 EXP, number of setae/spines: seven (0); up to six (1)
36	Male P5 EXP, medial and distal outer spines, relative length: about as long as proximal outer seta (0); shorter than proximal outer seta (1)
37	Male P5 EXP, shape of outer distal element: seta or pinnate spine (0); bare spine (1)
38	Male P5 EXP, medial outer spine: not transformed (0); transformed into short spine (1)
39	Male P5 EXP, distal outer spine: not transformed (0); transformed into short spine (1)
40	Female P5 EXP, distal outer spine: not transformed (0); transformed into short spine (1)
41	Female P5 EXP, middle distal seta or third or fourth seta from outer to inner margin: not issuing from a setophore (0); issuing from a setophore (1)
42	Female P5 EXP, middle inner seta or second from inner to outer margin: not issuing from a setophore, long, thin and smooth (0); issuing from a setophore (1)
43	Male P5 EXP, middle distal seta or third (fourth in <i>P. cibimae</i> ) from inner to outer margin: not issuing from a setophore, spine or thick seta (0); issuing from a setophore (1)
44	Male P5 EXP, distal outer pedunculated pore: absent (0); present (1)

or multistate (0–n). The state for each character can be seen in the character list (Table 3, see the Discussion section). Also, the data matrix is given (Table 4, see the Discussion section). The characters are not differently weighted. The polarisation of characters was done a priori (zero (0) represents the plesiomorphic condition, one (1) the apomorphic condition, and one (1) is plesiomorphic in comparison with two (2)) as in the ground pattern characters for Diosaccinae (Willen 2000). Additional decisions on character polarity were obtained by comparing the Diosaccinae ground pattern with the state of character present in the other Miraciidae and other Thalestridimorpha. The resulting cladogram is rooted. The term ‘ground pattern’ is used here in the sense of ‘Grundmuster’ (Ax 1984: 156) and refers to all plesiomorphies and autapomorphies present in each taxon (‘Stammart’ sensu Ax 1984). Unsupported nodes in the tree are hard collapsed. Characters are ACCTRAN (fast) optimized. We have obtained more than one (12) most parsimonious phylogenetic topology; hence, here we have applied strict consensus for the figure that we include within the body of the text. All possible phylogenetic trees are provided in Supplementary file 1.

## Results

### *Taxonomy*

Subclass Copepoda Milne Edwards, 1840  
Order Harpacticoida Sars, 1903  
Family Miraciidae Dana, 1846  
Subfamily Diosaccinae Sars, 1906

*Typhlamphiascus* Lang, 1944

### Type species

*Amphiascus typhlops* Sars, 1906, by original designation.



### Other species and subspecies

- T. blanchardi* (T. Scott & A. Scott, 1895) (originally described in *Stenhelia*)  
*T. bouligandi* Soyer, 1971  
*T. brevicornis* (I.C. Thompson & A. Scott, 1903) (originally described in *Stenhelia*)  
*T. capensis* Kunz, 1975 comb. nov.  
*T. confusus* (T. Scott, 1902) (originally described in *Stenhelia*)  
*T. confusus erythraeicus* Por, 1963  
*T. confusus gullmaricus* Por, 1963  
*T. dentipes* (I.C. Thompson & A. Scott, 1903) (originally described in *Stenhelia*)  
*T. gracilicaudatus* (I.C. Thompson & A. Scott, 1903) (originally described in *Stenhelia*)  
*T. gracilis* Por, 1963  
*T. higginsii* Chullasorn, 2009  
*T. lamellifer* (Sars, 1911) (originally described in *Amphiascus*)  
*T. latifurca* Por, 1968  
*T. medici* sp. nov.  
*T. ovale* Wells & Rao, 1987  
*T. pectinifer* Lang, 1965  
*T. tuerkayi* Ma & Li, 2017  
*T. unisetosus* Lang, 1965

### Species incertae sedis

- Stenhelia hirsuta* Thompson, 1893  
*T. accraensis* (T. Scott, 1894) (described in *Stenhelia*)  
*T. drachi* Soyer, 1963  
*T. longifurcatus* Rouch, 1962  
*T. lutincola* Soyer, 1963  
*T. typhloides* (Sars, 1911) (described in *Amphiascus*)

### Species inquirendae

- T. typhlops* (Sars, 1906) sensu Por (1963)  
*T. aff. confusus confusus* (T. Scott, 1902) sensu Moore (1976)  
*T. confusus confusus* (T. Scott, 1902) sensu Marinov & Apostolov (1985)  
*Typhlamphiascus* sp. in Vilela 1965  
*Typhlamphiascus* sp.? in Bodin 1964  
*Typhlamphiascus* sp.? in Bodin 1964  
*Typhlamphiascus* sp. I (?*confusus*) in Marinov 1977  
*Typhlamphiascus* sp. II in Marinov 1977

### Emended diagnosis

Miraciidae: Diosaccinae. Body fusiform; length: width ratio of caudal rami from about 1.0 to about 3.0. Rostrum not fused to cephalothorax, triangular, elongate, as long as first and second antennular segments combined, with pointed tip, with one subdistal sensilla on each side. Female genital and third urosomites distinct dorsally and/or laterally, completely fused ventrally forming genital double-somite; genital and third urosomites separated in males. Length: width ratio of caudal rami variable, from 1:1 to 3:1. Female antennule seven- to nine-segmented, with aesthetasc and seta fused basally on fourth segment, and with apical acrothek on last segment. Male antennule haplocer, eight–ten-segmented, with aesthetasc and seta fused basally on fifth segment, and with apical acrothek on last segment. Antennular setae typically smooth, except for few slightly setulose setae on penultimate and last articles in females and males. Antenna with allobasis; exopod three-segmented, armature formula 1-0-1,3,0. Mandibular palp

**Table 4** (continued on next page). Character matrix used to reconstruct the generic phylogenetic relationships within the Diosaccinae. Characters are multistate. 0 = plesiomorphic; 1-n = apomorphic; ? = unknown.

	Characters																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
<b>Terminals</b>																						
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Actopsyllus</i>	0	?	0	1	1	1	0	1	0	0	0	1	0	1	1	1	0	0	0	0	1	1
<i>Amonardia</i>	0	1	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
<i>Amphascooides</i>	0	1	0	1	0	1	0	1	0	0	1	0	0	1	1	1	0	0	0	0	1	1
<i>Amphiascus</i>	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Antiboreodiosaccus</i>	0	?	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
<i>Balucopsylla</i>	0	2	0	1	1	1	0	1	0	0	1	0	0	1	1	1	0	0	0	1	1	1
<i>Bulbamphiascus</i>	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
<i>Dactylopodamphiascopsis</i>	0	?	0	?	0	0	2	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
<i>Diosaccopsis</i>	0	?	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
<i>Diosaccus</i>	1	1	0	1	1	0	0	2	0	0	0	1	1	1	1	1	0	0	0	0	0	0
<i>Eoschizopera</i>	0	?	0	1	0	1	0	1	0	0	1	0	0	1	1	1	0	0	0	1	1	1
<i>Goffinella</i>	0	?	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
<i>Haloschizopera</i>	0	1	0	1	0	1	0	1	0	0	1	0	0	1	1	1	0	0	0	1	0	1
<i>Helmutkanzia</i>	?	?	0	?	0	1	0	1	0	0	1	0	0	1	1	0	0	0	0	1	1	1
<i>Ialysus</i>	0	?	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
<i>Metamphiascopsis</i>	0	1	0	?	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
<i>Miscegenus</i>	0	?	0	1	0	1	0	1	0	0	1	0	0	1	1	1	0	0	0	0	1	1
<i>Monardius</i>	?	?	0	?	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1
<i>Neomiscegenus</i>	0	1	0	1	0	1	0	1	0	0	0	0	0	1	1	1	0	0	0	0	1	1
<i>Paramphiascella</i>	0	1	0	1	0	1	0	1	0	0	0	0	0	1	1	1	0	0	0	0	1	1
<i>Paramphiascooides</i>	0	?	0	1	0	1	0	1	0	0	0	0	0	1	1	1	0	0	0	0	1	1
<i>Pararobertsonia</i>	0	?	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Pariachysus</i>	1	1	0	?	0	1	1	1	0	2	0	1	0	1	1	1	0	0	0	0	1	0
<i>Pholenota</i>	0	?	0	?	0	1	0	0	0	2	0	1	1	1	1	1	0	0	0	0	0	0
<i>Protopsammotopa</i>	0	1	0	0	1	1	0	1	0	2	0	0	0	1	1	1	1	1	1	1	1	1
<i>Psammotopa</i>	0	?	0	0	1	1	0	3	0	2	0	0	0	1	1	1	1	1	1	1	1	1
<i>Pseudamphiascopsis</i>	0	?	0	?	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0
<i>Pseudodiosaccopsis</i>	0	?	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
<i>Pseudodiosaccus</i>	0	?	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
<i>Rhyncholagena</i>	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1
<i>Robertgurneya</i>	0	2	0	0	1	0	1	0	0	0	1	1	0	1	1	1	0	0	0	0	1	1
<i>Robertsonia</i>	0	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
<i>Sarsamphiascus</i>	0	?	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
<i>Schizopera</i>	0	1	0	1	0	1	0	1	0	0	0	0	0	1	1	1	0	0	0	1	1	1
<i>Schizoperoides</i>	0	?	0	?	0	1	0	1	0	2	0	1	0	1	1	1	0	0	0	1	1	1
<i>Tydemanella</i>	0	?	0	?	0	0	0	1	0	1	0	0	0	?	?	?	?	?	?	?	?	?
<i>Typhlamphiascus</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Sinamphiascus</i>	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Spinodiosaccus</i> gen. nov.	0	0	1	1	0	1	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	1
<i>Dineticola</i> gen. nov.	0	?	0	?	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1
<i>Spinopedia</i> gen. nov.	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
<i>Pallarica</i> gen. nov.	0	?	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1

**Table 4** (continued). Character matrix used to reconstruct the generic phylogenetic relationships within the Diosaccinae. Characters are multistate. 0 = plesiomorphic; 1-n = apomorphic; ? = unknown.

	Characters																					
	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
<b>Terminals</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Outgroup</i>	1	0	1	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0
<i>Actopsyllus</i>	0	0	0	0	0	0	0	0	0	1	0	2	1	0	0	0	0	0	0	0	0	0
<i>Amonardia</i>	1	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	0	1	0
<i>Amphiascoides</i>	0	1	0	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	1	1	0
<i>Amphiascus</i>	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
<i>Antiboreodiosaccus</i>	1	0	1	0	0	1	0	0	1	1	1	1	1	0	1	1	1	1	1	1	1	0
<i>Balucopsylla</i>	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
<i>Bulbamphiascus</i>	0	1	0	1	0	1	0	0	1	0	0	0	1	1	1	1	1	1	1	1	1	0
<i>Dactylopodamphiascopsis</i>	0	0	0	0	0	0	0	0	0	1	0	?	1	0	0	0	0	0	1	0	?	0
<i>Diosaccopsis</i>	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
<i>Diosaccus</i>	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0
<i>Eoschizopera</i>	1	0	1	0	0	0	0	0	2	0	1	1	1	0	0	0	0	0	0	0	0	0
<i>Goffinella</i>	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Haloschizopera</i>	1	0	0	0	0	0	0	0	1	2	1	1	1	0	0	0	0	0	0	0	0	0
<i>Helmutkuntzia</i>	1	0	1	0	0	0	0	0	2	1	0	2	1	0	0	0	0	0	0	0	0	0
<i>Ialysus</i>	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	?	0	0	0
<i>Metamphiascopsis</i>	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	1	0
<i>Miscegenus</i>	0	1	0	1	0	0	0	0	1	1	1	?	1	0	0	0	0	0	0	1	?	0
<i>Monardius</i>	1	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	0	1	0
<i>Neomiscegenus</i>	1	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	1	1	0
<i>Paramphiascella</i>	1	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	1	1	0
<i>Paramphiascoides</i>	1	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	1	0	1	0
<i>Pararobertsonia</i>	0	1	0	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	1	1	0
<i>Pariachysus</i>	0	0	0	0	0	0	0	0	1	0	1	0	2	1	0	0	0	0	0	0	0	0
<i>Pholenota</i>	1	0	1	0	1	0	0	0	0	1	0	?	1	0	0	0	0	0	0	0	0	0
<i>Protopsammotopa</i>	1	0	1	0	1	0	0	0	2	1	1	1	1	0	0	0	0	0	0	0	0	0
<i>Psammotopa</i>	1	0	1	0	1	0	0	0	3	1	3	1	3	1	0	0	0	0	0	0	0	0
<i>Pseudamphiascopsis</i>	0	0	0	0	0	0	0	0	1	0	?	?	1	0	0	0	0	0	1	1	?	0
<i>Pseudodiosaccopsis</i>	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Pseudodiosaccus</i>	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Rhyncholagena</i>	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	1	1	1	0
<i>Robertigurneya</i>	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	1	1	1	0
<i>Robertsonia</i>	0	1	0	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	1	1	0
<i>Sarsamphiascus</i>	0	0	0	0	0	1	0	0	1	0	1	0	1	0	0	0	0	0	1	0	1	0
<i>Schizopera</i>	1	0	1	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0	1	0
<i>Schizoperoides</i>	?	?	?	?	?	?	?	?	2	1	0	?	1	0	0	0	0	0	1	1	?	0
<i>Tydemanella</i>	0	0	0	0	0	0	0	0	1	0	0	?	1	0	0	0	0	0	1	1	?	0
<i>Typhlamphiascus</i>	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1	1	1	0
<i>Sinamphiascus</i>	0	1	0	1	0	1	0	0	1	1	0	0	1	0	0	0	0	0	1	1	1	1
<i>Spinodiosaccus</i> gen. nov.	0	1	0	1	0	1	0	0	1	0	0	?	1	0	?	1	1	1	1	1	1	0
<i>Dineticola</i> gen. nov.	0	0	0	0	0	0	0	0	0	1	0	?	1	0	?	0	0	0	1	0	0	0
<i>Spinopedia</i> gen. nov.	0	1	0	1	0	1	1	1	1	1	0	0	1	1	1	0	0	0	1	0	1	0
<i>Pallarica</i> gen. nov.	0	1	0	1	0	1	0	0	?	1	0	0	0	1	0	0	0	0	1	1	1	0

biramous; endopod one-segmented, larger than exopod; exopod two-segmented. Maxillule biramous; rami one-segmented. Maxilla with three endites; endopod two-segmented. Maxilliped subchelate; (syn)coxa with two to four, basis with two setae; endopod one-segmented, with claw and variable number of accompanying setae. P1–P4 with three-segmented rami. Male P1 basis sexually dimorphic, with normal or modified (elongate, blunt) inner spine, without or with variable number of inner accessory spines (two–eight). Male P2 sexually dimorphic, two-segmented; first segment with one inner seta, second segment with two inner setae, two subdistal elements (one of which thick and blunt) and two elements (one medial, one apical) issuing from elongate cylindrical extension fused to segment basally. P5 EXP typically longer than wide, with four to six setae in the female and male; P5 endopodal lobe with four to five setae in the female, with two setae in the male; two innermost elements of the female P5 endopodal lobe and armature of the male P5 endopodal lobe bifurcate distally.

Armature formula of P1–P5 as follows:

	EXP	ENP/ENP lobe
P1	0-1-0,2,3	1-1-1,1,1
P2	1-1-1(0),2,3	♀ 1-2-1,2,1 / ♂ dimorphic
P3	1-1-1(0),2,3	1-1-2(1),2,1
P4	1-1-2(0,3),2,3	1-1(0) <sup>2</sup> -2(1),2,1
P5 ♀ / ♂	♀ 4-6 <sup>1</sup> / ♂ 4-6	♀ 4-5 / ♂ 2

<sup>1</sup> The report of eight setae on the female P5 EXP of *T. blanchardi* is most probably erroneous.

<sup>2</sup> *Typhlamphiascus typhlops* is known to lack inner armature on the P4 ENP2. The inner seta of P4 ENP2 of *T. capensis* comb. nov. might have become detached from the supporting segment as indicated by the interrupted cuticle (Kunz 1975).

Sexual dimorphism expressed in the male antennule (see above), P1 basis, P2 ENP (see above), P5 (see above), structure of P6, and in the separated genital and third urosomites.

*Typhlamphiascus medici* sp. nov.

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Figs 1–10

**Etymology**

The specific epithet from the Latin ‘*medicī*’, ‘doctor’, ‘physician’, is dedicated in honour and to the memory of all physicians and health personnel for their self-sacrifice during the fight against the COVID-19 pandemic. It is in the genitive singular, gender masculine.

**Material examined**

**Holotype**

MEXICO • ♀ (preserved in alcohol); Sinaloa State, Mazatlán, Urías coastal system, stn 2 (see also Gómez 2020a: 43, fig. 1); 23.1587° N, 106.3326° W; 1.8 m depth; 18 Jan. 2019; S. Gómez leg.; organic carbon content 3.99%, organic matter content 6.86%, sand 80.42%, clay 8.29%, silt 11.28%; ICML-EMUCOP-180119-40.

**Allotype**

MEXICO • ♂ (preserved in alcohol); same collection data as for holotype; ICML-EMUCOP-180119-43.

**Other paratypes**

MEXICO • 3 ♀♀ (preserved in alcohol); same collection data as for holotype; ICML-EMUCOP-180119-103 • 2 ♀♀, 2 ♂♂ (preserved in alcohol); same collection data as for holotype; ICML-EMUCOP-180119-46 • 1 ♀ (dissected); same collection data as for holotype; ICML-EMUCOP-180119-41 • 1 ♀ (dissected); same collection data as for holotype; ICML-EMUCOP-180119-42 • 1 ♂ (dissected); same collection data as for holotype; ICML-EMUCOP-180119-44 • 1 ♂ (P1 and P2 dissected, rest intact and preserved in alcohol); same collection data as for holotype; ICML-EMUCOP-180119-45.

**Other material**

MEXICO • 8 CV, 4 CIV, 1 CII (preserved in alcohol); same collection data as for holotype; ICML-EMUCOP-180119-47 • 1 ♀, 2 ♂♂, 2 CV (preserved in alcohol); Sinaloa State, Mazatlán, Uriás coastal system, stn 4 (see also Gómez 2020a: 43, fig. 1); 23.1840° N, 106.3579° W; 0.7 m depth; 18 Jan. 2019; S. Gómez leg.; organic carbon content 1.13%, organic matter content 1.94%, sand 82.44%, clay 8.27%, silt 9.29%; ICML-EMUCOP-180119-48 • 1 CV, 1 CIV, 1 CI (preserved in alcohol); Sinaloa State, Mazatlán, Uriás coastal system, stn 5 (see also Gómez 2020a: 43, fig. 1); 23.2056° N, 106.3715° W; 0.6 m depth; 18 Jan. 2019; S. Gómez leg.; organic carbon content 0.99%, organic matter content 1.71%, sand 78.61%, clay 6.72%, silt 14.67%; ICML-EMUCOP-180119-49 • 1 ♂, 1 CIII (preserved in alcohol); same collection data as for preceding; ICML-EMUCOP-180119-50 • 1 ♀, 2 CIV, 1 CII (preserved in alcohol); same collection data as for preceding; ICML-EMUCOP-180119-51 • 1 CV, 1 CIII, 2 CII (preserved in alcohol); Sinaloa State, Mazatlán, Uriás coastal system, stn 6 (see also Gómez 2020a: 43, fig. 1); 23.2123° N, 106.3780° W; 1.4 m depth; 18 Jan. 2019; S. Gómez leg.; organic carbon content 1.65%, organic matter content 2.84%, sand 61.44%, clay 14.57%, silt 23.99%; ICML-EMUCOP-180119-52 • 1 ♂, 1 CV, 1 CIV (preserved in alcohol); same collection data as for preceding; ICML-EMUCOP-180119-53 • 1 ♂ (preserved in alcohol); same collection data as for preceding; ICML-EMUCOP-180119-54 • 1 ♀, 1 CIV (preserved in alcohol); Sinaloa State, Mazatlán, Uriás coastal system, stn 10 (see also Gómez 2020a: 43, fig. 1); 23.1815° N, 106.4214° W; 6.0 m depth; 18 Jan. 2019; S. Gómez leg.; organic carbon content 1.2%, organic matter content 2.07%, sand 69.12%, clay 7.91%, silt 22.97%; ICML-EMUCOP-180119-55 • 3 CIV (preserved in alcohol); same collection data as for preceding; ICML-EMUCOP-180119-56.

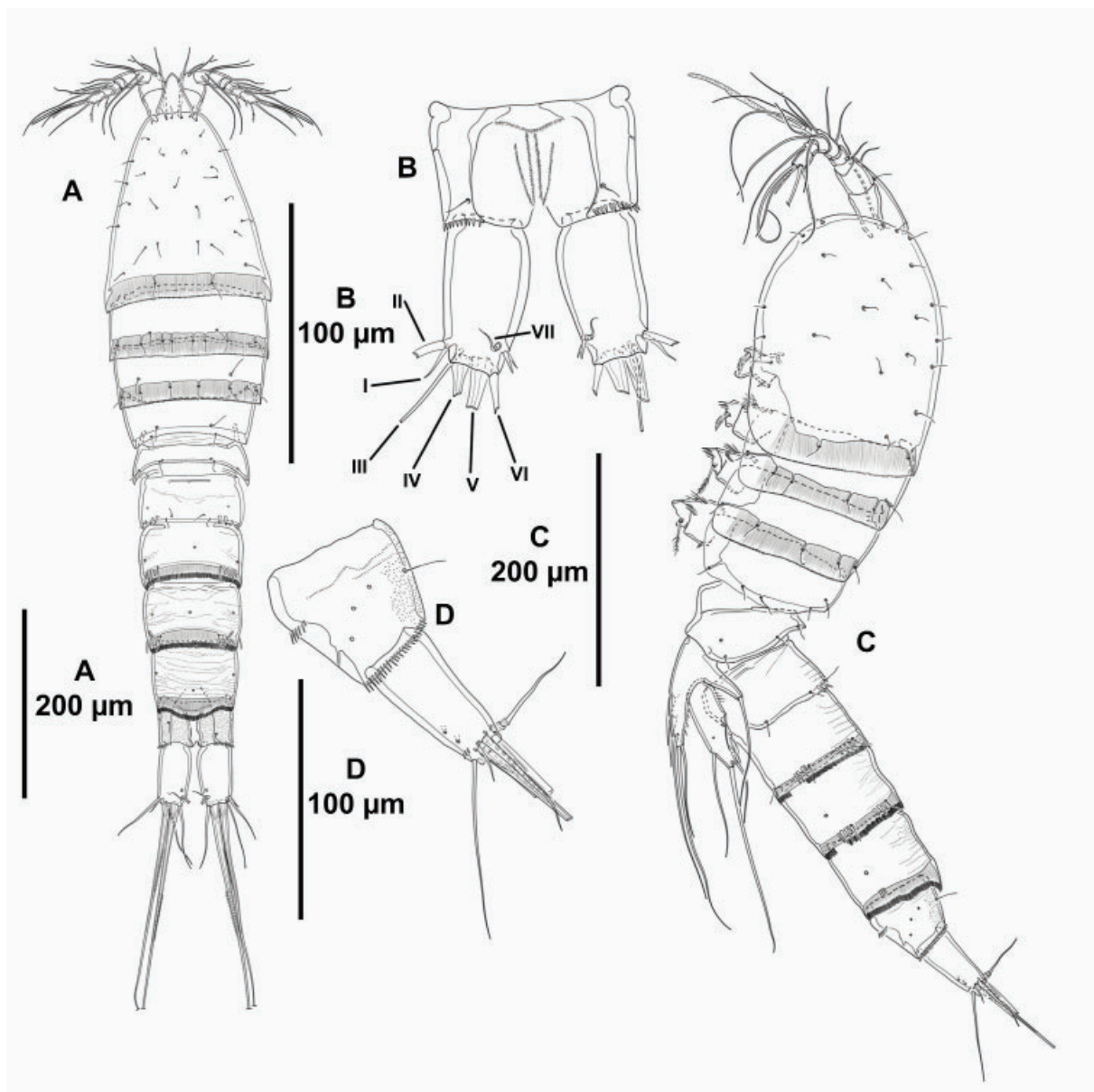
**Description****Female**

GENERAL. Total body length measured from tip of rostrum to posterior margin of caudal rami ranging from 705 to 850 µm (mean 762 µm; n = 5; total body length of holotype 850 µm); habitus fusiform, widest at posterior end of cephalothorax in dorsal view, tapering posteriad (Fig. 1A).

PROSOME (Figs 1A–B, 2A). Consisting of cephalothorax with fused first pedigerous somite and second to fourth free pedigerous somites; prosomites without expansions nor spinular ornamentation; posterior hyaline frill of cephalothorax, second and third pedigerous somites broad, with posterior margins finely serrated, striated, of fourth pedigerous somite visibly narrower, finely serrated, without striations.

UROSOME (Figs 1A–D, 2A). Consisting of fifth pedigerous somite (first urosomite), genital double-somite (genital – second urosomite – and third urosomites fused), two free urosomites, anal somite and caudal rami; urosomites without expansions. First urosomite narrower than preceding somites in dorsal view (Fig. 1A), without spinular ornamentation, with posterior sensilla as depicted, with one lateral pore on each side (Fig. 1C), posterior frill as in preceding somite dorsally and laterally (Fig. 1A, C). Genital double-somite (Figs 1A, C, 2A) rectangular, slightly longer than wide, with sensilla and minute surface spinules dorsolaterally as shown; anterior and posterior halves (second – genital – urosomite and third urosomite, respectively) distinct dorsally and laterally (Fig. 1A, C), completely fused ventrally (Fig. 2A); dorsolateral posterior margin of anterior half serrated and with two large spinules on each side

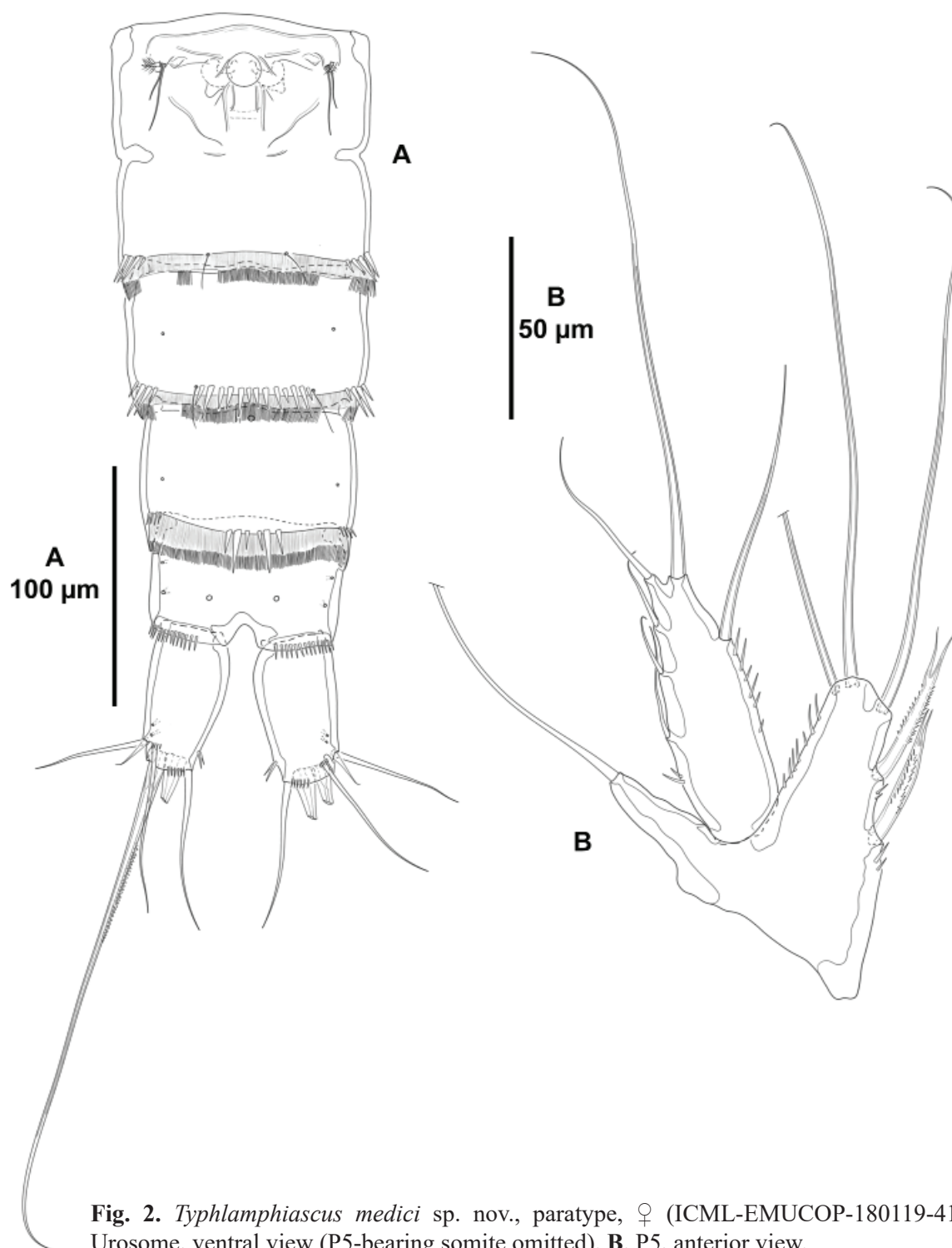
(Fig. 1A, C); posterior half of genital double-somite with dorsal (Fig. 1A) and lateral (Figs 1C, 2A) large posterior spinules, posterior hyaline frill deeply incised and striated, the latter continuous dorsolaterally (Fig. 1A, C) and interrupted ventrally (Fig. 2A); P6 at anterior third of genital somite (anterior half of genital double-somite) and with genital field as shown (Fig. 2A). Fourth urosomite largely as in posterior half of genital double-somite, but with additional paired lateroventral pores and posterior medial transverse spinular row (Figs 1A, C, 2A). Fifth urosomite without sensilla, with one lateral row of small spinules (Fig. 1C) and with paired lateroventral pores (Figs 1C, 2A), with short medial row of large spinules ventrally (Fig. 2A), with continuous deeply incised posterior hyaline frill, the latter with medial part slightly crescentic dorsally (Fig. 1A). Anal somite slightly wider than long in dorsal view (Fig. 1A–B), without anal operculum, cleft medially dorsally (Fig. 1A–B) and ventrally (Fig. 2A), with two posterior sensilla dorsally (Fig. 1A–D), with lateral and ventral pores as shown (Figs 1C–D, 2A),



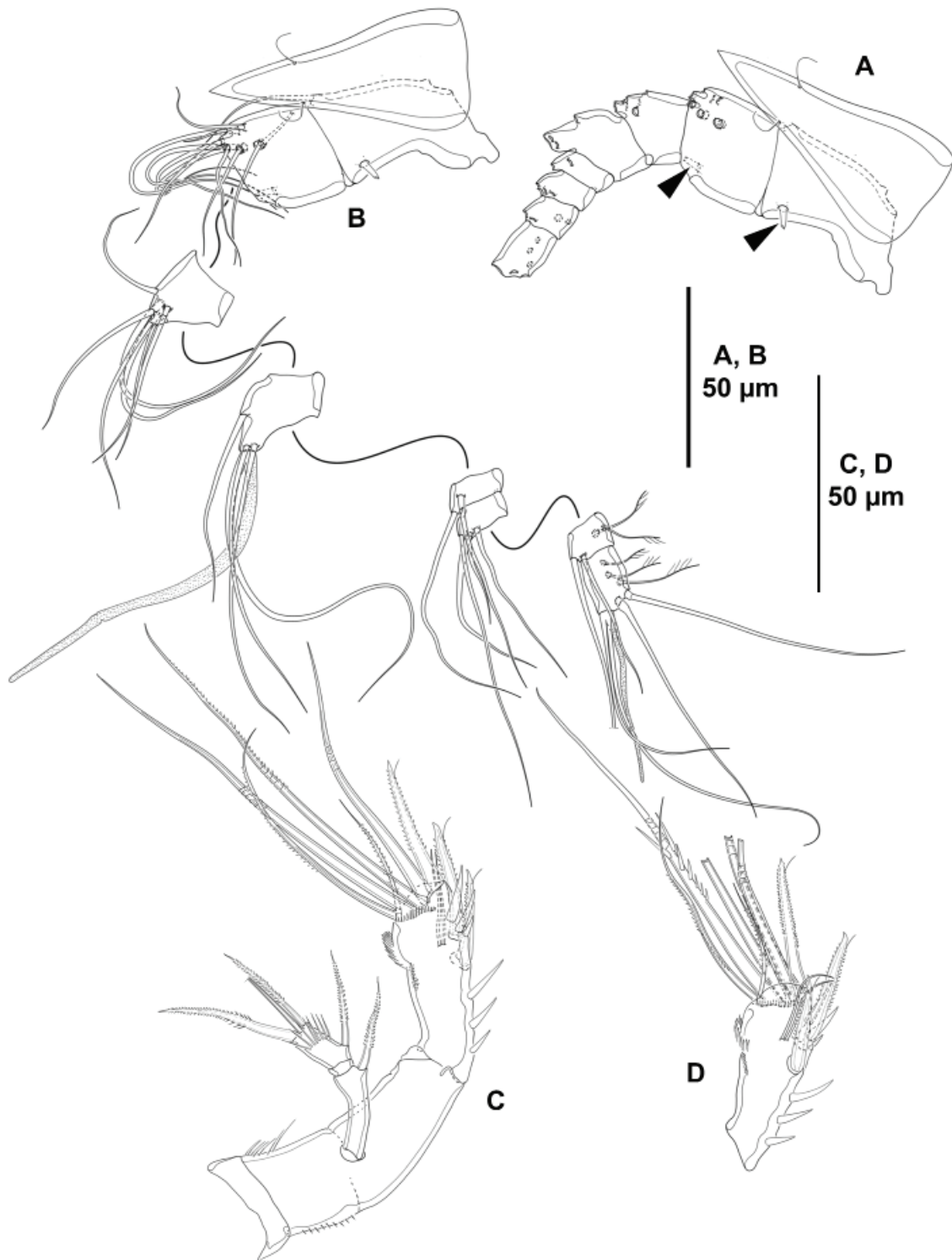
**Fig. 1.** *Typhlamphiascus medici* sp. nov., holotype, ♀ (ICML-EMUCOP-180119-40). **A.** Habitus, dorsal view. **B.** Anal somite and caudal rami, dorsal view. **C.** Habitus, lateral view. **D.** Anal somite and left caudal ramus, lateral view.



and with small spinules close to joint with caudal rami. Caudal rami well-developed (Figs 1A–D, 2A), about 1.7 times as long as wide and with straight outer and slightly convex inner margin (Fig. 1A–B), with pores as shown; with seven setae (Fig. 1B) as follows: setae I and II situated subdistally on outer margin, the former very small and ventral to the latter; seta III displaced ventrally close to outer margin; setae IV and V normal, with fracture plane, the former shorter; seta VI arising at inner distal corner; dorsal seta VII issuing subdistally, close to inner margin, triarticulated.



**Fig. 2.** *Typhlamphiascus medici* sp. nov., paratype, ♀ (ICML-EMUCOP-180119-41). **A.** Urosome, ventral view (P5-bearing somite omitted). **B.** P5, anterior view.



**Fig. 3.** *Typhlamphiascus medici* sp. nov., paratype, ♀ (ICML-EMUCOP-180119-41). **A.** Rostrum and antennule (armature omitted for simplicity; arrows indicate tube pores on first and second segments). **B.** Rostrum and antennule showing armature. **C.** Antenna with aberrant outermost geniculate seta (without spinular ornamentation), and with only two free geniculate setae. **D.** Free endopodal segment of another antenna.

ROSTRUM (Figs 1A, C, 3A–B). Not fused to cephalothorax, triangular, pointed, with one sensilla arising at distal third on each side, reaching distal margin of second antennular segment.

ANTENNULE (Fig. 3A–B). Eight-segmented; all segments smooth; first and second segments with tube pore (arrowed in Fig. 3A); all setae smooth except for two and three biarticulated setulose setae on seventh and eighth segments, respectively; outer subdistal seta of eighth segment biarticulated basally, neighbouring seta swollen basally. Armature formula: 1(1); 2(11); 3(7); 4(3+(1+ae)), 5(2); 6(4); 7(4); 8(5+acro). Acrothek consisting of two setae and one aesthetasc fused basally.

ANTENNA (Fig. 3C–D). With small unornamented coxa. Allobasis with remains of former division between basis and first endopodal segment, slightly longer than free endopodal segment, with outer slender spinules proximally, without abexopodal seta. Exopod three-segmented; first segment longer than second and third segments combined, second segment smallest; first and second segments unornamented, the former with one, the latter without seta; third segment with subapical row of spinules, armed with three setae, of which one bare, the other two bipinnate. Free endopodal segment with proximal and subdistal inner strong spinules as shown, and with two outer frills; armed with two lateral inner flagellate spines and two slender setae (the latter set close to each other), one inner apical flagellate spine, three single geniculate setae, one slender bipinnate short seta and one strongly spinulose geniculate outer seta fused basally to slender pinnate element.

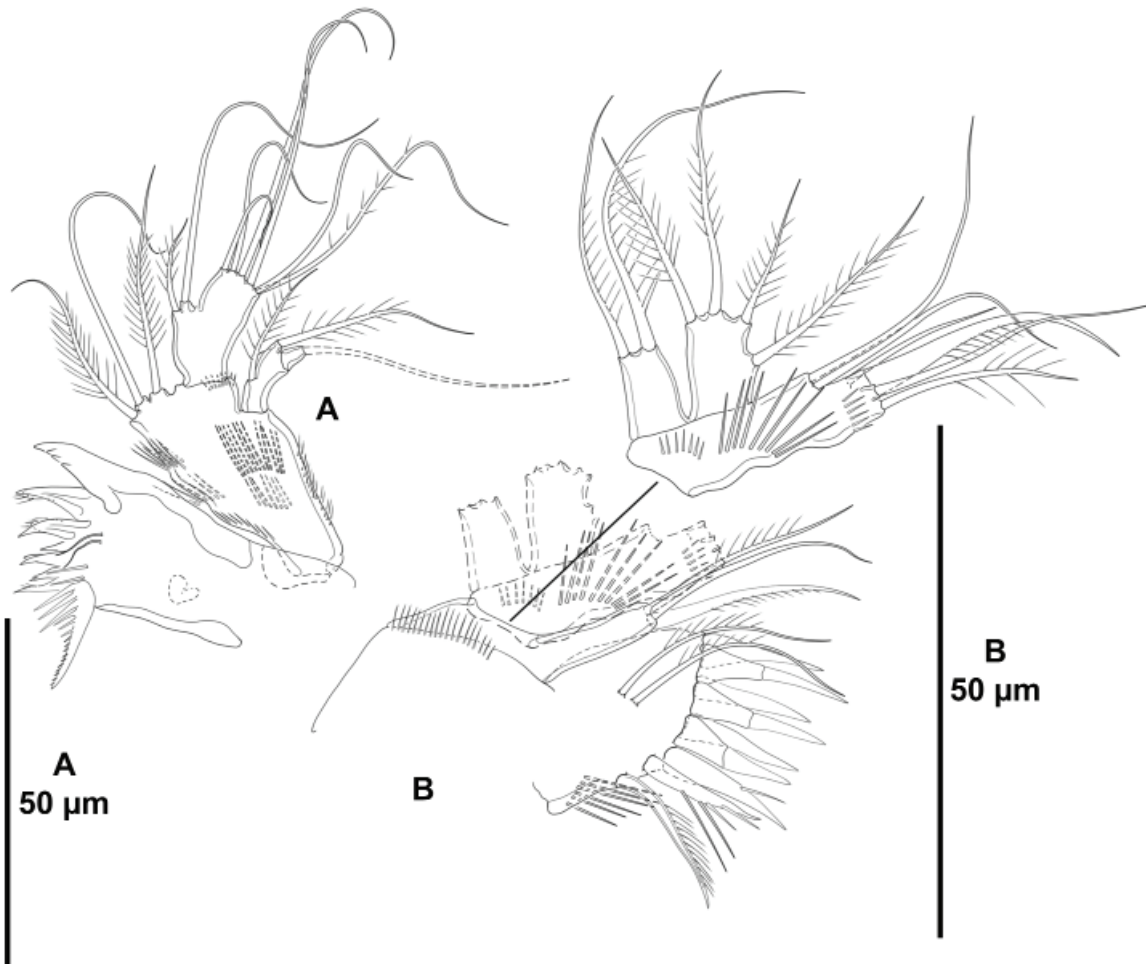
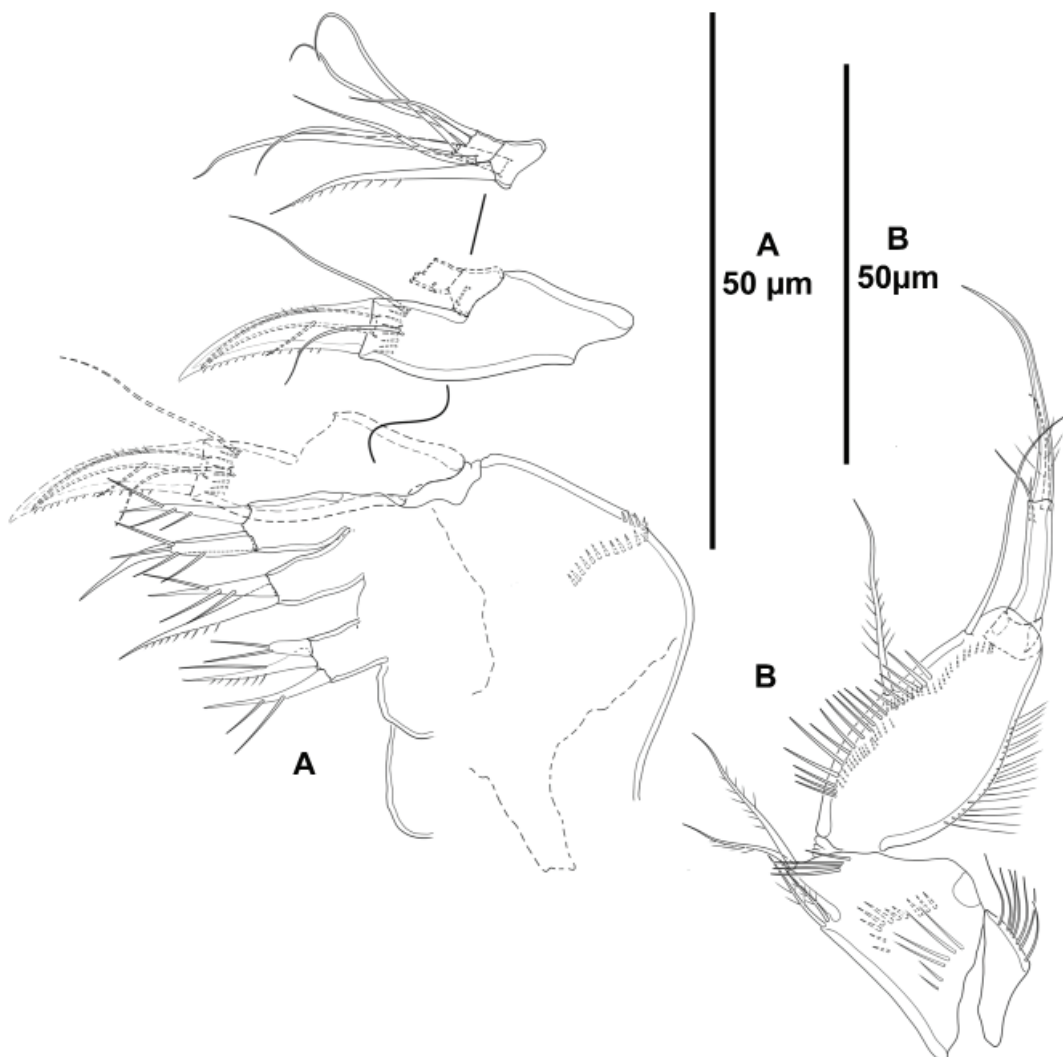


Fig. 4. *Typhlamphiascus medici* sp. nov., paratype, ♀ (ICML-EMUCOP-180119-41). A. Mandible. B. Maxillule.

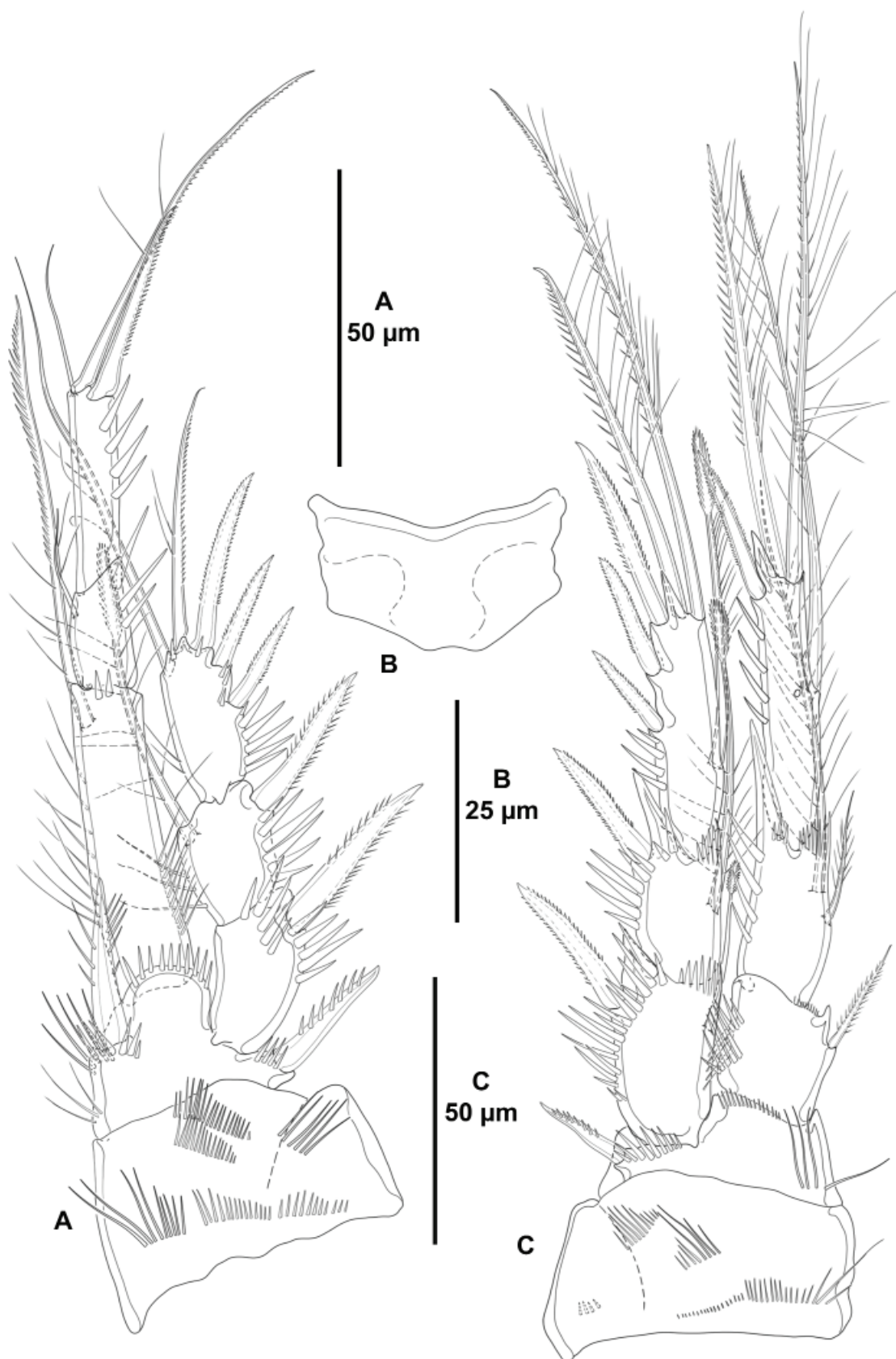
**MANDIBLE** (Fig. 4A). With well-developed gnathobasis bearing strong multi- and bicuspidate teeth as shown, subdistally with two small slender setae and two spinules medially, and with one strongly spinulose element. Basis massive, with spinules as depicted, with three inner setae. Exopod two-segmented; first segment longer than second, the former with one lateral and one distal seta, the latter with one apical element. Endopod one-segmented, visibly larger than exopod; with two lateral and six distal setae.

**MAXILLULE** (Fig. 4B). With arthrite ornamented with some slender spinules and armed with two surface setae, seven distal spines as shown, one spinulose element and one recurved stiff pinnate seta. Coxal endite with three setae. Basis with spinular row as depicted and armed with two lateral, one subdistal and three distal elements, one of which visibly stronger. Rami one-segmented, exopod with two, endopod with four elements – two distal, one inner subdistal and one inner medial seta.

**MAXILLA** (Fig. 5A). With large syncoxa ornamented with small outer spinules; with three endites; proximal endite smallest, with three setae; middle and distal endites nearly subequal in length, the former with two, the latter with three setae. Basis drawn out into strong claw with minute pinnae, additionally



**Fig. 5.** *Typhlamphiascus medici* sp. nov., paratype, ♀ (ICML-EMUCOP-180119-41). A. Maxilla. B. Maxilliped.



**Fig. 6.** *Typhlamphiascus medici* sp. nov., paratype, ♀ (ICML-EMUCOP-180119-41). **A.** P1, anterior view. **B.** Intercoxal sclerite of P1, anterior view. **C.** P2, anterior view.



with strong spine bearing one long spinule and two slender setae – one anterior, one posterior. Endopod two-segmented; first segment with two, second segment with one lateral and four distal setae.

MAXILLIPED (Fig. 5B). Subchelate. Praecoxa small, trapezoidal, ornamented with slender outer spinules. Coxa trapezoidal, with proximal, medial and subdistal spinules as shown; with two inner small setae



**Fig. 7.** *Typhlamphiascus medici* sp. nov., paratype, ♀ (ICML-EMUCOP-180119-41). **A.** P3, anterior view. **B.** P4, anterior view.



issuing at distal fourth and two long apical setae. Basis longer than coxa, oval, with outer slender longitudinal spinules, and one posterior and one anterior row of spinules as depicted, with one medial inner and one subdistal inner seta. Endopod one-segmented, elongate, with three setae – one lateral, one subdistal and one small distal – and apical claw.

P1 (Fig. 6A–B). With broad unornamented intercoxal sclerite (Fig. 6B). Coxa massive, with several spinular rows as shown. Basis with inner and outer spinulose spines; with slender long inner spinules proximally and close to insertion of inner spine, and with shorter but stronger spinules at base of inner and outer seta, and distally on medial distal rounded protrusion. Exopod three-segmented, arising at a lower level than that of the endopod and reaching slightly beyond ENP1; ENP:EXP length ratio 1.5; exopodal segments subequal in length, with strong outer spinules as shown; first segment without, second segment with one inner seta with comb tip; third segment with five elements. Endopod three-segmented, arising from pedestal; ENP1 about four times as long as wide, as long as second and third segments combined, with outer and inner longitudinal rows of slender spinules, with one inner stiff, long, strongly pectinate seta; second and third segments ornamented with strong outer spinules as shown, the former shorter, nearly as long as wide and half as long as the latter, with one inner, slender, short seta; third segment elongate with one inner distal slender seta, one apical long element and one outer distal spine.

P2 (Fig. 6B). Narrow intercoxal sclerite (not shown) with acute distal projection on each side, largely as in P3. Praecoxa (not shown) as in P3. Coxa with three anterior rows of spinules – one proximal and two medial transverse – and with posterior small spinules close to proximal outer margin. Basis with long slender spinules proximally close to inner margin, with small spinules between rami, and with comparatively larger spinules at base of exopod and at base of outer pinnate spine. Rami three-segmented, endopod and exopod subequal in absolute length. Exopod three-segmented, arising at a lower level than that of the endopod, not reaching tip of ENP; exopodal segments with strong outer spinules as shown; EXP1 and EXP2 with outer distal acute projection, on EXP1 shorter, both segments with coarse inner distal hyaline frill and inner seta with comb tip, on EXP1 visibly shorter; EXP3 with six elements – three outer spines, two apical elements and one inner seta with comb tip. Endopod three-segmented, arising from pedestal; endopodal segments with strong outer spinules as shown; ENP1 shortest, as long as wide, with small distal spinules close to small inner projection, without outer distal projection nor inner hyaline frill, with one short inner seta; ENP2 elongate, 1.7 times as long as wide and 0.6 times as long as ENP3, with strong outer spinules and with small spinules at base of outer distal acute projection, with coarse inner distal frill, with two inner setae of which proximal one short; ENP3 longest, elongate, 4.8 times as long as wide, with medial outer pore, with four elements (one inner and two apical setae, and one outer spine), with acute projection between outer spine and inner apical seta.

P3 (Fig. 7A). Narrow intercoxal sclerite with acute distal projection on each side. Praecoxa small, with transverse distal row of slender spinules close to outer margin. Coxa and basis as in P2 except for outer setiform element of basis on P3. Rami three-segmented, endopod and exopod subequal in absolute length. Exopod largely as in P2 except for additional posterior pore on P3 EXP1. Endopod largely as in P2 except for one inner seta only on P3 ENP2 and two inner setae on P3 ENP3.

P4 (Fig. 7B). With intercoxal sclerite, praecoxa, coxa and basis as in P3. Exopod longer than endopod; EXP:ENP length ratio 1.3; largely as in P3 except for two inner setae on P4 EXP3 of which distalmost one visibly thicker and strongly pectinate. Endopod reaching slightly beyond middle of EXP3; largely as in P3 except for stiffer inner seta on P4 ENP2, and one inner seta only on P4 ENP3.

Armature formula of P1–P4 as follows:

	EXP	ENP
P1	0-1-0,2,3	1-1-1,1,1
P2	1-1-1,2,3	1-2-1,2,1
P3	1-1-1,2,3	1-1-2,2,1
P4	1-1-2,2,3	1-1-1,2,1

P5 (Fig. 2B). With outer seta of BENP arising from long setophore. Endopodal lobe triangular, reaching middle of exopod; with small spinules along outer margin and at base of inner setae; with five elements – one outer subdistal, one apical and one inner subdistal normal seta, and two inner bifurcate elements. Exopod elongate, 2.8 times as long as wide; with spinules along inner margin and with few proximal outer spinules; with six elements – three outer slender, short setae, two apical elements, of which outermost one shorter, and one inner seta.

P6 (Fig. 2A). With three setae – one short bipinnate element, and one medial and one inner bare seta of which medial one shorter.

### Male

GENERAL. Total body length measured from tip of rostrum to posterior margin of caudal rami ranging from 675 to 900  $\mu\text{m}$  (mean 731  $\mu\text{m}$ ;  $n = 5$ ; total body length of allotype 680  $\mu\text{m}$ ).

PROSOME (Fig. 8A). As in female.

UROSOME (Fig. 8A–B). As in female except for second – P6-bearing somite – and third urosomites separated, and for continuous spinular rows and hyaline frill of third and fourth urosomites ventrally.

SEXUAL DIMORPHISM. Expressed in the ventral somatic ornamentation, antennule, basis of P1, P2 ENP, P5 and P6.

ANTENNULE (Fig. 9A–B). Ten-segmented, haplocer. All segments smooth; first and second segments with tube pore. All setae smooth except for two and three biarticulated setulose setae on ninth and tenth segments, respectively; outer subdistal seta of tenth segment biarticulated basally, neighbouring seta swollen basally. Armature formula: 1(1); 2(11); 3(5); 4(3); 5(7+(1+ae)); 6(1); 7(1+2 spines); 8(1+2 spines); 9(4); 10(5+acro). Acrothek consisting of two setae and one aesthetasc fused basally.

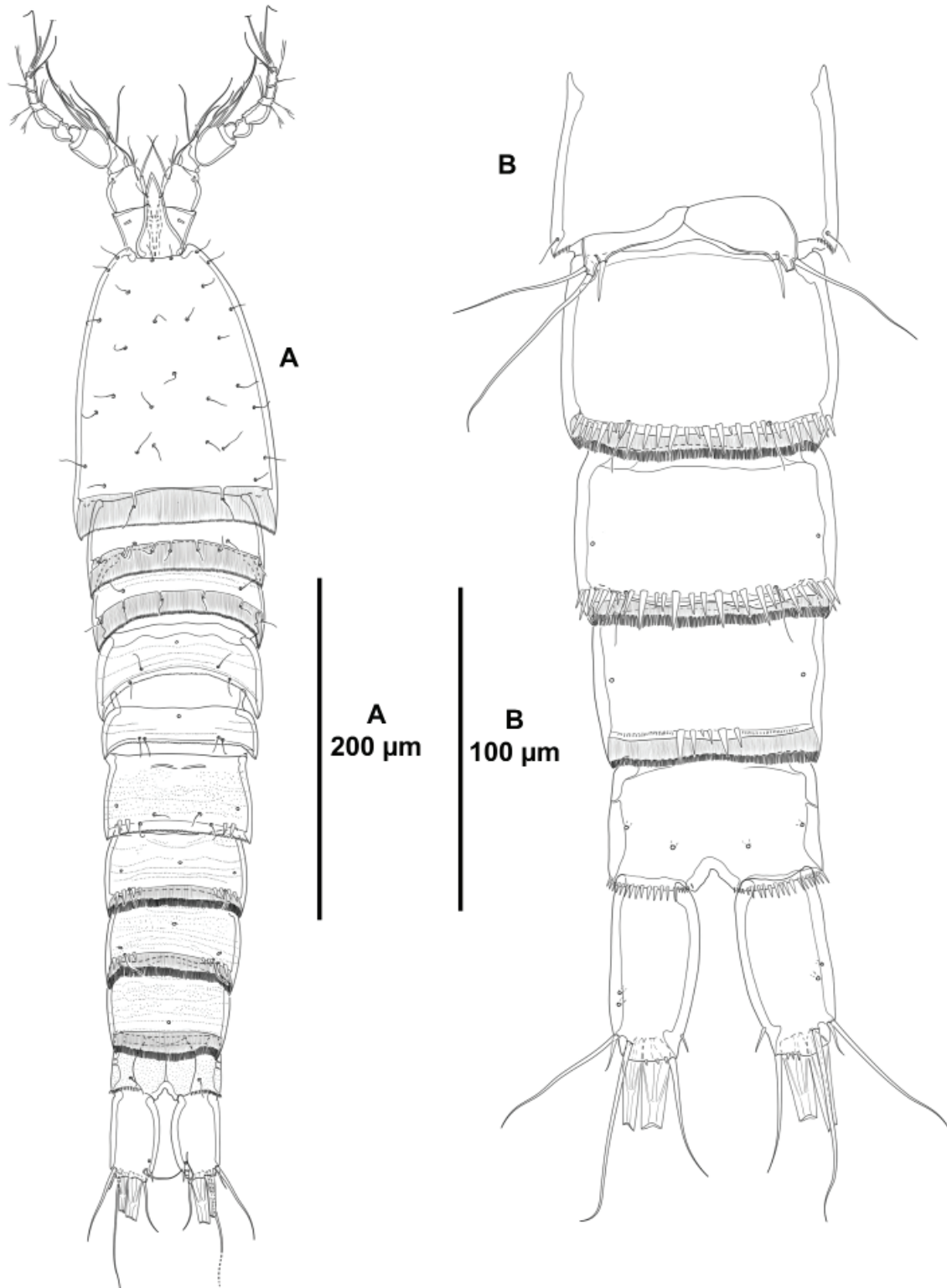
ANTENNA, MANDIBLE, MAXILLULE, MAXILLA AND MAXILLIPED (not shown). As in female.

P1. As in female except for basis without slender inner, long spinules, and with three inner accessory spines and a proximal inner, nose-like outgrowth in the male (Fig. 9C).

P2 EXP (not shown). As in female. Endopod (Fig. 10A) sexually dimorphic, two-segmented; ENP1 0.7 times length of ENP2, with sinuous inner margin, with proximal and medial outer slender spinules, with one short inner seta; ENP2 oval, with longitudinal row of outer slender, long spinules, with two short inner setae arising from pedestal, subdistally with one posterior strong, blunt element, and with one anterior stiff, bare seta with subapical rounded expansion and pointed tip, with one lateral and one apical seta arising from elongate cylindrical extension fused to segment basally.

P3 AND P4 (not shown). As in female.

P5 (Fig. 10B). With outer seta of baseoendopod arising from long setophore. Endopodal lobe reaching middle of exopod, with inner and outer spinules as shown, with two distal bifurcate setae of which outermost one slightly shorter. Exopod rectangular, 2.5 times as long as wide, with longitudinal row of inner spinules and medial pore, with few proximal outer spinules, with six setae – three outer elements



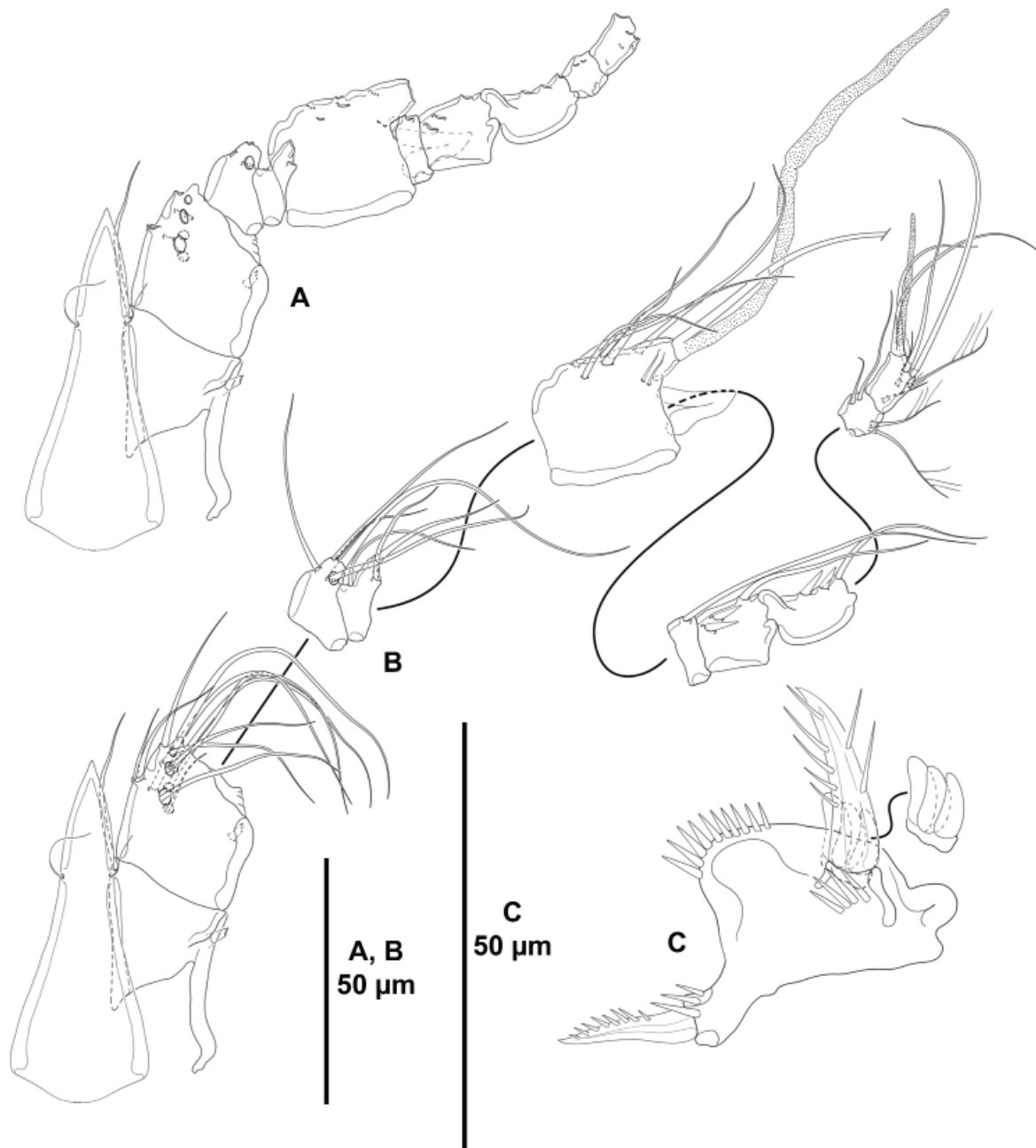
**Fig. 8.** *Typhlamphiascus medici* sp. nov. A. Allotype, ♂ (ICML-EMUCOP-180119-43); habitus, dorsal view. B. Paratype, ♂ (ICML-EMUCOP-180119-44); urosome, ventral view (P5-bearing somite omitted).

of which proximalmost visibly longer, one subdistal outer seta arising from setophore and two distal setae of which innermost one  $\frac{1}{3}$  length of outermost and with bifurcate tip.

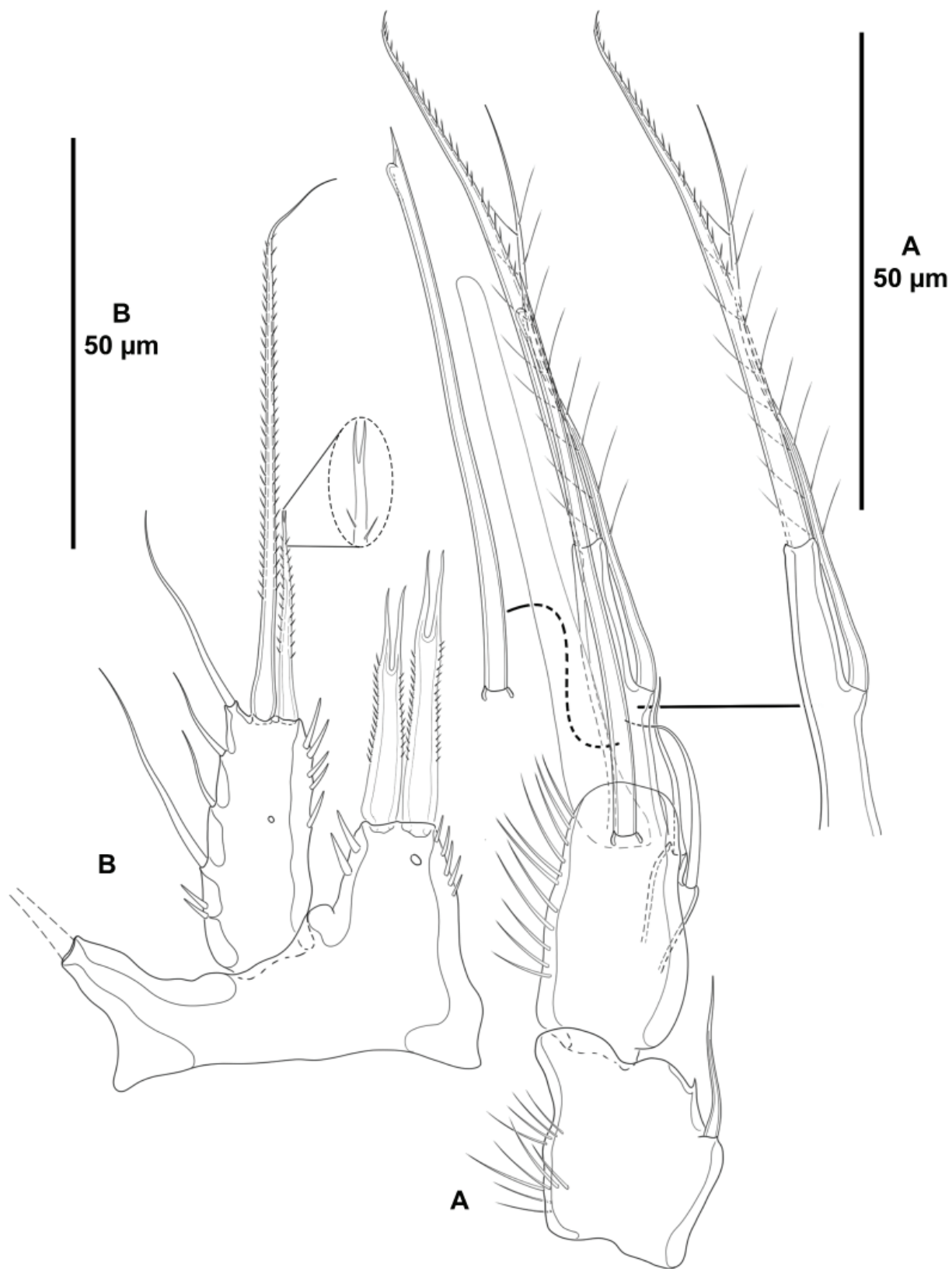
P6 (Fig. 8B). Asymmetrical, each leg with three setae of which innermost one shortest and spiniform, medial and outermost ones slender, medial one longest.

### Variability

The left dorsal sensilla of the anal somite of the holotype is situated more proximally than the right sensilla. One female possesses five instead of six setae on one mandibular endopod and two instead of three maxillary endites on one maxilla.



**Fig. 9.** *Typhlamphiascus medici* sp. nov., paratype, ♂ (ICML-EMUCOP-180119-44). A. Rostrum and antennule (armature omitted for simplicity). B. Rostrum and antennule showing armature. C. P1 basis, anterior view.



**Fig. 10.** *Typhlamphiascus medici* sp. nov., paratype, ♂ (ICML-EMUCOP-180119-44). A. P2 ENP. B. P5, anterior view.

*Spinodiosaccus* gen. nov.

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**Type and only species**

*Spinodiosaccus primus* gen. et sp. nov., by monotypy.

**Diagnosis** (based on *Spinodiosaccus primus* gen. et sp. nov.)

Miraciidae: Diosaccinae. Body fusiform. Rostrum not fused to cephalothorax, elongate, almost as long as the first, second and third antennular segments combined, with one subdistal sensilla on each side issuing at the third quarter of its length. Pro- and urosomites without extensions; with a flexible unsclerotized cuticle between prosome and urosome, the latter seemingly more evident in the male. Female genital double-somite (genital – second urosomite – and third urosomites fused) completely fused ventrally, with a dorsolateral cuticular rib marking former division between somites. Anal somite trapezoidal, without anal operculum. Caudal rami short, 1.6 times as wide as long in dorsal view, unornamented, with slender tube pore ventrally; with seven setae. Female antennule eight-segmented, with aesthetasc and seta fused basally on fourth segment and with apical acrothek on last segment. Male antennule haplocer, 11-segmented, with aesthetasc and seta fused basally on fifth segment and with apical acrothek on last segment. Antennular setae typically smooth. Antenna with allobasis; exopod three-segmented, armature formula 1-1-1,3,0. Mandibular palp biramous; endopod one-segmented, exopod two-segmented. Maxillule biramous; rami one-segmented. Maxilla with three endites; ENP one-segmented. Maxilliped subchelate; (syn)coxa with four, basis with two setae; ENP one-segmented, with claw and three accompanying setae. P1–P4 with three-segmented rami. P1–P2 EXP shorter than endopod, P3 EXP and ENP of approximately the same length, P4 ENP shorter than EXP. Male P1 basis sexually dimorphic, with inner unipinnate spine and inner modified accessory spine. Male P2 sexually dimorphic, two-segmented; first segment with one inner seta; second segment with two inner, one inner subdistal almost straight element, and two setae (one medial, one apical) issuing from elongate cylindrical extension fused to segment basally, and one strong outer subdistal spine, the latter strongly tapering distally. P2–P4 EXP1 without, EXP2 with inner seta; P2–P4 ENP1 with inner seta; P2 ENP2 with two, P3–P4 ENP2 with one inner seta, inner distal seta of EXP3 visibly shorter than other elements of same segment. Both P5 EXP separated in the female, baseoendopods fused medially in the male; rami of P5 distinct in both sexes; P5 EXP with six setae in both sexes, whip-like in the female, two medial outer elements transformed into short spines in the male; P5 endopodal lobe with five setae in the female, with two setae in the male.

Armature formula of P1–P5 as follows:

	EXP	ENP/ENP lobe
P1	0-0-0,2,3	1-1-1,1,1
P2	0-1-2,2,3	♀ 1-2-1,2,1 / ♂ dimorphic
P3	0-1-2,2,3	1-1-2,2,1
P4	0-1-3,2,3	1-1-1,2,1
P5 ♀/♂	♀ 6 / ♂ 6	♀ 5 / ♂ 2

Sexual dimorphism expressed in the male antennule, P1 basis, P2 ENP, P5, P6, and in the genital and third urosomite separated in males.

**Etymology**

The prefix ‘spino’ from the Latin ‘spīna’, ‘spine’, refers to the two medial elements of the male P5 EXP modified into strong short spines. Gender masculine.



### Apomorphies of *Spinodiosaccus* gen. nov.

This new genus can easily be recognised by i) the male A1 with 11 segments resulting from the re-expression of the plesiomorphic condition, ii) the absence of an inner seta on the P1 EXP2 and iii) the absence of inner armature on P2–P4 EXP1.

### *Spinodiosaccus primus* gen. et sp. nov.

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Figs 11–18

### Etymology

The specific epithet comes from the Latin ‘p̄rīmus’, ‘first’, and refers to the first – and type – species described for *Spinodiosaccus* gen. nov. It is in the nominative singular, gender masculine.

### Material examined

#### Holotype

MEXICO • ♀ (preserved in alcohol); Sinaloa State, Mazatlán, Urías coastal system, stn 5 (see also Gómez 2020a: 43, fig. 1); 23.2056° N, 106.3715° W; 0.6 m depth; 18 Jan. 2019; S Gómez leg.; organic carbon content 0.99%, organic matter content 1.71%, sand 78.61%, clay 6.72%, silt 14.67%); ICML-EMUCOP-180119-57.

#### Allotype

MEXICO • ♂ (preserved in alcohol); same collection data as for holotype; ICML-EMUCOP-180119-58.

#### Paratypes

MEXICO • 7 ♀♀, 5 ♂♂ (preserved in alcohol); same collection data as for holotype; ICML-EMUCOP-180119-59 • 1 ♀ (preserved in alcohol); same collection data as for holotype; ICML-EMUCOP-180119-60 • 2 ♀♀, 3 ♂♂ (preserved in alcohol); same collection data as for holotype; ICML-EMUCOP-180119-61 • 1 ♀ (dissected); same collection data as for holotype; ICML-EMUCOP-180119-64 • 1 ♀ (dissected); same collection data as for holotype; ICML-EMUCOP-180119-65 • 1 ♀ (dissected); same collection data as for holotype; ICML-EMUCOP-180119-66 • 1 ♂ (dissected); same collection data as for holotype; ICML-EMUCOP-180119-67 • 1 ♂ (dissected); same collection data as for holotype; ICML-EMUCOP-180119-68 • 1 ♂ (dissected); same collection data as for holotype; ICML-EMUCOP-180119-69 • 1 ♀ (preserved in alcohol); Sinaloa State, Mazatlán, Urías coastal system, stn 6 (see also Gómez 2020a: 43, fig. 1); 23.2123° N, 106.3780° W; 1.4 m depth; 18 Jan. 2019; S. Gómez leg.; organic carbon content 1.65%, organic matter content 2.84%, sand 61.44%, clay 14.57%, silt 23.99%); ICML-EMUCOP-180119-63.

#### Other material

MEXICO • 3 ♀♀, 6 ♂♂, 4 CV (preserved in alcohol); Sinaloa State, Mazatlán, Urías coastal system, stn 2 (see also Gómez 2020a: 43, fig. 1); 23.1587° N, 106.3326° W; 1.8 m depth; 18 Jan. 2019; S. Gómez leg.; organic carbon content 3.99%, organic matter content 6.86%, sand 80.42%, clay 8.29%, silt 11.28%); ICML-EMUCOP-180119-70 • 1 ♀, 1 ♂ (preserved in alcohol); Sinaloa State, Mazatlán, Urías coastal system, stn 4 (see also Gómez 2020a: 43, fig. 1); 23.1840° N, 106.3579° W; 0.7 m depth; 18 Jan. 2019; S. Gómez leg.; organic carbon content 1.13%, organic matter content 1.94%, sand 82.44%, clay 8.27%, silt 9.29%); ICML-EMUCOP-180119-71 • 1 ♀ (preserved in alcohol); same collection data as for preceding; ICML-EMUCOP-180119-72 • 2 CV (preserved in alcohol); same collection data as for preceding; ICML-EMUCOP-180119-73 • 1 CV (preserved in alcohol); same collection data as for holotype; ICML-EMUCOP-180119-62 • 1 CV, 1 CIII (preserved in alcohol); Sinaloa State, Mazatlán, Urías coastal system, stn 6 (see also Gómez 2020a: 43, fig. 1); 23.2123° N, 106.3780° W; 1.4 m depth;

18 Jan. 2019; S. Gómez leg.; organic carbon content 1.65%, organic matter content 2.84%, sand 61.44%, clay 14.57%, silt 23.99%; ICML-EMUCOP-180119-74 • 2 ♂♂ (preserved in alcohol); same collection data as for preceding; ICML-EMUCOP-180119-75 • 2 ♀♀, 2 ♂♂ (preserved in alcohol); same collection data as for preceding; ICML-EMUCOP-180119-76 • 1 ♀, 1 ♂ (preserved in alcohol); Sinaloa State, Mazatlán, Urías coastal system, stn 9 (see also Gómez 2020a: 43, fig. 1); 23.1904° N, 106.4121° W; 5.4 m depth; 18 Jan. 2019; S. Gómez leg.; organic carbon content 1.41%, organic matter content 2.43%, sand 64.81%, clay 8.09%, silt 27.11%; ICML-EMUCOP-180119-77 • 4 ♂♂, 1 CV (preserved in alcohol); same collection data as for preceding; ICML-EMUCOP-180119-78 • 3 ♂♂, 1 CV (preserved in alcohol); same collection data as for preceding; ICML-EMUCOP-180119-79 • 1 ♂ (preserved in alcohol); Sinaloa State, Mazatlán, Urías coastal system, stn 10 (see also Gómez 2020a: 43, fig. 1); 23.1815° N, 106.4214° W; 6.0 m depth; 18 Jan. 2019; S. Gómez leg.; organic carbon content 1.2%, organic matter content 2.07%, sand 69.12%, clay 7.91%, silt 22.97%; ICML-EMUCOP-180119-80 • 1 ♂ (preserved in alcohol); same collection data as for preceding; ICML-EMUCOP-180119-81.

## Description

### Female

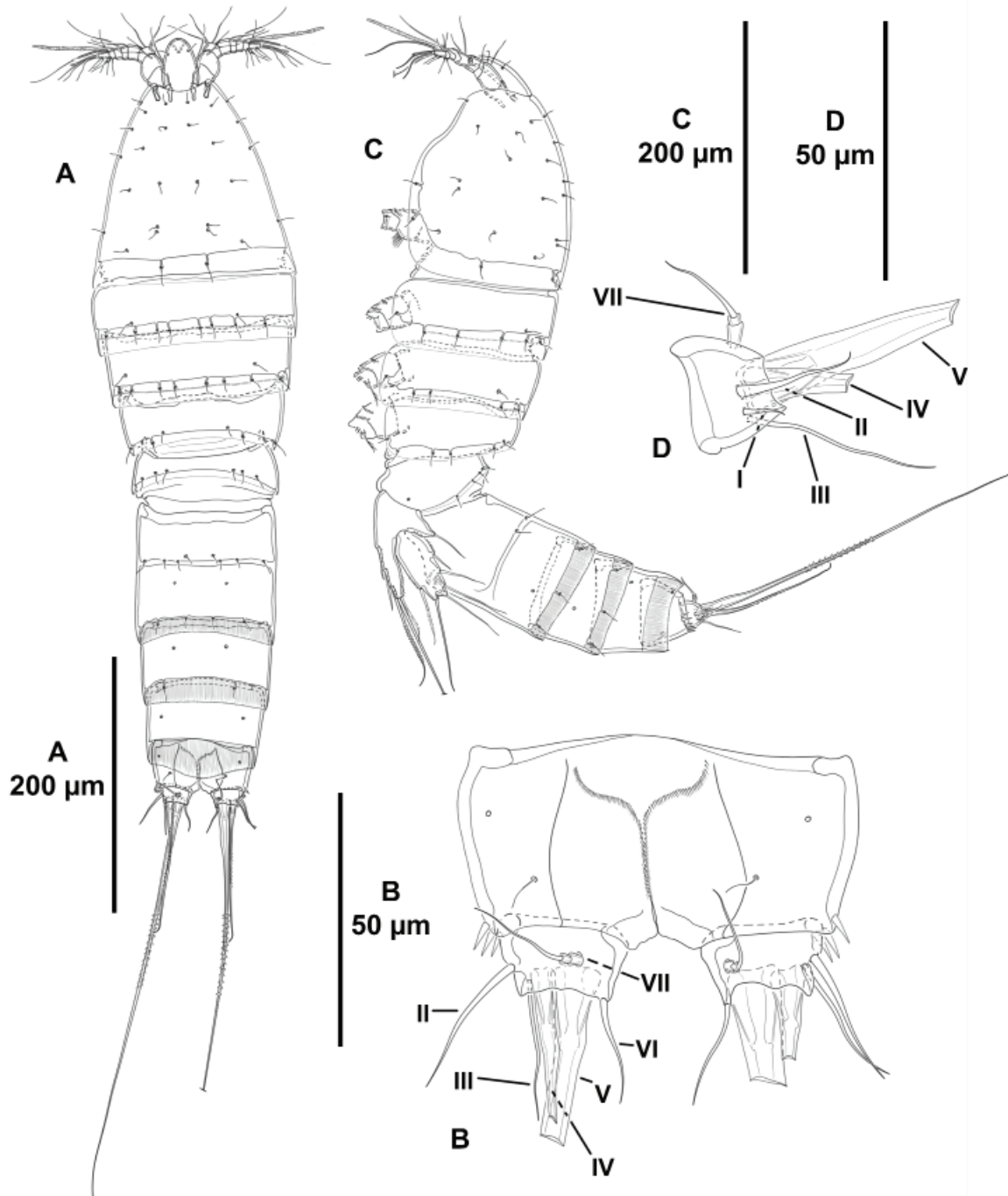
**GENERAL.** Total body length measured from tip of rostrum to posterior margin of caudal rami ranging from 510 to 695  $\mu\text{m}$  (mean 605.4  $\mu\text{m}$ ;  $n = 13$ ; total body length of holotype 695  $\mu\text{m}$ ); habitus fusiform, widest at posterior end of cephalothorax in dorsal view, tapering posteriad (Fig. 11A).

**PROSOME** (Fig. 11A, C). Consisting of cephalothorax, with fused first pedigerous somite, and second to fourth free pedigerous somites; prosomites without expansions nor spinular ornamentation; posterior hyaline frill of cephalothorax, second and third pedigerous somites broad, of P4-bearing somite visibly narrower, with posterior margins plain; posterior frill of second and third pedigerous somites with transverse row of minute spinules.

**UROSOME** (Figs 11A–D, 12A). Consisting of fifth pedigerous somite (first urosomite), genital double-somite (genital – second urosomite – and third urosomites fused), two free urosomites, anal somite and caudal rami; urosomites without expansions. First urosomite narrower than preceding somites in dorsal view (Fig. 11A), without spinular ornamentation, with posterior sensilla as depicted, with one lateral pore on each side (Fig. 11C), posterior frill as in preceding somite dorsally and laterally (Fig. 11A, C). Genital double-somite (Figs 11A, C, 12A) rectangular, slightly longer than wide, with sensilla as shown, without spinular ornamentation; original division between anterior and posterior halves (second – genital – urosomite and third urosomite, respectively) marked by inner cuticular rib dorsally and laterally (Fig. 11A, C), completely fused ventrally (Fig. 12A); posterior half of genital double-somite with two dorsal pores and one lateroventral pore on each side, with posterior hyaline frill finely serrated and striated; P6 at anterior third of genital somite (anterior half of genital double-somite) and with genital field as shown (Fig. 12A). Fourth urosomite largely as in posterior half of genital double-somite, but with additional medial pore ventrally and posterior ventrolateral transverse spinular row on frill (Figs 11A, C, 12A). Fifth urosomite without sensilla or spinules, with two dorsal and two ventral pores, posterior hyaline frill as in preceding somites (Figs 1A, C, 12A). Anal somite wider than long in dorsal view (Fig. 11A–B), without anal operculum, cleft medially dorsally (Fig. 11A–B) and ventrally (Fig. 12A), with two posterior sensilla dorsally, two dorsolateral pores (Fig. 11A–C) and two ventral pores (Fig. 12A), dorsally without spinules, with one ventrolateral and one short ventral spinular row on each side close to joint with caudal rami as shown (Fig. 12A). Caudal rami short, twice as wide as long in dorsal view (Fig. 11A–B), unornamented, with slender tube pore ventrally; with seven setae (Figs 1B, D, 2A) as follows: setae I and II situated almost medially on outer margin, the former very small and ventral to the latter; seta III displaced ventrally close to outer margin; setae IV and V normal, with fracture plane, the former shorter; seta VI arising at inner distal corner; dorsal seta VII issuing subdistally, close to inner margin, triarticulated.

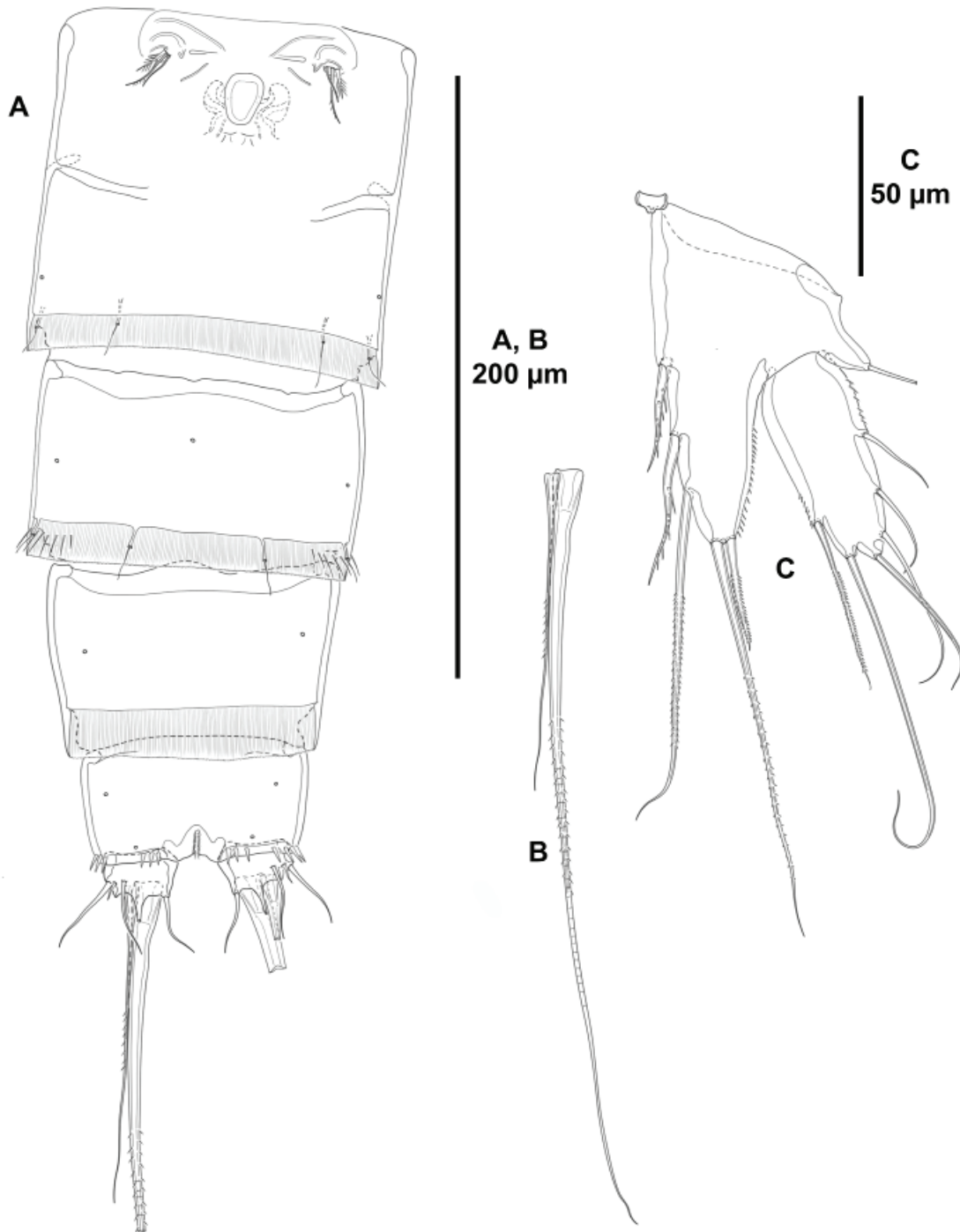
ROSTRUM (Fig. 13A). Not fused to cephalothorax, elongate, triangular, with blunt tip, with one sensillum arising at distal third on each side, without pore, reaching distal margin of second antennular segment.

ANTENNULE (Fig. 13B–C). Eight-segmented; all segments smooth, except for one proximal and one subdistal short spinular row on first segment; all setae smooth; with two and four biarticulated setae on penultimate and last segments, respectively. Armature formula: 1(1); 2(10); 3(6); 4(3+(1+ae)); 5(2); 6(4); 7(4); 8(5+acro). Acrothek consisting of two setae and one aesthetasc fused basally.

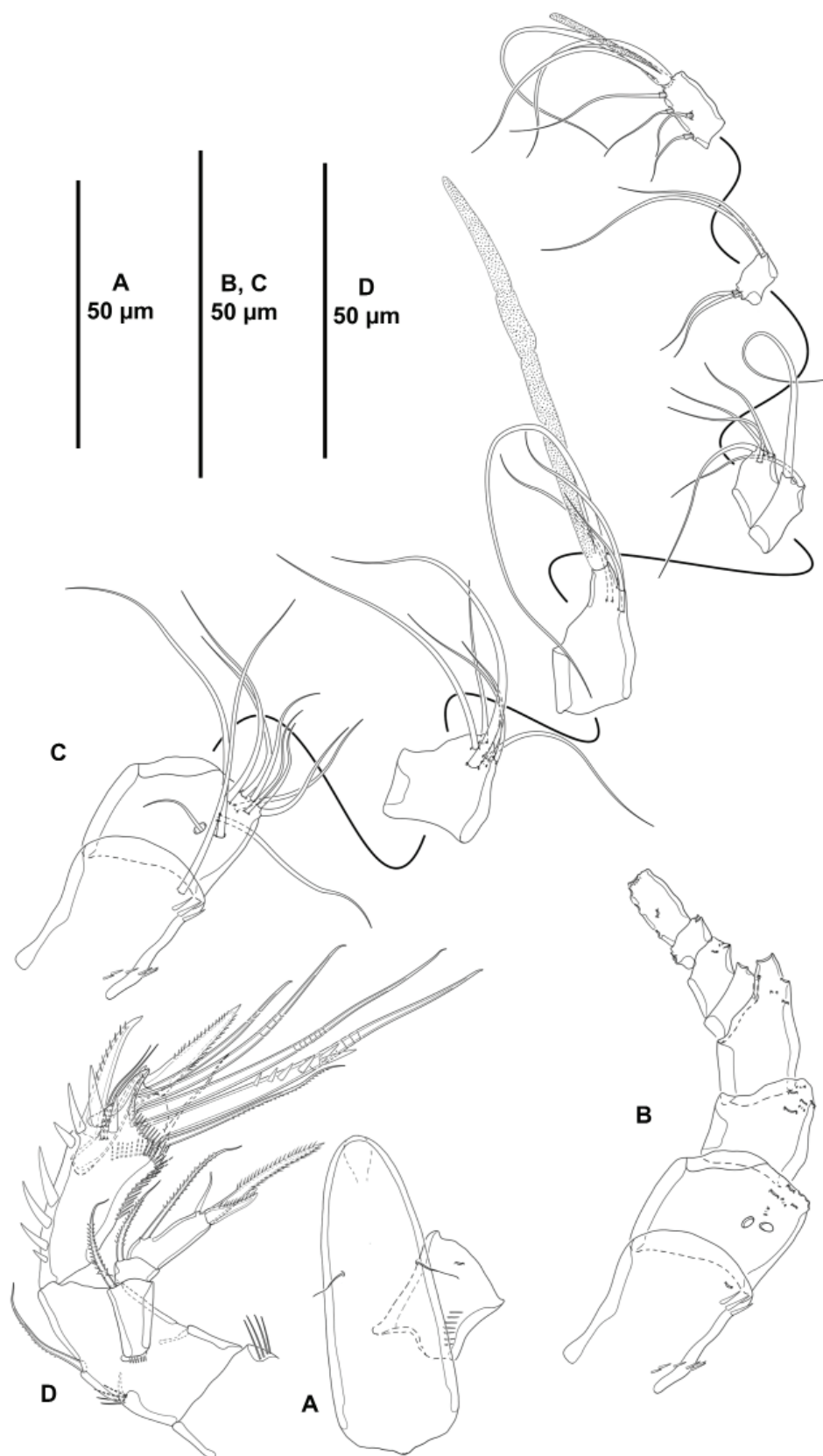


**Fig. 11.** *Spinodiosaccus primus* gen. et sp. nov., holotype, ♀ (ICML-EMUCOP-180119-57). **A.** Habitus, dorsal view. **B.** Anal somite and caudal rami, dorsal view. **C.** Habitus, lateral view. **D.** Left caudal ramus, lateral view.

ANTENNA (Fig. 13D). With small coxa ornamented with outer spinules. Allobasis with remains of former division between basis and first endopodal segment, as long as free endopodal segment, with outer spinules proximally, with one abexopodal seta. Exopod three-segmented; first and third ones subequal in length, second segment smallest; first and second segments unornamented, with one seta each; third segment unornamented, with four elements – one proximal bipinnate, one small subdistal and two distal spine-like elements. Free endopodal segment with proximal and subdistal inner strong spinules, and



**Fig. 12.** *Spinodiosaccus primus* gen. et sp. nov., paratype, ♀ (ICML-EMUCOP-180119-64). **A.** Urosome, ventral view (P5-bearing somite omitted). **B.** Caudal setae IV and V, ventral view. **C.** P5, anterior view.

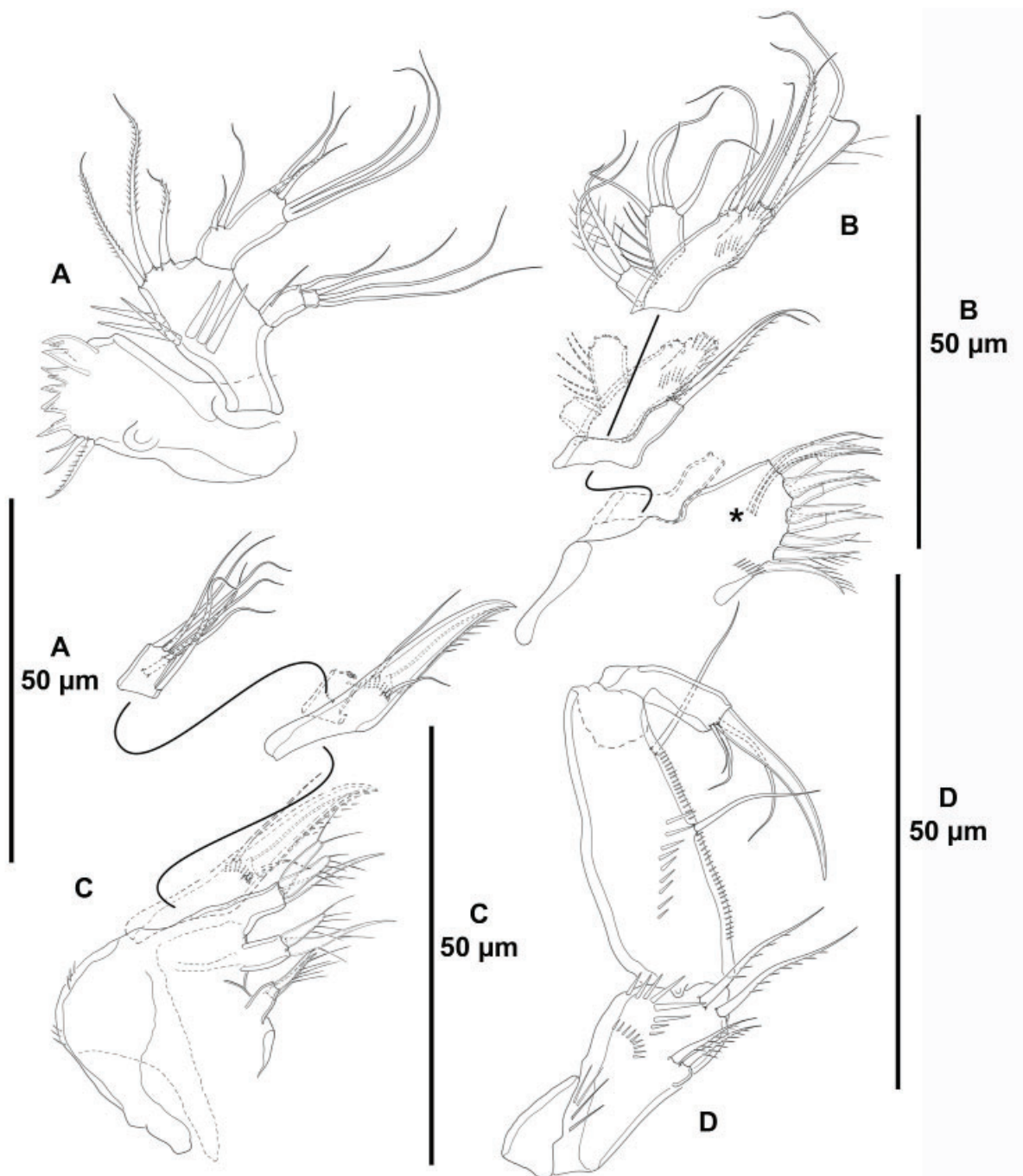


**Fig. 13.** *Spinodiosaccus primus* gen. et sp. nov., paratype, ♀ (ICML-EMUCOP-180119-64). A. Rostrum, dorsal view. B. Antennule (armature omitted for simplicity). C. Antennule showing armature. D. Antenna.



with row of outer small spinules as shown; armed with two lateral inner spines and two slender setae, the latter set close to each other, one inner apical spine, three single geniculate setae, one slender seta, and one strongly spinulose geniculate outer seta fused basally to slender pinnate element.

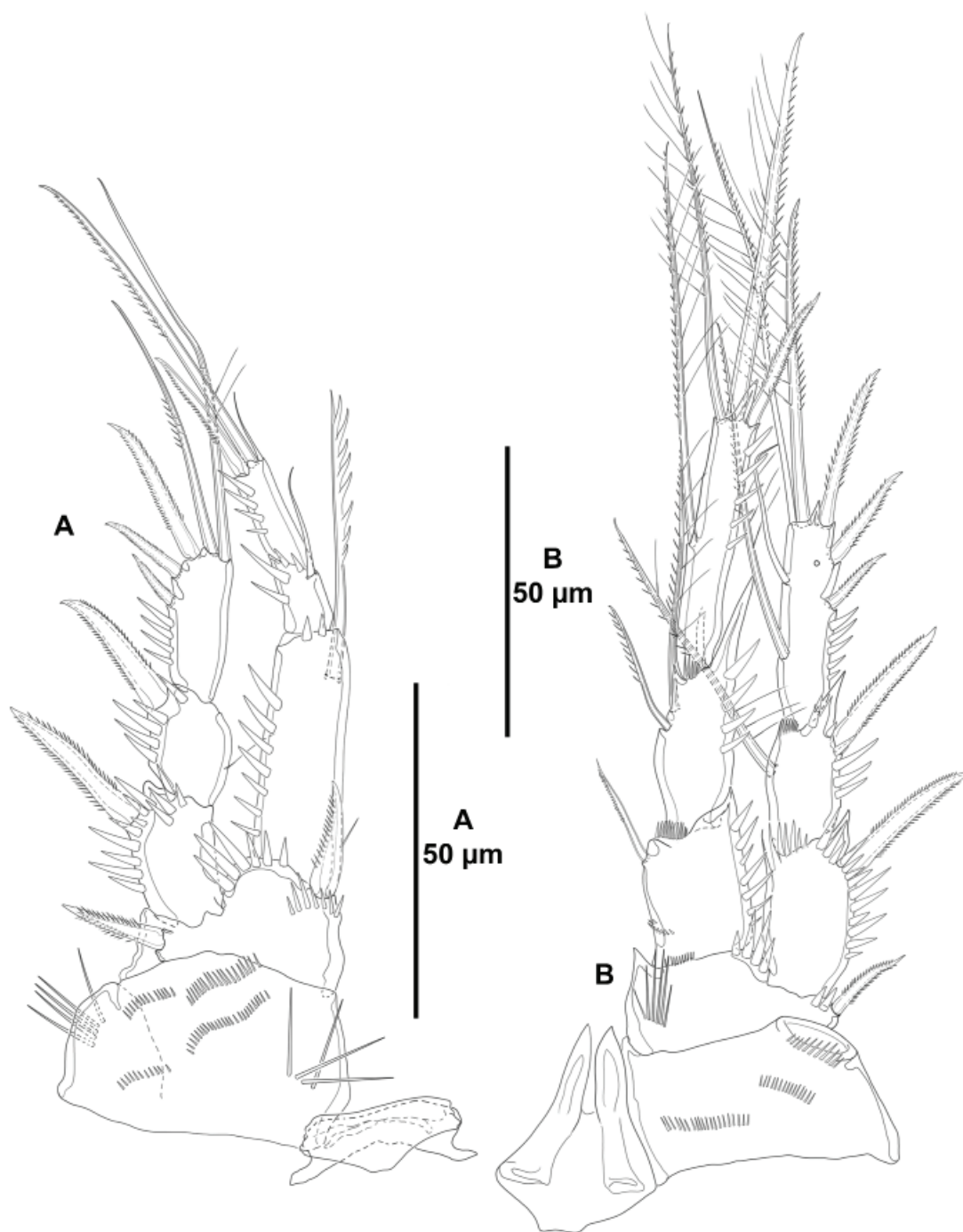
**MANDIBLE** (Fig. 14A). With well-developed gnathobasis bearing strong multi- and bicuspidate teeth as shown, with two long spinules and one pinnate seta. Basis massive, with strong spinules, with three inner setae. Exopod two-segmented; first segment longer than second, the former with one lateral and one distal seta, the latter with three apical elements. Endopod one-segmented, visibly larger than exopod; with two lateral and six distal setae, of which three fused basally.



**Fig. 14.** *Spinodiosaccus primus* gen. et sp. nov., paratype, ♀ (ICML-EMUCOP-180119-64). A. Mandible. B. Maxillule (asterisk indicates two surface setae). C. Maxilla. D. Maxilliped.

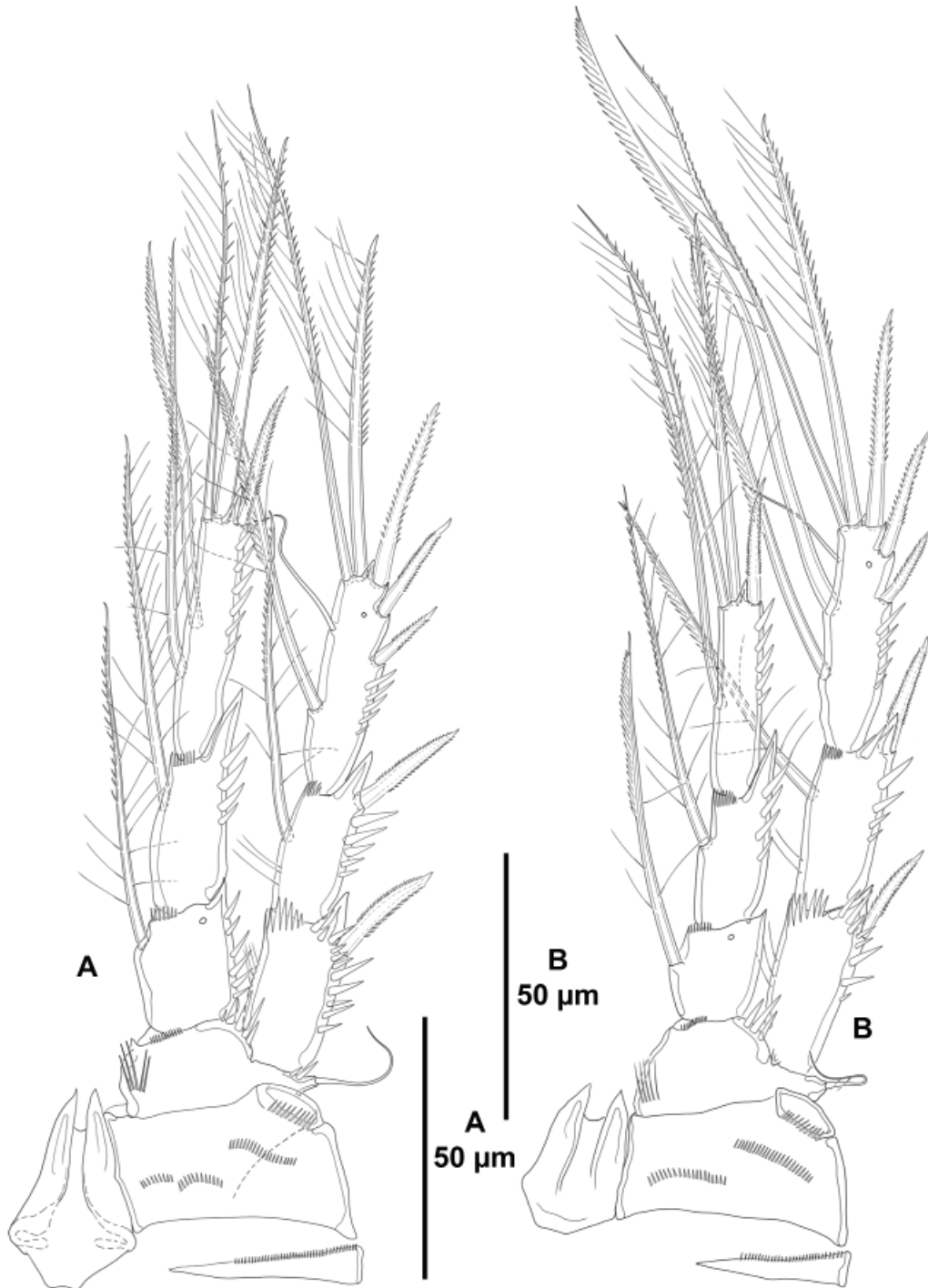


MAXILLULE (Fig. 14B). With arthrite ornamented with some slender spinules and armed with two surface setae (the latter indicated with an asterisk on figure), seven distal spines as shown, one spinulose element and one recurved, stiff pinnate seta. Coxal endite with two setae. Basis with spinular rows as depicted and armed with three lateral, one subdistal and three distal elements, one of which visibly stronger. Rami one-segmented, exopod unornamented and with two setae, endopod with longitudinal spinular row and with four elements – one inner subdistal, two distal and two outer subdistal setae.



**Fig. 15.** *Spinodiosaccus primus* gen. et sp. nov., paratype, ♀ (ICML-EMUCOP-180119-65). **A.** P1, anterior view. **B.** P2, anterior view.

MAXILLA (Fig. 14C). With large syncoxa ornamented with small outer spinules; with three endites; proximal endite smallest, with two setae; middle endite longer than proximal endite, with two setae; distal endite longest, with three setae. Basis drawn out into strong claw, additionally with pinnate spine, and two slender setae – one anterior, one posterior. Endopod one-segmented, with one proximal, one medial, one subdistal and four apical setae.



**Fig. 16.** *Spinodiosaccus primus* gen. et sp. nov., paratype, ♀ (ICML-EMUCOP-180119-65). **A.** P3, anterior view. **B.** P4, anterior view.

MAXILLIPED (Fig. 14D). Subchelate. Praecoxa small. Coxa elongate, with proximal, medial and subdistal spinules as shown; with two inner small setae issuing at middle of segment and two long apical setae. Basis longer than coxa, elongate, with medial row of small spinules and with longitudinal row of minute outer spinules, with one medial inner and one subdistal inner seta. Endopod one-segmented, elongate, with apical claw and three setae of different lengths.

P1 (Fig. 15A). With unornamented intercoxal sclerite. Coxa massive, with several spinular rows as shown. Basis with inner and outer spinulose spines; with strong spinules at top of crescentic medial extension, and with smaller spinules at base of inner spine. Exopod three-segmented, arising at a lower level than that of endopod and reaching tip of ENP2; ENP:EXP length ratio 1.2; exopodal segments with strong outer spinules as shown; second segment shortest, third segment longest; first and second segments without inner armature, outer spine of first segment longer than that of second segment; third segment with five elements of which outer proximal and medial spines shorter than those of preceding segments. Endopod three-segmented, arising from pedestal; ENP1 about 2.8 times as long as wide, 1.4 times as long as second and third segments combined, with outer longitudinal row of strong spinules, with one inner stiff, long, strongly pectinate seta; second and third segments with strong outer spinules as shown, the former shorter, slightly longer than wide, with one inner seta; third segment elongate, 1.5 times as long as preceding segment, with one inner distal slender seta, one apical long element and one outer distal spine.

P2 (Fig. 15B). With narrow intercoxal sclerite unornamented, with acute distal projection on each side. Coxa with three anterior rows of spinules. Basis with small inner acute outgrowth, with long slender inner spinules, with minute spinules at base of endopod, and with strong spinules between rami and at base of outer spine. Rami three-segmented, endopod longer than exopod. Exopod three-segmented, arising at a lower level than that of the endopod, reaching slightly above the middle of ENP3; exopodal segments with strong outer spinules as shown; EXP1 and EXP2 with outer distal acute projection, of EXP1 shorter, inner distal frill of first segment coarse, of second segment small, first segment without, second segment with inner seta; EXP3 with subdistal outer pore and seven elements – three outer spines, two apical elements and two inner setae of which distalmost one visibly shorter. Endopod three-segmented, arising from pedestal; endopodal segments with strong outer spinules as shown; ENP1 shortest, slightly longer than wide, with posterior small spinules proximally, with small inner distal spinules and with outer short acute projection, with one short inner seta; ENP2 elongate, twice as long as wide and 0.6 times as long as ENP3, with small inner distal spinules, with long outer distal acute projection, with two inner setae of which proximal shorter; ENP3 longest, elongate, six times as long as wide, with four elements (one inner and two apical setae, and one outer spine), with acute projection between outer spine and inner apical seta.

P3 (Fig. 16A). With triangular praecoxa ornamented with transverse row of minute spinules. Intercoxal sclerite and coxa as in P2. Basis largely as in P2, but with smaller inner distal outgrowth and setiform outer element. Rami three-segmented, endopod slightly longer than exopod. Exopod largely as in P2. Endopod largely as in P2 except for lack of posterior spinules and with outer subdistal pore on ENP1, for inner seta of P3 ENP1 comparatively longer, for one long seta only on P3 ENP2, and for two inner setae on P3 ENP3.

P4 (Fig. 16B). With intercoxal sclerite, praecoxa, and coxa as in P3. Basis as in P3 except for lack of inner distal outgrowth. Exopod longer than endopod; EXP:ENP length ratio 1.3; largely as in P3 except for three inner setae on P4 EXP3 of which medial one visibly thicker and strongly pectinate. Endopod reaching slightly beyond middle of EXP3; largely as in P3 except for one inner seta only on P4 ENP3.

Armature formula of P1–P4 as follows:

	EXP	ENP
P1	0-0-0,2,3	1-1-1,1,1
P2	0-1-2,2,3	1-2-1,2,1
P3	0-1-2,2,3	1-1-2,2,1
P4	0-1-3,2,3	1-1-1,2,1

P5 (Fig. 12C). With outer seta of baseoendopod arising from setophore. Endopodal lobe triangular, reaching distal third of exopod; with small spinules along outer margin; with five elements – one outer and one inner apical and one inner subdistal long setae, and two inner spiniform elements. Exopod elongate, 2.2 times as long as wide; with spinules at base of innermost seta and on outer margin proximally; with six elements – three outer slender setae, two apical elements of which outermost one shorter and one inner seta.

P6 (Fig. 12A). With three setae – one short bipinnate element, and one medial and one inner slender seta.

### Male

GENERAL. Total body length measured from tip of rostrum to posterior margin of caudal rami ranging from 380 to 510  $\mu\text{m}$  (mean 455  $\mu\text{m}$ ;  $n = 8$ ; total body length of allotype 510  $\mu\text{m}$ ).

PROSOME (Fig. 17A). As in female.

UROSOME (Fig. 17A–B). As in female except for second – P6-bearing somite – and third urosomites separated, for medial row of eight ventral spinules on third urosomite, and for lack of spinules on hyaline frill of fourth urosomite.

SEXUAL DIMORPHISM. Expressed in ventral somatic ornamentation (see above), antennule, and basis of P1, P2 ENP, P5 and P6.

ANTENNULE (Fig. 18A–B). 11-segmented, haplocer. All segments smooth, except for proximal and subdistal spinular rows on first segment. All setae smooth except for two and four biarticulated setae on tenth and eleventh segments, respectively. Armature formula: 1(1); 2(11); 3(6); 4(1); 5(5+(1+ae)); 6(2); 7(2+2 spines); 8(0); 9(1); 10(4); 11(5+acro). Acrothek consisting of two setae and one aesthetasc fused basally.

ANTENNA, MANDIBLE, MAXILLULE, MAXILLA AND MAXILLIPED (not shown). As in female.

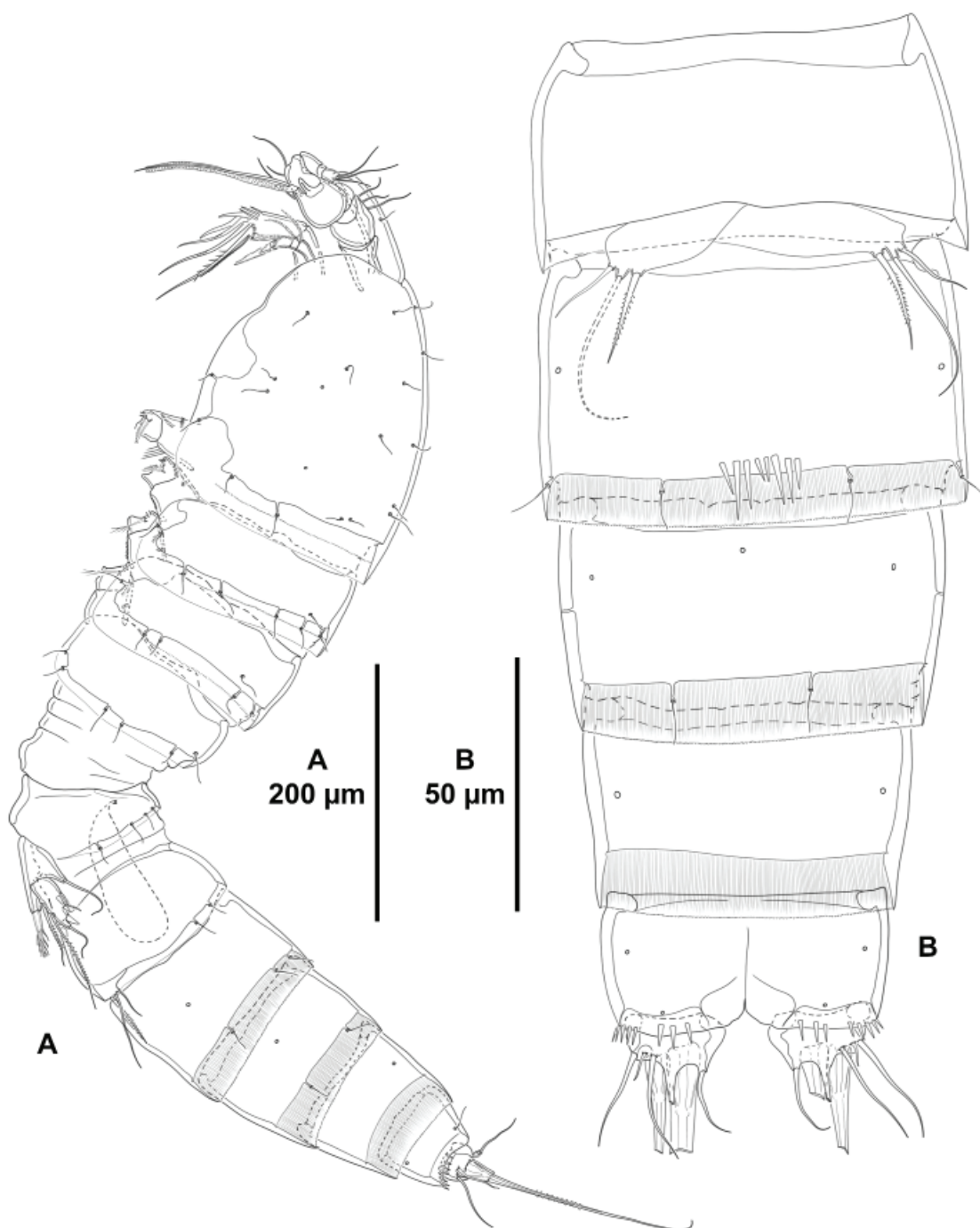
P1. As in female except for basis without slender inner long spinules, without spinules at base of inner spine and with inner modified accessory spine (Fig. 18C).

P2 EXP (not shown). As in female. Endopod (Fig. 18D) sexually dimorphic, two-segmented; ENP1 as long as ENP2 (excluding distal cylindrical extension of ENP2), with longitudinal row of outer spinules, with outer distal acute outgrowth, with one inner short seta; proximal part of ENP2 rectangular, distal extension cylindrical, 2.4 times as long as wide excluding distal cylindrical extension, with longitudinal row of outer spinules, with two inner setae arising from pedestal of which proximal (seta I on Fig. 18D) visibly shorter, subdistally with one strong inner and almost straight element (element III on Fig. 18D), with one lateral and one apical seta (setae IV and V on Fig. 18D) arising from distal elongate cylindrical

extension fused to segment basally and with strong outer subdistal element strongly tapering distally (element VI on Fig. 18D).

P3 AND P4 (not shown). As in female.

P5 (Fig. 18E). With outer seta of baseoendopod arising from setophore. Endopodal lobe reaching middle of exopod, with outer spinules as shown, with two distal modified setae as shown of which outermost



**Fig. 17.** *Spinodiosaccus primus* gen. et sp. nov. **A.** Allotype, ♂ (ICML-EMUCOP-180119-58); habitus, lateral view. **B.** Paratype, ♂ (ICML-EMUCOP-180119-67); urosome, ventral view (P5-bearing somite omitted).

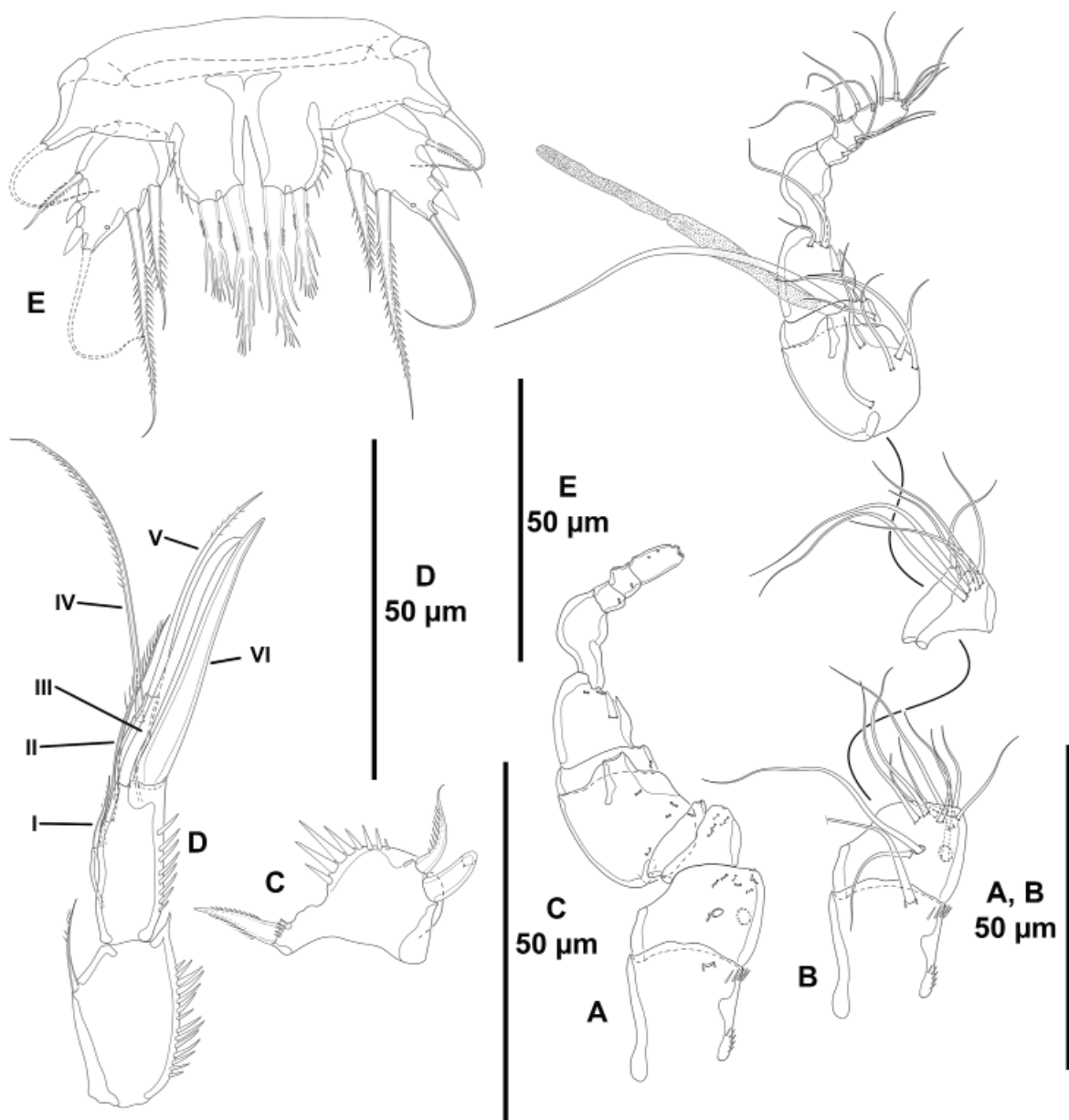


one shorter. Exopod triangular, 1.6 times as long as wide, with inner subdistal pore, with six setae – one proximal bipinnate seta, one medial and one subdistal short strong spines of which medial one shorter, one distal seta arising from setophore and two inner setae of which proximal one shorter.

P6 (Fig. 17B). Asymmetrical, only one leg functional, each leg with three setae of which innermost one bipinnate, medial longest and bare, outermost shortest and bare.

### Variability

Both caudal setae I spiniform in one female. One male possesses only one outer spine on P5 EXP.



**Fig. 18.** *Spinodiosaccus primus* gen. et sp. nov. A–B, E. Paratype, ♂ (ICML-EMUCOP-180119-68). C–D. Paratype, ♂ (ICML-EMUCOP-180119-69). A. Antennule (armature omitted for simplicity). B. Antennule showing armature. C. Basis of P1, anterior view. D. P2 ENP. E. P5, anterior view.



*Bulbamphiascus* Lang, 1944

**Type species**

*Canthocamptus imus* Brady, 1872, by original designation.

**Other species**

*Bulbamphiascus denticulatus* (Thompson, 1893), *B. incus* Gee, 2005, *B. plumosus* Mu & Gee, 2000 and *B. scilloniensis* Gee, 2005.

**Species incertae sedis**

*Bulbamphiascus chappuisi* Rouch, 1962.

**Amended diagnosis**

Miraciidae: Diosaccinae. Body fusiform. Rostrum not fused to cephalothorax, triangular, elongate, with rounded apical margin, almost as long as first, second and third antennary segments combined, with one subdistal sensilla on each side at third quarter of its length. Pro- and urosomites without extensions; with a flexible unsclerotized cuticle between prosome and urosome. First urosomite (P5-bearing somite) narrower than preceding somites in dorsal view. Female genital double-somite (genital – second urosomite – and third urosomites fused) completely fused ventrally, with a dorsolateral cuticular rib marking former division between somites. Anal somite trapezoidal, without anal operculum. Caudal rami 1.6 times as wide as long in dorsal view, with seven setae. Female antennule eight-segmented, with aesthetasc and seta fused basally on fourth segment and with apical acrothek on last segment. Male antennule haplocer, 10-segmented, with aesthetasc and seta fused basally on fifth segment, and with apical acrothek on last segment. Antennular setae typically smooth. Antenna with allobasis and abexopodal seta; exopod three-segmented, armature formula 1-1-1,3,0. Mandibular palp biramous; endopod one-segmented, exopod two-segmented. Maxillule biramous; rami one-segmented. Maxilla with three endites, proximal and middle endites with two, distal endite with three elements; ENP one-segmented. Maxilliped subchelate; (syn)coxa with four, basis with two setae, ENP one-segmented with claw and three accompanying setae. P1–P4 with three-segmented rami. Male P1 basis sexually dimorphic, with inner unipinnate spine and inner modified accessory spine. P1 EXP shorter than ENP, reaching tip of ENP2; EXP2 with inner seta; ENP1 with inner seta; ENP3 longer than the ENP2, with one inner seta, a distal long and geniculate seta, and an outer spine. P2–P4 EXP and ENP of approximately the same length; P2–P4 EXP1 with inner seta; inner distal seta of EXP3 visibly shorter than other elements of same segment; P2 ENP2 with two setae, proximal shorter. Male P2 ENP sexually dimorphic, two-segmented; first segment with one inner seta; second segment with two inner setae, one inner subdistal sigmoid element, one subdistal and one distal seta arising from cylindrical extension fused basally to segment, and one strong distal outer element strongly tapering distally. P5 EXP with six setae in female and male; one or two medial outer elements transformed into short spines. P5 endopodal lobe with five setae in female, with two setae in male; armature of male P5 endopodal lobe strongly bipinnate.

Armature formula of P1–P5 as follows:

	EXP	ENP/ENP lobe
P1	0-1-0,2,3	1-1-1,1,1
P2	1-1-2,2,3	♀ 1-2-1,2,1 / ♂ dimorphic
P3	1-1-2,2,3	1-1-2,2,1
P4	1-1-3,2,3	1-1-1,2,1
P5 ♀/♂	♀ 6/♂ 6	♀ 5/♂ 2

Sexual dimorphism expressed in male antennule, P2 ENP, P5, P6, and in genital and third urosomites being separated.

### Apomorphies for *Bulbamphiascus*

We did not detect any apomorphy for *Bulbamphiascus*. However, *Bulbamphiascus* is part of a larger monophyletic group composed of *Spinodiosaccus* gen. nov., *Spinopedia* gen. nov. and *Pallarica* gen. nov. (Fig. 19). The subdistal outer element of the male P2 ENP2 with almost parallel margins, viz slightly tapering distally, is considered here as part of the ground pattern of this monophyletic group and is regarded as a potential synapomorphy for this clade. The modification of this spine into a strong tapering element is regarded here as secondary and is a synapomorphy for *Bulbamphiascus* and *Spinodiosaccus* gen. nov. The combination of an outer subdistal tapering spine and a sigmoid inner subdistal element on the male P2 ENP2 is unique to *Bulbamphiascus* (the outer subdistal spine on the male P2 ENP2 of

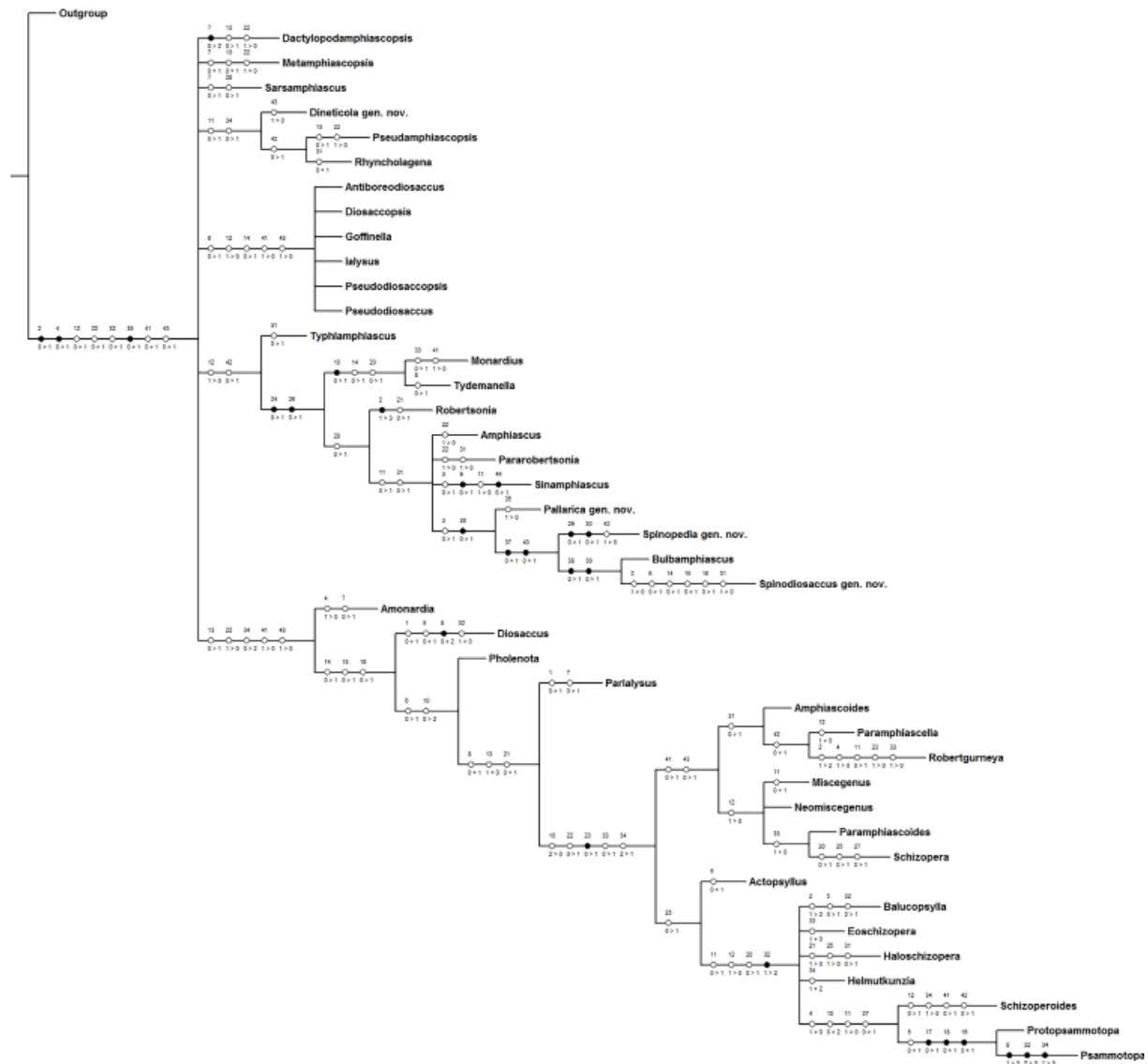


Fig. 19. Strict consensus cladogram of the generic relationships within the Diosaccinae.

*Spinodiosaccus* gen. nov. also tapers distally, but the inner subdistal element on the same segment of this species is rather straight).

*Bulbamphiascus chappuisi* is here relegated to incertae sedis due to the shape of the rostrum and furca, and to the morphology of the male P2 ENP, the illustrations of which (see Rouch 1962: 247, figs 29–33) are too schematic, preventing any further comparison.

***Spinopedia* gen. nov.**

urn:lsid:zoobank.org:act:F6DD1CA7-26EE-476D-AC00-2C4401B63014

*Bulbamphiascus* Lang, 1944: 19, pro parte.

**Type and only species**

*Bulbamphiascus spinulosus* Mu & Gee, 2000 (= *Spinopedia spinulosa* (Mu & Gee, 2000) comb. nov.), by monotypy.

**Diagnosis**

Miraciidae: Diosaccinae. Body fusiform; body surface seemingly covered with minute denticles. Rostrum not fused to cephalothorax, triangular, elongate, with round apical margin, almost as long as first and second antennular segments combined, with one subdistal sensilla on each side at third quarter of its length. Pro- and urosomites without extensions; with a flexible unsclerotized cuticle between prosome and urosome. First urosomite (P5-bearing somite) narrower than preceding somites in dorsal view. Genital double-somite (genital – second urosomite – and third urosomites fused) completely fused ventrally, with a dorsolateral cuticular rib marking original division between genital and third urosomites. Telson trapezoidal, without anal operculum. Caudal rami short, about 1.5 times as wide as long in dorsal view, with seven setae. Female antennule eight-segmented, with aesthetasc and seta fused basally on fourth segment and with apical acrothek on last segment. Male antennule haplocer, 10-segmented, with aesthetasc and seta fused basally on fifth segment and with apical acrothek on last segment. Setae of first and second antennular segments typically bipinnate, smooth in remaining segments. Antenna with allobasis and abexopodal seta; exopod three-segmented, armature formula 1-1-1,3,0. Mandibular palp biramous; endopod one-segmented, larger than exopod, the latter two-segmented. Maxillule biramous; rami one-segmented. Maxilla with three endites, proximal and middle endites with two, distal endite with three elements; ENP one-segmented. Maxilliped subchelate; (syn)coxa with four, basis with two setae; ENP one-segmented, with claw and three accompanying setae. P1–P4 with three-segmented rami. Male P1 basis sexually dimorphic, with inner unipinnate spine and inner modified accessory spine. P1 EXP shorter than ENP, reaching tip of ENP2; P1 ENP1 with strong bipinnate inner seta; P1 ENP3 2.5 times as long as ENP2, with one small inner seta, a distal long geniculate seta and one outer spine; P1 EXP2 with inner seta; P2–P4 EXP and ENP of approximately the same length. P2–P4 EXP1 with inner seta; inner distal seta of P2–P4 EXP3 visibly smaller than other inner setae on same segment. P2 ENP2 with two setae, proximalmost shorter. P2–P4 basis with inner chitinous projection. Male P2 ENP sexually dimorphic, two-segmented; first segment with one inner seta; second segment completely covered by spinules and setules of different lengths, with two inner setae subequal in length, two elements (one medial, one apical) issuing from elongate cylindrical extension fused to segment basally, and with one inner subdistal sigmoid blunt element and one outer subdistal blunt spine with almost parallel margins, viz slightly tapering distally, of which the former is shorter. P5 EXP longer than wide, comparatively shorter in male, with six setae in both sexes; two medial outer elements modified into stiff short spines in male; distal outer spine foliaceous in female. P5 endopodal lobe with five setae in female, with two setae in male; armature of male P5 endopodal lobe strongly bipinnate.

Armature formula of P1–P5 as follows:

	EXP	ENP/ENP lobe
P1	0-1-0,2,3	1-1-1,1,1
P2	1-1-2,2,3	♀ 1-2-1,2,1 / ♂ dimorphic
P3	1-1-2,2,3	1-1-2,2,1
P4	1-1-3,2,3	1-1-1,2,1
P5 ♀/♂	♀ 6 / ♂ 6	♀ 5 / ♂ 2

Sexual dimorphism expressed in male antennule, P2 ENP, P5, P6, and in separated genital and third urosomites.

### Etymology

The prefix ‘spino’ from the Latin ‘spīna’, ‘spine’, and the suffix ‘pedia’ from the Latin ‘pēs’, ‘pedis’, ‘foot’, refers to the presence of a spinular patch on the male P2 ENP1, and to the presence of several spinules and setules covering the male P2 ENP2. Gender feminine.

### Apomorphies for *Spinopedia* gen. nov.

Two apomorphies for *Spinopedia* have been detected: i) presence of an inner subdistal spinular patch on the male P2 ENP1 and ii) male P2 ENP2 completely covered with spinules and setules of different lengths. In addition, the subdistal inner seta of the female P5 EXP arises directly from the ramus (i.e., the seta does not arise from a setophore) (character 42 in Table 3 ; see also Fig. 19). The lack of a setophore for the subdistal inner seta of the female P5 EXP is regarded here as autapomorphic for the genus and is a result of reversal. The presence of a setophore for the inner subdistal seta of the female P5 EXP is autapomorphic for a larger group of genera to which *Spinopedia* gen. nov. belongs (Fig. 19) and seems to have evolved convergently in more than one evolutionary lineage within the Diosaccinae (Fig. 19).

### *Pallarica* gen. nov.

urn:lsid:zoobank.org:act:78F45B32-1B47-41BB-99E0-E7F8327E3333

*Bulbamphiascus* Lang, 1944: 19, pro parte.

### Type and only species

*Bulbamphiascus cibimae* Pallares, 1982 (= *Pallaricia cibimae* (Pallares, 1982) comb. nov.), by monotypy.

### Diagnosis

Miraciidae: Diosaccinae. Body fusiform. Rostrum not fused to cephalothorax, triangular, elongate, with round apical margin, almost as long as first, second and third antennular segments combined, with one subdistal sensilla at third quarter of its length, on each side. Pro- and urosomites without expansions. Genital double-somite (genital – second urosomite – and third urosomites fused) completely fused ventrally, with a dorsolateral cuticular rib marking original division between somites. Caudal rami about 1.5 times as wide as long in dorsal view; with seven setae. Female antennule eight-segmented, with aesthetasc and seta fused basally on fourth segment, and with apical acrothek on last segment. Antennular setae typically smooth. Antenna with allobasis and abexopodal seta; exopod three-segmented, armature formula 1-1-1,3,0. Mandibular palp biramous; endopod one-segmented, larger than exopod, the latter two-segmented. Maxillule biramous; rami one-segmented. Maxilla with three endites, proximal and middle endites with two, distal endite with three elements; ENP two-segmented.

Maxilliped subchelate; (syn)coxa with three, basis with two setae; ENP one-segmented, with claw and three accompanying setae. P1–P4 with three-segmented rami. Male P1 basis sexually dimorphic, with inner unipinnate spine and inner modified accessory spine. P1 EXP shorter than ENP, reaching tip of ENP2; P1 ENP1 with strong bipinnate inner seta; ENP3 2.5 times as long as ENP2, with one small inner seta, a long distal geniculate seta, and an outer spine; EXP2 with inner seta. P2–P4 EXP and ENP of approximately same lengths; P2–P4 EXP1 with inner seta; inner distal seta of P2–P4 EXP3 visibly shorter than other inner setae on same segment. P2 ENP2 with two setae, proximalmost small. Male P2 ENP sexually dimorphic, two-segmented; first segment with one inner seta; second segment with two inner setae, two elements (one medial, one apical) issuing from elongate cylindrical extension fused to segment basally, and inner subdistal element almost straight and outer subdistal element slightly thicker and longer than the former and with almost parallel margins (i.e., slightly tapering distally). P5 EXP longer than wide in female, comparatively shorter in male, with six setae in female and seven setae in male; two medial outer elements stiff short spine-like in male, slender and smooth in female. P5 endopodal lobe with five setae in female, with two setae in male; armature of male P5 endopodal lobe strongly bipinnate.

Armature formula of P1–P5 as follows:

	EXP	ENP
P1	0-1-0,2,3	1-1-1,1,1
P2	1-1-2,2,3	♀ 1-2-1,2,1 / ♂ dimorphic
P3	1-1-2,2,3	1-1-2,2,1
P4	1-1-3,2,3	1-1-1,2,1
P5 ♀/♂	♀ 6/♂ 6	♀ 5/♂ 2

Sexual dimorphism expressed in male antennule, P2 ENP, P5, P6, and in separated genital and third urosomites.

### Etymology

This genus is dedicated to Rosa E. Pallares for her contribution to the taxonomy of harpacticoid copepods from Argentina. Gender feminine.

### Apomorphies for *Pallarica* gen. nov.

This genus is unique by the possession of seven setae on the male P5 EXP, which is regarded here as apomorphic for the genus. The presence of an additional seta is regarded here as a character reversal.

### *Dinetia* gen. nov.

urn:lsid:zoobank.org:act:570211A6-5E4D-42CA-A26D-61E2F0E6BC6A

Syn. *Bulbamphiascus* Lang, 1944: 19, pro parte.

### Type and only species

*Bulbamphiascus minutus* Dinet, 1971 (= *Dinetia minuta* (Dinet, 1971) comb. nov), by monotypy.

### Diagnosis

Miraciidae: Diosaccinae. Body fusiform. Width:length ratio of caudal rami 0.8–1.2. Rostrum not fused to cephalothorax, elongate, with rounded tip. Female antennule eight-segmented, with aesthetasc

and seta fused basally on fourth segment. Antennular setae typically smooth. Antenna with allobasis and abexopodal seta; EXP three-segmented, armature formula 1-1-1,3,0. Mandibular palp extremely reduced. Maxillule biramous; rami one-segmented. Maxilla with three endites. Maxilliped subchelate; (syn)coxa with two, basis with two setae; ENP one-segmented, with claw and two accompanying setae. P1–P4 with three-segmented rami. P1 EXP shorter than ENP1, reaching its distal third; P1 ENP1 with strong bipinnate inner seta; ENP3 about twice as long as ENP2, with one small inner seta, a long distal geniculate seta and an outer spine; P1 EXP2 with inner seta, EXP3 with three outer spines, proximal one shortest, and two geniculate distal setae. P2–P4 EXP1 with inner seta; P2–P4 EXP3 with reduced inner armature. P2 ENP1 with inner setae; ENP2 with two setae of approximately same length. Female P5 EXP longer than wide, with six setae – three outer, two distal and one inner element. P5 endopodal lobe with five setae.

Armature formula of P1–P5 as follows:

	EXP	ENP
P1	0-1-0,2,3	1-0(1?)-1,1,1
P2	1-1-1,2,3	1-2-1.2.1
P3	1-1-1,2,3	1-1-2,2,1
P4	1-1-2,2,3	1-1-2,2,1
P5 ♀/♂	♀ 6/♂ 6	♀ 5/♂ 2

Male unknown.

### Etymology

This genus is dedicated to Alain Dinet for his contribution to the taxonomy of harpacticoid copepods from France. Gender feminine.

### Apomorphies for *Dinetia* gen. nov.

The exclusion of *Bulbamphiascus minutus* from that genus and from any other genus presented here, and its reallocation into *Dinetia* gen. nov., is supported by, for example, the lack of the short inner distal seta on P2–P4 EXP3. *Bulbamphiascus minutus* probably bears a sister-group relationship with *Pseudamphiascopsis* Lang, 1944 and *Rhyncholagena* Lang, 1944, with which it forms a monophyletic group (see Fig. 19). These three genera share the longer P1 ENP1 relative to the P1 EXP. Given that *B. minutus* could not be included in *Bulbamphiascus* or into any other diosaccin genus, and pending the discovery of the male of this species, we propose a new genus, *Dinetia* gen. nov., for *B. minutus*. The assessment and significance of character 43 for *D. minuta* comb. nov. (see Table 3) is still pending until the male is described.

### Phylogenetic statistics and resolution

Our partial phylogenetic analysis resulted in 12 most parsimonious topologies with 126 steps, CI of 42, and RI of 77 (see Supplementary File 1). The strict consensus topology (nine branches collapsed) returned the following clades of unclear phylogenetic affinities between each other: a) a small clade composed by *Dinetia* gen. nov., *Pseudamphiascopsis* and *Rhyncholagena*; b) a clade formed by *Antiboreodiosaccus* Lang, 1944, *Diosaccopsis* Brian, 1925, *Goffinella* Wilson, 1932, *Ialysus* Brian, 1927, *Pseudodiosaccopsis* Lang, 1944 and *Pseudodiosaccus* T. Scott, 1906; c) a clade formed by *Typhlamphiascus* Lang, 1944, *Monardius* Huys, 2009, *Tydemanella* A. Scott, 1909, *Robertsonia* Brady, 1880, *Amphiascus* Sars, 1905, *Pararobertsonia* Lang, 1944, *Sinamphiascus* Mu & Gee, 2000, *Pallarica*



gen. nov., *Spinopedia* gen. nov., *Bulbamphiascus* and *Spinodiosaccus* gen. nov.; d) a clade composed of *Amonardia* Lang, 1944, *Diosaccus* Boeck, 1872, *Pholenota* Vervoort, 1964, *Parialysus* Nicholls, 1941, *Amphiascoides* Nicholls, 1941b, *Paramphiascella* Lang, 1944, *Robertgurneya* Apostolov & Marinov, 1988, *Miscegenus* Wells, Hicks & Coull, 1982, *Neomiscegenus* Karanovic & Ranga Reddy, 2004, *Paramphiascoides* Wells, 1967, *Schizopera* Sars, 1905, *Actopsyllus* Wells, 1967, *Balucopsylla* Rao, 1972, *Eoschizopera* Wells & Rao, 1976, *Haloschizopera* Lang, 1944, *Helmutkunzia* Wells & Rao, 1976, *Schizoperoides* Por, 1968, *Protopsamnotopa* Geddes, 1968 and *Psammotopa* Pennak, 1942. The phylogenetic position of the genera *Dactylopodamphiascopsis* Lang, 1944, *Metamphiascopsis* Lang, 1944 and *Sarsamphiascus* Huys, 2009 remains uncertain. It is important to highlight the high level of character convergence within the Diosaccinae.

Clades a–d above are present in the 12 most parsimonious topologies (see Supplementary File 1), but their relationships are not consistent. The positions of the clade *Dinetia* gen. nov.–*Rhyncholagena* and the genera *Sarsamphiascus*, *Metamphiascopsis* and *Dactylopodamphiascopsis* are unclear, sometimes forming a clade with *Typhlamphiascus*–*Spinodiosaccus* gen. nov. (6 times), sometimes forming a clade with *Amonardia*–*Psammotopa* (6 times). The same happens to the clade *Antiboreodiosaccus*–*Pseudodiosaccus* which appears either as the sister group of the remaining Diosaccinae or as the sister group of a clade including *Dinetia* gen. nov.–*Rhyncholagena*, *Sarsamphiascus*, *Metamphiascopsis*, *Dactylopodamphiascopsis* and *Typhlamphiascus*–*Spinodiosaccus* gen. nov.

#### **Key to the species of *Typhlamphiascus* Lang, 1944**

1. P4 ENP3 with two inner setae (five setae in all). Female: P5 EXP with tip normal or hook-like. Male: P1 basis with inner seta normal or modified, elongate .....2 [Por's group I (Pors 1963)]
  - P4 ENP3 with one inner seta (four setae in all). Female: P5 EXP with tip normal. Male: P1 basis with inner seta normal, not modified .....11 [Por's group II (Pors 1963)]
2. Female P5 EXP with tip hook-like; endopodal lobe with apical outer seta very small .....3
  - Female P5 EXP with tip normal .....4
3. Female: antennule seven-segmented; P5 EXP and endopodal lobe with five setae each, endopodal lobe with apical inner element spiniform; P4 EXP3 with three inner setae (male unknown) .....*T. dentipes* (I.C. Thompson & A. Scott, 1903)
  - Female: antennule eight-segmented; P5 EXP and endopodal lobe with five setae each, endopodal lobe with apical inner element setiform; P4 EXP3 with two inner setae (male unknown) .....*T. blanchardi* (T. Scott & A. Scott, 1895) <sup>1</sup>
4. Female: antennule eight-segmented; P5 EXP with five, endopodal lobe with four setae. Male: P1 basis with inner spine not modified, with three to five inner accessory spines; P5 EXP with four, endopodal lobe with two bifurcate setae .....*T. gracilicaudatus* (I.C. Thompson & A. Scott, 1903) <sup>6</sup>
  - These characters not combined .....5
5. Female: antennule eight-segmented; P5 EXP with four, endopodal lobe with five setae. Male: P1 basis with inner element modified, elongate; P5 EXP with four, endopodal lobe with two bifurcate setae .....*T. longifurcatus* Rouch, 1962
  - These characters not combined .....6
6. Female: P5 EXP and endopodal lobe with five setae each .....7
  - Female: P5 EXP with six setae, endopodal lobe with five setae .....8

7. Female: caudal rami 1.4–1.5 times as long as wide, shorter than anal somite; P5 second exopodal seta from outer to inner margin 1.5 times as long as third element; third seta 1.7 times as long as first seta and longer than exopod; innermost (fifth) seta 1.2 times as long as fourth seta. Male: P1 basis with inner spine normal, with seven to eight inner accessory spines; P5 EXP with five setae, endopodal lobe with two setae; P5 second exopodal seta from outer to inner margin shorter than first seta .....*T. gracilis* Por, 1963 <sup>7</sup>  
 – Female: caudal rami twice as long as wide, as long as anal somite; P5 second exopodal seta from outer to inner margin 4.5 times as long as third element; third seta as long as first seta and shorter than exopod; innermost (fifth) seta 2.3 times as long as fourth seta. Male: P1 basis with inner spine modified, elongate, with three inner accessory spines; P5 EXP with five setae, endopodal lobe with two setae; P5 second exopodal seta from outer to inner margin longer than first seta ....  
 .....*T. drachi* Soyer, 1963
8. P4 EXP3 without inner armature, formula 0,2,3. Female: antennule nine-segmented (male unknown) .....*T. accraensis* (T. Scott, 1894)  
 – P4 EXP3 with two inner setae, formula 2,2,3. Female: antennule eight-segmented .....9
9. Caudal rami 1.2 times as long as wide, shorter than anal somite ...*T. capensis* Kunz, 1975 comb. nov.  
 – Caudal rami twice as long as wide, as long as anal somite .....10
10. Caudal rami as long as anal somite, rather cylindrical, with inner margin slightly concave. Female: second antennular segment about 1.5 times as wide as long; P5 EXP with three outer setae subequal in length; outermost seta of P5 endopodal lobe long, reaching well beyond tip of exopod. Male: P1 basis with three inner accessory spines, inner seta normal, not modified; P5 EXP with six setae, endopodal lobe with two bifurcate setae; P5 innermost exopodal seta bifurcate .....*T. lutincola* Soyer, 1963  
 – Caudal rami 1.5 times as long as anal somite, elongate, elliptic. Female: second antennular segment three times as long as wide; P5 EXP with outer proximal seta very long, medial and subdistal outer setae small and subequal in length. Male: second antennular segment three times as long as wide; P1 basis without inner accessory spines, inner seta modified, elongate; P5 EXP with four setae, endopodal lobe with two bifurcate setae; P5 innermost exopodal seta normal ...*T. bouligandi* Soyer, 1971
11. P3 ENP3 with one inner seta, formula 1,2,1 .....12  
 – P3 ENP3 with two inner setae, formula 2,2,1 .....13
12. P2–P3 EXP3 without inner armature, formula 0,2,3; caudal rami nearly twice as long as wide (length:width ratio 1.8). Male: P1 basis with three inner accessory spines; P5 EXP with six normal (not bifurcated) setae, endopodal lobe with two bifurcate setae .....*T. higginsii* Chullasorn, 2009  
 – P2–P3 EXP3 with one inner seta, formula 1,2,3; caudal rami slightly more than two times as long as broad (length:width ratio 2.3) (male unknown) .....*T. unisetosus* Lang, 1965
13. Caudal rami slightly more than three times as long as wide (length:width ratio 3.2). Female: P5 EXP with six setae, endopodal lobe with four setae. Male: P1 basis with eight inner accessory spines; P5 EXP with four normal setae, endopodal lobe with two bifurcated elements .....  
 .....*T. tuerkayi* Ma & Li, 2017  
 – Female: P5 EXP with six, endopodal lobe with five setae .....14
14. P4 ENP2 without inner seta; caudal rami from 1.7 to 2.2 times as long as wide. Male: P1 basis with four <sup>3</sup> or from seven to eight <sup>4</sup> inner accessory spines; P5 EXP with six normal setae, endopodal lobe with two bifurcated elements .....*T. typhlops* (Sars, 1906) <sup>2,8</sup>  
 – P4 ENP2 with inner seta .....15

15. P1 EXP3 with four elements; caudal rami three times as long as wide (male unknown) .....  
 .....*T. brevicornis* (I.C. Thompson & A. Scott, 1903)  
 – P1 EXP3 with five elements .....16
16. Caudal rami less than 1.5 times as long as wide .....17  
 – Caudal rami more than 1.5 times as long as wide .....18
17. Caudal rami about as long as wide. Female: P5 EXP elongate. Male: P1 basis with three inner accessory spines; P5 EXP with five setae .....*T. latifurca* Por, 1968  
 – Caudal rami length:width ratio from 1.3 to 1.5. Female: P5 EXP oval. Male: P1 basis with eight inner accessory spines; P5 EXP with six setae .....*T. ovale* Wells & Rao, 1987
18. Caudal seta V characteristically deformed proximally, with inner blunt outgrowth .....  
 .....*T. typhloides* (Sars, 1911)  
 – Caudal seta V normal .....19
19. Length:width ratio of caudal rami variable, from about 1.7 to 3.1 times as long as wide, with concave inner margins, with lenticular, biconvex thickening of external chitinous walls, with one spinule on inner distal margin. Female: ventral surface of posterior half of genital double-somite without medial spinules, with two posterior transverse sets of three to five spinules, each close to outer margin; ventral surface of fourth urosomite with one medial spinular row of 21 to 30 spinules and one posterior transverse row of 15 to 24 spinules; ventral surface of fifth urosomite with two medial sets of three to ten spinules on each side or with a medial continuous row of about 24 spinules, and with short posterior row of four to six medial spinules or with three sets of spinules of which medial one with ten spinules and marginal sets with three to four spinules; ventral surface of anal somite without spinular ornamentation. Male: ventral surface of third urosomite with two medial transverse sets of four spinules each or with medial continuous spinular row of eight to ten transverse spinules, posterior margin with transverse row of 14 to 26 spinules; ventral surface of fourth urosomite with two medial sets of four to eight transverse spinules or with short medial row of four transverse spinules, and with posterior transverse row of 16 to 24 spinules; ventral surface of fifth urosomite without medial spinules or with two medial sets of four transverse spinules, posterior margin with transverse row of four to 12 spinules; P1 basis with three to five inner accessory spines; P5 EXP with six setae, endopodal lobe with two bifurcate setae .....  
 .....*T. confusus confusus* (T. Scott, 1902)<sup>5,7</sup>  
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<sup>1</sup> The female P5 EXP was described with eight setae (Scott & Scott 1895: pl. 15 (9)), but this is most probably erroneous.

<sup>2</sup> Two samples of *T. typhlops* in Lang's collection at the Museum of Natural History in Stockholm possess an inner seta on P4ENP2 and were considered as representatives of *T. typhlops* by Por (1963).

<sup>3</sup> After Sars (1906b).

<sup>4</sup> After Por (1963) and Chislenko (1967).

<sup>5</sup> This species is highly variable. It is highly advisable to check the available descriptions.

<sup>6</sup> See also Por (1967).

<sup>7</sup> See also Bodin (1968).

<sup>8</sup> See also Klie (1941).

## Discussion

### *Typhlamphiascus medici* sp. nov.

The highly complex taxonomy of *Typhlamphiascus* results from poor and incomplete original descriptions, in which the somatic spinular ornamentation was omitted and one or several appendages were not appropriately described, arguing that they resemble those of other congeners or species of somewhat related genera (for example, see Scott (1894) for *T. accraensis*; Thompson & Scott (1903) for *T. gracilicaudatus*; Por (1968) for *T. latifurca*; Scott (1902) and Sars (1911) for *T. confusus confusus*; Por (1963) for *T. c. erythraeicus*). This complexity is fuelled also by the high variability of some species (see Por (1963) and Lang (1965) for a discussion of *T. c. confusus*, *T. c. erythraeicus* and *T. c. gullmaricus*), but also by observational misinterpretations. This has led to a failure to detect potential (aut)apomorphies for the objective definition of the genus and its species.

In the last revision of *Typhlamphiascus*, Por (1963) proposed to subdivide the genus into two species groups based on the inner armature complement – total number of setae/spines – on P4 ENP3. Por (1963) defined his group I by the presence of two inner setae (five elements in all) on the P4 ENP3 and his group II by the presence of one seta only (four elements in all) on the same segment. This criterion has been followed since and has proved to be useful for identification purposes. Por also suggested that this group might be characterized by the female genital somite and third urosomite being separated only laterally, but fused dorsally and ventrally. We could not find enough evidence for this, but the female genital and the third urosomites seem to be divided laterally only in *T. gracilis* (see Por 1963: 198; *T. gracilicaudatus*, see Por 1963: 199; *T. bouligandi*, see Soyer 1971: 275, fig. 6a; *T. drachi*, see Soyer 1963a: 821, fig. 1a). The condition of *T. accraensis*, *T. blanchardi*, *T. capensis*, *T. dentipes* and

*T. longifurcatus* remains uncertain, and the genital and third urosomites are divided dorsolaterally in *T. lutincola* (see Soyer 1963b: 235, fig. 1a). As for group II, the genital and third urosomites are divided dorsolaterally in most species, but this condition is inconclusive for *T. brevicornis*, and they seem to be divided laterally in *T. lamellifer*, *T. typhloides* and *T. typhlops*. The genital and third urosomites of *T. latifurca* were described as separated dorsally and ventrally (see Por 1968: 40–41, pl. 3 fig. 13). This needs to be confirmed.

Also, we observed that the female P5 EXP in Por's group I can be either normal or with the tip deformed into a hook-like process, and the inner spine of the P1 basis of the males can be either a normal, unmodified spine or it can be modified into an elongate, unornamented element with blunt tip, and that the P5 EXP of the females in Por's group II is always normal and the inner spine of the P1 basis of the males is always non-modified. Also, in group I there seems to be a tendency towards the reduction of the apical setae on the female P5 endopodal lobe. This reduction is more pronounced in *T. dentipes* and *T. blanchardi*. A similar, though less pronounced tendency is observable also in *T. ovale* of group II.

Por's group I is currently composed of *T. blanchardi*, *T. dentipes*, *T. gracilis*, *T. gracilicaudatus*, and – probably – *T. typhloides* (Por 1963). Sars (1911: 391) noted that *T. typhloides* differs very little from *T. confusus*, and it most probably belongs to Por's group II. Group I also includes *T. lutincola*, *T. drachi* (Lang 1965), *T. accraensis*, *T. l. capensis* (Ma & Li 2017) and also *T. longifurcatus*. Ma & Li (2017) erroneously allocated *T. longifurcatus* to group II. The males of *T. accraensis*, *T. l. capensis*, *T. blanchardi* and *T. dentipes* remain unknown, but the inner spine on the male P1 basis is not modified in the males of *T. gracilicaudatus*, *T. gracilis* or *T. lutincola*, but *T. bouligandi*, *T. drachi* and *T. longifurcatus* share a potentially synapomorphic modified elongate inner spine on the P1 basis. The number of inner accessory spines (modified spinules?) on the male P1 basis is highly variable within this group. Inner accessory spines on the male P1 basis are absent in *T. bouligandi*. *Typhlamphiascus lutincola* and *T. drachi* possess three inner accessory spines, *T. gracilicaudatus* displays from three to five inner accessory spines and *T. gracilis* possesses from seven to eight inner accessory spines. The armature formulae of P1–P4 is constant throughout the entire group, but *T. dentipes* is unique and differs from *T. blanchardi* – with which it shares the modified inner spine on the male P1 basis – and from the rest of the species of group I in the number of inner elements on the P4 EXP3 (with three setae in *T. dentipes*, but with two setae in *T. blanchardi* and in the rest of the species of group I). The armature complement of the male and female P5 endopodal lobe is fairly constant within group I (five setae in the females except for the female of *T. gracilicaudatus* with four setae; two setae in the males), but the number of setae on the male and female EXP varies from four (as in the males of *T. gracilicaudatus* and *T. bouligandi*, and in the female and male of *T. longifurcatus*), to five (as in the females of *T. gracilicaudatus* and *T. dentipes*, and in the males and females of *T. gracilis* and *T. drachi*), and six (as in the females of *T. accraensis*, *T. l. capensis* and *T. bouligandi*, and in the male and female of *T. lutincola*). The supranumerary armature complements of the female P5 EXP of *T. blanchardi* (eight elements), as reported by Scott & Scott (1895), is most probably erroneous. Also, the shape of the female P5 EXP is rather constant within group I and within the genus, but *T. blanchardi* and *T. dentipes* share having the tip of the female P5 EXP modified into a hook-like process, as well as a marked tendency towards the reduction of the apical setae of the female P5 endopodal lobe. These two characters could constitute potential synapomorphies for these two species.

Por's group II is currently composed of *T. higginsii*, *T. brevicornis*, *T. c. confusus*, *T. c. erythraeicus*, *T. c. gullmaricus*, *T. l. lamellifer*, *T. latifurca*, *T. ovale*, *T. pectinifer*, *T. tuerkayi*, *T. typhloides*, *T. typhlops*, *T. unisetosus* and *T. medici* sp. nov. Kunz (1975) described a new subspecies of *T. l. lamellifer*, *T. l. capensis* from South Africa, without any justification for attributing the latter to this species. *Typhlamphiascus l. lamellifer* possesses one seta only on the P4 ENP3 (Por's group II), but two setae are present on the same segment in *T. l. capensis* (Por's group I). The armature complement of the



P4 ENP3 has been consistently used to separate Por's groups I and II. In our opinion, the differences between these two taxa are beyond the differences that could be expected between a nominotypical species and its subspecies, and *T. l. capensis* probably represents a different species. Thus, we propose to consider *T. l. lamellifer* and *T. l. capensis* as distinct species and to give the latter full species rank as *T. capensis* Kunz, 1975 comb. nov. The inner spine on the male P1 basis is not modified in all the species and subspecies of this group; the males of *T. unisetosus* and *T. brevicornis* remain unknown, but the number of inner accessory spines on the male P1 basis is highly variable. *Typhlamphiascus lamellifer* possesses two inner accessory spines; *T. higginsi*, *T. latifurca*, *T. pectinifer* and *T. medici* sp. nov. possess three inner accessory spines; from three to five inner accessory spines can be found in *T. c. confusus*; *T. c. erythraeicus* possesses four inner accessory spines; *T. c. gullmaricus* possesses from five to seven inner accessory spines; *T. ovale* and *T. tuerkayi* possess eight inner accessory spines. The number of inner accessory spines seems to be highly variable in *T. typhlops*. Sars (1906b) described four inner accessory spines on the male P1 basis of this species, but Por (1963) and Chislenko (1967) reported from seven to eight inner accessory spines. The armature complements of P1–P4 are fairly constant in the species of group II, and only three species – *T. higginsi*, *T. unisetosus*, and *T. typhlops* – deviate from the most common armature formulae of P1–P4 EXP/ENP (P1: 0-0-0,2,3/1-1-1,1,1; P2: 1-1-1,2,3/1-2-1,2,1; P3: 1-1-1,2,3/1-1-2,2,1; P4: 1-1-2,2,3/1-1-1,2,1). *Typhlamphiascus typhlops* seems to occupy an isolated position given the lack of inner armature on P4 ENP2 (armature formula 1-0-1,2,1). Interestingly, Por (1963) had the opportunity to inspect two samples of *T. typhlops* in Lang's collection and observed the presence of an inner seta on P4 ENP2. Por considered this as the true condition for the P4 ENP2 of *T. typhlops*. Kunz (1975) described the P4 ENP2 of *T. capensis* comb. nov. without inner seta, but he suggested that this seta might have become detached from the supporting segment as indicated by the interrupted cuticle in the place where the inner seta might once have been, and suggested that the lack of this seta might be of little importance. *Typhlamphiascus higginsi* and *T. unisetosus* share the reduced inner armature complement of P3 ENP3 from two to one seta. Additionally, *T. higginsi* is unique within the genus by its lack of inner armature on the P2–P3 EXP3. The armature complements of the female P5 EXP and endopodal lobe (six and five setae, respectively) are constant in group II, and only one species, *T. tuerkayi*, possesses four setae on the endopodal lobe. The armature complement of the male P5 endopodal lobe is constant throughout the genus (with two bifurcate setae); not so the armature complements of the P5 EXP, which varies from four setae in *T. tuerkayi*, to five elements as in *T. latifurca*, and six as in *T. higginsi*, *T. c. confusus*, *T. lamellifer*, *T. ovale*, *T. medici* sp. nov. and *T. pectinifer* (males of *T. unisetosus* and *T. brevicornis* unknown). Noteworthy, *T. lutincola* of Por's group I, and *T. pectinifer* and *T. medici* sp. nov. of group II are unique within the genus in that they share a bifurcated innermost seta on the male P5 EXP. The bifurcated innermost seta on the male P5 EXP in *T. pectinifer* – known from Monterrey Bay (California, USA) (Lang 1965) and Tierra del Fuego (Argentina) (Pallares 1975) – and in *T. medici* sp. nov., but also in *T. lutincola*, known from the French Mediterranean (Soyer 1963a), could constitute a potential synapomorphy for these three species.

Twenty-three nominotypical species and two subspecies – *T. confusus erythraeicus* and *T. c. gullmaricus* – are here recognised in *Typhlamphiascus*. Of these, six species – *Stenhelium hirsutum*, *Typhlamphiascus accraensis*, *T. drachi*, *T. longifurcatus*, *T. lutincola* and *T. typhloides* – are considered as incertae sedis (Lang 1948; Wells 2007). Soyer (1971) described *T. bouligandi* from the French Catalan coast. He described his newly found species with antennular basis, the armature of the antennal exopod as 1-1-0;3;0 – second exopodal segment with one seta – and the mandibular exopod as one-segmented with one lateral and two apical setae. Similar observational mistakes appear in the original descriptions of *Typhlamphiascus accraensis* and *T. brevicornis* (with one seta on the second exopodal segment of the antenna; *T. brevicornis* also with one-segmented mandibular exopod with three setae). Additionally, the record of three species and subspecies – *T. typhlops* sensu Por (1963), *T. aff. confusus confusus* sensu Moore (1976), *T. confusus confusus* sensu Marinov & Apostolov (1985) – and five morphospecies – *Typhlamphiascus* sp. (Vilela 1965), *Typhlamphiascus* sp. ? (Bodin 1964), *Typhlamphiascus* sp. ? (Bodin



1964), *Typhlamphiascus* sp. I (?*confusus*) (Marinov 1977) and *Typhlamphiascus* sp. II (Marinov 1977) – have been relegated to species inquirendae and have naturally been omitted from recent keys to the species of *Typhlamphiascus* (e.g., Wells 2007; Chullasorn 2009; Ma & Li 2017). Only one out of the six species incertae sedis, *S. hirsuta*, has been systematically excluded from most recent keys and species lists (e.g., Wells 2007; Chullasorn 2009; Ma & Li 2017). The exclusion of this species is obvious given the dubious and controversial original description by Thompson (1893: 194–195, pl. 31, figs 1–13) (see also Lang 1948: 712).

To the best of our knowledge, the last diagnosis of the genus *Typhlamphiascus* was presented by Lang (1948: 705). The genus has been defined subjectively on a combination of features and no apomorphies have been detected for the genus, nor have any synapomorphy been found to unite all its species objectively, and the relationships between the species of *Typhlamphiascus* have been based on morphological similarities only.

Chullasorn (2009: 506) gave a list of autapomorphies for *T. higginsii*. These are: (i) male P1 basis with three inner accessory spines, (ii) reduced number of setae/spines on P3 ENP3 from five to four, (iii) reduced number of setae/spines on P4 ENP3 from five to four, (iv) P1 EXP1 reaching tip of ENP2, (v) caudal rami two times as long as wide, (vi) seven minute spinules on each side of the female genital somite, (v) fourth and fifth female urosomites with posterior spinular row ventrally and (vi) caudal rami twice as long as wide, with two small spinules at the base of caudal seta VII. In our opinion, these are not true autapomorphies for *T. higginsii*, since all of them are shared by one or more species within the genus. For example, the presence of three inner accessory spines on the male P1 basis is shared by a larger set of species (*T. gracilicaudatus*, *T. lutincola*, *T. drachi*, *T. c. confusus*, *T. latifurca*, *T. pectinifer* and *T. medici* sp. nov.), the reduced number of setae/spines on P3 ENP3 from five to four is also present in *T. unisetosus* and the reduced number of setae/spines on P4 ENP3 from five to four is present in all the species of Por's group II. The only potential (aut)apomorphy that we could detect for *T. higginsii* is the loss of the inner armature on P2–P3 EXP3. In her description of the maxilliped of *T. higginsii*, Chullasorn (2009) confused the basis with the syncoxa, a first endopodal segment with the basis, and a second endopodal segment with the one-segmented endopod. She also reversed P1 and P2, as well as P3 and P4 in her figures (Chullasorn 2009: 498, fig. 3 and 499, fig. 4, respectively). Also, her figures of the ventral and dorsal views of the urosome of *T. higginsii* (Chullasorn 2009: 500, fig. 5a–b) are reversed, and so are the male maxilliped and maxilla (Chullasorn 2009: 502, fig. 7).

In their description of *Typhlamphiascus tuerkayi*, Ma & Li (2017) suggested a close relationship between their species and both *T. ovale* and *T. higginsii* based on (i) the presence of ventral hyaline frills on the posterior edge of the posterior half of the genital double-somite, and fourth and fifth urosomites, (ii) presence of one inner seta on P1–P4 EXP2, (iii) presence of an inner seta on P2–P4 EXP1, (iv) presence of one inner seta on P1–P4 ENP1, (v) P1 ENP3 with three setae, (vi) female P2 ENP2 with two inner setae, (vii) female P5 EXP with six setae and (viii) endopodal lobe of the male P5 with two bifid elements. However, all these features are common to the whole genus and are not indicative of a close relationship between *T. tuerkayi* on one hand and *T. ovale* and *T. higginsii* on the other. Also, Ma & Li (2017) described the mandibular endopod as two-segmented – first segment with one, second segment with two setae – but on their figure (Ma & Li 2017: 994, fig. 2d) the mandibular exopod appears as one-segmented with two setae.

Briefly, given the complex taxonomy of the genus and the lack of potential (syn)apomorphies, any hypothesis on the phylogenetic relationships of the species of *Typhlamphiascus* is at this moment futile and an in-depth revision of the genus is needed. At this point it seems that (i) Por's criterion (Por 1963) to subdivide the genus into two species groups on the armature complement of the P4 ENP3 is probably useful for identification purposes only, (ii) that some species seem to be related by the shape

of the female P5 EXP and shape of the apical elements on the female P5 endopodal lobe (*T. blanchardi* and *T. dentipes*), the sexually dimorphic inner spine of the male P1 basis (*T. bouligandi*, *T. drachi* and *T. longifurcatus*), the presence of a bifurcated inner element on the male P5 EXP (*T. lutincola*, *T. pectinifer* and *T. medici* sp. nov.) and the reduced armature of the P3 ENP3 from five to four (*T. higginsii* and *T. unisetosus*) and (iii) that the only species with a potential (aut)apomorphy (without inner armature on P2 EXP3) is *T. higginsii* (see Tables 1–2).

*Typhlamphiascus medici* sp. nov. belongs to Por's group II. The new species proposed herein share the armature complements of the female P1–P5 with all species of group II except for *T. typhlops* (without inner seta on P4 ENP2; but see above), *T. unisetosus* (with only one inner seta on P3 ENP3), *T. higginsii* (with only one inner seta on P3 ENP3 and without inner armature on P2–P3 EXP3) and *T. tuerkayi* (with only four setae on the P5 endopodal lobe). The males of *T. unisetosus* and *T. brevicornis* remain unknown and the males of some other species have been described incompletely. The male antennules of the species for which these appendages have been described have been shown to be nine-segmented, and only *T. higginsii* and *T. medici* sp. nov. were described with eight- and ten-segmented male antennules, respectively. The nine-segmented condition of the male antennule in *T. ovale*, *T. pectinifer* and *T. tuerkayi* is most probably the result of a failure to detect the separate third and fourth segments which are common in podogenontan harpacticoids (Willen 2000). Similarly, the eight-segmented condition of the male antennule of *T. higginsii* is most probably the result of a failure to detect the separated third and fourth segments, but also the sixth segment. The latter seems to be incorporated into the fifth segment in Chullasorn (2009: 502, fig. 7a) and requires confirmation. In our opinion it is highly probable that all species of *Typhlamphiascus* possess ten-segmented male antennules, as shown for *T. medici* sp. nov. The setation pattern of the male P5 endopodal lobe with two bifurcate setae is constant throughout the genus and group II; not so the armature complements of the exopod which varies in group II from four (*T. tuerkayi*) to five (*T. latifurca*) and six setae (*T. higginsii*, *T. confusus*, *T. lamellifer*, *T. ovale*, *T. pectinifer*, *T. medici* sp. nov. and *T. typhlops*). As noted above, *T. pectinifer*, *T. medici* sp. nov. and *T. lutincola* share the bifurcated innermost seta of the male P5 EXP. The number of inner accessory spines on the male P1 basis is variable in *T. c. confusus* (from three to five), *T. c. gullmaricus* (from five to seven) and *T. typhlops* (four inner accessory spines were observed by Sars 1906a, but from seven to eight by Por 1963 and Chislenko 1967). Four inner accessory spines have been reported in *T. c. erythraeicus*, and only two were observed in *T. lamellifer*. *Typhlamphiascus medici* sp. nov., *T. higginsii*, *T. latifurca* and *T. pectinifer* share the presence of three inner accessory spines on the male P1 basis. *Typhlamphiascus medici* sp. nov. is more similar to and probably bears a close relationship with *T. pectinifer* and *T. lutincola*, as suggested by the bifurcated condition of the inner distal bifurcate seta on the male P5 EXP. Besides the armature complement of P1–P5, the male armature complements of the male P5 and the bifurcate inner seta on the P5 male EXP, *T. pectinifer* and *T. medici* sp. nov. are unique also in the combination of having three inner accessory spines on the male P1 basis and six setae on the male P5 EXP. The Mexican material could be attributed to a new subspecies of *T. pectinifer*. Besides the features shared by these two species, this reasoning might find support also in their distribution. *Typhlamphiascus pectinifer* was described from Monterey Bay, central California, USA, about 2000 km from the type locality of *T. medici* sp. nov. in the mouth of the Gulf of California. *Typhlamphiascus pectinifer* was also reported from Tierra del Fuego, Argentina (Pallares 1975). Pallares' material fits Lang's description (Lang 1965), including the ventral spinular ornamentation of the last urosomites, but a more detailed examination of the South American population would be necessary to confirm its identity. A scenario where the original population from the Central Eastern Pacific split and gave birth to two different species through vicariance is feasible. The latter view is grounded in some differences to support the presence of two related species. These are: (i) subdistal inner ornamentation of caudal rami (with a row of spinules forming a comb in *T. pectinifer*, but with very few spinules in the Mexican species), (ii) dorsolateral spinular ornamentation of both halves of the genital double-somite, and fourth urosomite in the female, and of the genital, third and fourth urosomites in the male (without dorsolateral

spinular ornamentation in *T. pectinifer*, but with some spinules in *T. medici* sp. nov.), (iii) relative length of the caudal setae (comparatively shorter in *T. pectinifer*), (iv) relative length of the two innermost setae of the female P6 (visibly longer in the Mexican material), (v) number of midventral spinules on the female fourth urosomite (with five spinules in Lang's species, but with 13 spinules in *T. medici* sp. nov.), (vi) number of midventral spinules on the female and male fifth urosomite (a continuous row of spinules in *T. pectinifer*, but with only six spinules in *T. medici* sp. nov.), (vii) relative length of the outer proximal seta of the female P5 EXP (relatively longer in the new species), (viii) relative length of the inner setae on the female P2 ENP2 (short and subequal in length in *T. pectinifer*, but subdistal seta visibly longer than proximal element in the Mexican species), (ix) relative length of the inner setae on the male P2 ENP2 (visibly shorter in *T. pectinifer*) and (x) probably the shape of the innermost element of the male P6 (seemingly setiform in *T. pectinifer*, but spiniform in the new species). The two large tube pores observed in the first and second antennular segments in females and males of the new species have not been observed before. The presence of this pair of tube pores is deemed to be a potential apomorphy for the species, but its absence in other species still needs confirmation.

Our analyses showed *Typhlamphiascus* as the first offshoot of the *Typhlamphiascus*–*Spinodiosaccus* gen. nov. monophylum, before the acquisition of characters 24 and 26 (P2 and P3 EXP3 with short distal seta on the inner margin) which support the monophylum *Monardius*–*Spinodiosaccus* gen. nov.

#### **Phylogenetic position of *Dinetia* gen. nov., *Pallarica* gen. nov., *Spinopedia* gen. nov., *Spinodiosaccus* gen. nov. and *Bulbamphiascus***

The complete clarification of the phylogenetic affinities within the Diosaccinae is far beyond the scope of this study. A more exhaustive analysis of a more complete data set including more characters (i.e., structure and setation of mouth parts, armature number and shape of swimming legs, homology of the inner armature of the male P1 basis and of the male P2 ENP) and as many species as possible would be necessary. Instead, our main objective was to test the monophyletic status of the genus *Bulbamphiascus* as defined by Mu & Gee (2000). To accomplish this, and considering the high level of character convergence within the Diosaccinae (which probably fostered the establishment of non-monophyletic genera based solely on the setal formulae of P1–P5), we included species of all genera, but restricted our analyses to the type species of the non-monophyletic genera. Our results on the phylogeny within the Diosaccinae are preliminary – its phylogeny is not fully resolved – but they reflect the phylogenetic relationships between *Bulbamphiascus* and the newly proposed genera. Given the preliminary nature of our results, the characters considered will not be discussed in detail. Instead, we will focus on the characters that contribute to the monophyletic status of i) a clade composed of *Dinetia* gen. nov., *Pseudamphiascopsis* and *Rhyncholagena* and ii) a clade composed of *Pallarica* gen. nov., *Spinopedia* gen. nov., *Bulbamphiascus* and *Spinodiosaccus* gen. nov.

The genus *Bulbamphiascus* was originally proposed by Lang (1944) and was defined as different from *Amphiascus* and other diosaccin genera primarily on the structure of the P1 endopod, the setal formula of P2–P5, and the usually bulbous shape of the distal outer seta on the P5 EXP (Mu & Gee 2000). They (Mu & Gee 2000) gave a brief historical account of the genus and offered an amended diagnosis, in which they included some characters that we consider important synapomorphies for a more inclusive group of genera related to *Bulbamphiascus*, i.e., distal inner seta of P2–P4 EXP3 weakly developed (characters 24, 26, 28 in the present study; Table 3, Fig. 19), and P5 with medial and distal outer spines – sometimes – swollen at its base (or short and blunt) (characters 38 and 39 in the present study; Table 3, Fig. 19). Character 28 is a unique synapomorphy for a monophyletic clade represented by *Robertsonia*, *Amphiascus*, *Pararobertsonia*, *Sinamphiascus*, *Pallarica* gen. nov., *Spinopedia* gen. nov., *Bulbamphiascus* and *Spinodiosaccus* gen. nov. Characters 24 and 26 (see Table 3, Fig. 19) place *Monardius* and *Tydemanella* as the sister group of a clade supported by character 28 which seems to have appeared convergently also in *Sarsamphiascus*, the latter with an uncertain phylogenetic affinity

with other groups. The original description of the type of *Sarsamphiascus*, *S. minutus* (Claus, 1863), is too incomplete, and Sars (1906a) omitted the P3. The male P2 ENP2 of *S. minutus* as illustrated by Sars (1906a: pl. 96) resembles that of *Pallarica* gen. nov. and *Spinopedia* gen. nov. in that the inner subdistal spine is blunt and only slightly sigmoid, and the outer subdistal spine is blunt and tapers slightly distally.

The diagnosis of *Bulbamphiascus* by Mu & Gee (2000) and our own results indicate that the medial and subdistal outer elements of the female and male P5 EXP being reduced to short and basally bulbous elements is the only potential autapomorphy for the genus. This assumption lead to an alternative scenario where the new species attributed here to *Spinodiosaccus* gen. nov. would actually be a derived form of *Bulbamphiascus*, and the loss of the inner seta of P1 EXP2 and the inner seta of P2–P4 EXP1 should be interpreted as a secondary loss. However, in light of current research and upon re-diagnosis of *Bulbamphiascus*, the morphological homogeneity within this genus points towards a scenario in which *Spinodiosaccus* gen. nov. appears as an early offshoot of the *Bulbamphiascus*–*Spinodiosaccus* lineage. On the other hand, given the poor and sketchy descriptions of most species, it is difficult to detect any autapomorphy for *Bulbamphiascus*. Although we have not coded any character for the male P2 ENP2, the combination of the outer subdistal tapering spine and the inner subdistal sigmoid element in the male P2 ENP2 in *Bulbamphiascus* is regarded here as a potential apomorphy for that genus. Following this line of reasoning, *Spinodiosaccus* gen. nov. is defined by the presence of six autapomorphic character states: i) male antennule 11-segmented (character 2 in Table 3, Fig. 19), a unique reversion within the Diosaccinae, ii) loss of the inner seta of P1 EXP2 (character 6 in Table 3, Fig. 19), iii) loss of the inner seta of P2 EXP1 (character 14 in Table 3, Fig. 19), iv) loss of the inner seta of P3 EXP1 (character 15 in Table 2, Fig. 19), v) loss of the inner seta of P4 EXP1 (character 16 in Table 3, Fig. 19) and vi) absence of an anterior tube pore on the male P3 EXP3 (character 31 in Table 3, Fig. 19). Also, character 28 (presence of a short distal inner seta on P4 EXP3) is a potential synapomorphy for, at least, *Amphiascus*, *Pararobertsonia*, *Sinamphiascus*, *Pallarica* gen. nov., *Spinopedia* gen. nov., *Bulbamphiascus* and *Spinodiosaccus* gen. nov. Characters 14–16 appeared convergently within the monophyletic clade *Amonardia*–*Psammotopa* (see Fig. 19). Similarly, character 6 appeared convergently in the sub-clade *Pholenota*–*Psammotopoa* and in the clade *Antiboreodiosaccus*–*Pseudodiosaccus*. The anterior tube pore on the male P3 EXP3 occurs convergently in many different genera within Diosaccinae, namely *Amphiascus*, *Amphiascoides*, *Bulbamphiascus* (Mu & Gee 2000), *Haloschizopera* (Gee & Fleeger 1990), *Paramphiascella*, *Robertgurneya*, *Rhyncholagena*, *Sinamphiascus* (Nam & Lee 2012), *Spinopedia* gen. nov. and *Typhlamphiascus*. The condition within *Robertsonia*, *Pararobertsonia* and *Pallarica* gen. nov. must be re-investigated, since such structures as tube pores were frequently neglected in older descriptions.

Interestingly, the largest monophylum in which *Bulbamphiascus* and allied genera are included is supported only in the total consensus cladogram by the reversion of character 12 (see Table 3) – P1 ENP1 shorter or slightly longer than EXP. The plesiomorphic condition where the P1 EXP is considerably shorter than ENP1 is shared in all remaining genera of Diosaccinae. In the total consensus cladogram, the reversion of character 12 also appears as an independent evolution in the clade *Antiboreodiosaccus*–*Pseudodiosaccus*, which is also characterised by the reversion of characters 41 and 43, which also supports the monophyletic status of the clade *Amonardia*–*Psammotopa*. This clearly separates these monophyletic clades from the large monophylum containing *Typhlamphiascus*–*Spinodiosaccus* gen. nov. However, *Antiboreodiosaccus*–*Pseudodiosaccus* does not appear as closely related to *Amonardia*–*Psammotopa* in any of the 12 most parsimonious trees (see Supplementary File 1). This renders the synapomorphic condition of character 12 but also of characters 41 and 43 unclear, and the topology and optimization in Fig. 19 would be an artefact of the total consensus algorithm.

*Bulbamphiascus cibimae* is unique within the Diosaccinae by the male P5 EXP having seven setae (character 35 in Table 3). The medial and subdistal outer elements of the male P5 EXP of *B. cibimae*



display some degree of reduction in size but are not spine-like blunt and are not swollen basally as in other species of the genus. This justifies the exclusion of *B. cibimae* from *Bulbamphiascus* and its reallocation in a new genus, *Pallarica* gen. nov. as *P. cibimae* comb. nov., also characterized by the apomorphic reduction in length of the medial and subdistal seta of the male P5 EXP. On the other hand, the reduced medial and subdistal outer spines of the male P5 EXP is regarded here as synapomorphic for *Pallarica* gen. nov., *Spinopedia* gen. nov., *Bulbamphiascus* and *Spinodiosaccus* gen. nov. These four genera also share the same morphology of the armature of the A2 EXP3, i.e., with one distal seta, one spine and a longer spiniform element (character 3 in Table 3 ). Character 3 is also shared with *Sinamphiascus* and indicates that this genus should be included in this clade as the most basal taxon. The male P2 ENP2 is very similar in *Pallarica* gen. nov. and *Spinopedia* gen. nov.

The establishment of *Spinopedia* gen. nov. is clearly supported by the spinular ornamentation on the male P2 ENP1 and ENP2. In addition, the second inner seta from inner to outer margin of the female P5 EXP does not arise from a setophore but inserts directly on the inner edge of the ramus. *Spinopedia* gen. nov. bears a sister-group relationship with *Bulbamphiascus* and *Spinodiosaccus* gen. nov., as indicated by the reduction of the subdistal outer element of the male P5 EXP into a short, bare spine-like element, but *Spinodiosaccus* gen. nov. differs from *Bulbamphiascus* and *Spinopedia* gen. nov. in the well-developed subdistal outer seta of the female P5 EXP.

Among all the genera proposed here, *Dinetia* gen. nov. is the only one that does not belong to the same larger monophyletic clade *Pallarica*–*Spinodiosaccus*. *Dinetia* gen. nov. cannot be included within any of the remaining clades either. In fact, it seems closely related to *Pseudamphiascopsis* and *Rhyncholagena*, with uncertain phylogenetic affinities with the remaining monophyla. The male of *Dinetia* gen. nov. remains unknown and the supposed apomorphic status of character 43 (see Table 3 ) for this genus – which was coded as ‘?’ – is rather the result of the program’s algorithm used in this study for the phylogenetic analysis. The same happens for the supposed synapomorphic status of character 34 – male P5 EXP with five spines – for *Dinetia* gen. nov., *Pseudamphiascopsis* and *Rhyncholagena*, and character 11 – P1 ENP3 elongate, at least 1.5 times as long as ENP2 – is the only synapomorphy for this group of genera. However, it is not clear whether the *Dinetia*–*Rhyncholagena* clade is a true monophyletic clade or if these genera are clumped together by convergent characters. *Bulbamphiascus minutus*, the type species of *Dinetia* gen. nov., does not share important diagnostic characters with *Bulbamphiascus*, e.g., presence of a short inner distal seta on P2–P4 EXP3, and cannot be included in the latter. Dinet (1971) expressed some doubts about the membership of *B. minutus* in that genus and suggested some affinities with *Typhlamphiascus*. He placed his newly described species in *Bulbamphiascus* based on superficial similarities of the P5 and relative length of the caudal rami, and the general shape of the antennule, antenna and maxilliped. However, as recognized by Dinet (1971), *B. minutus* lacks the bulbous setae on the female P5 EXP. Also, the general shape of the female antennule is common to the Diosaccinae, Dinet’s descriptions of the mouth parts are too sketchy to allow further comparisons (see Dinet 1971), and the caudal rami of *B. minutus* are longer than in other species of *Bulbamphiascus* except for *B. chappuisi*, which is relegated here as species incertae sedis, and taper distally.

Our results show that most genera are arranged into three large monophyletic groups–*Antiboreodiosaccus*–*Pseudodiosaccus*, *Typhlamphiascus*–*Spinodiosaccus* and *Amonardia*–*Psammotopa* – the remaining groups being less speciose and of unclear phylogenetic affinities. The *Amonardia*–*Psammotopa* clade can easily be identified by the male P5 EXP having four or five setae (but three in *Psammotopa*). The remaining characters showed reversal along the topology in an almost haphazard manner. The *Typhlamphiascus*–*Spinodiosaccus* clade can easily be characterized by having the P1 ENP1 at most slightly longer than EXP (character 12); this character seems to have evolved convergently in the *Antiboreodiosaccus*–*Pseudodiosaccus* clade as well as in *Balucopsylla*–*Helmutkunzia*, *Protopsammotopa*, but also in *Psammotopa*. The *Typhlamphiascus*–*Spinodiosaccus* clade is also characterized by the presence of a

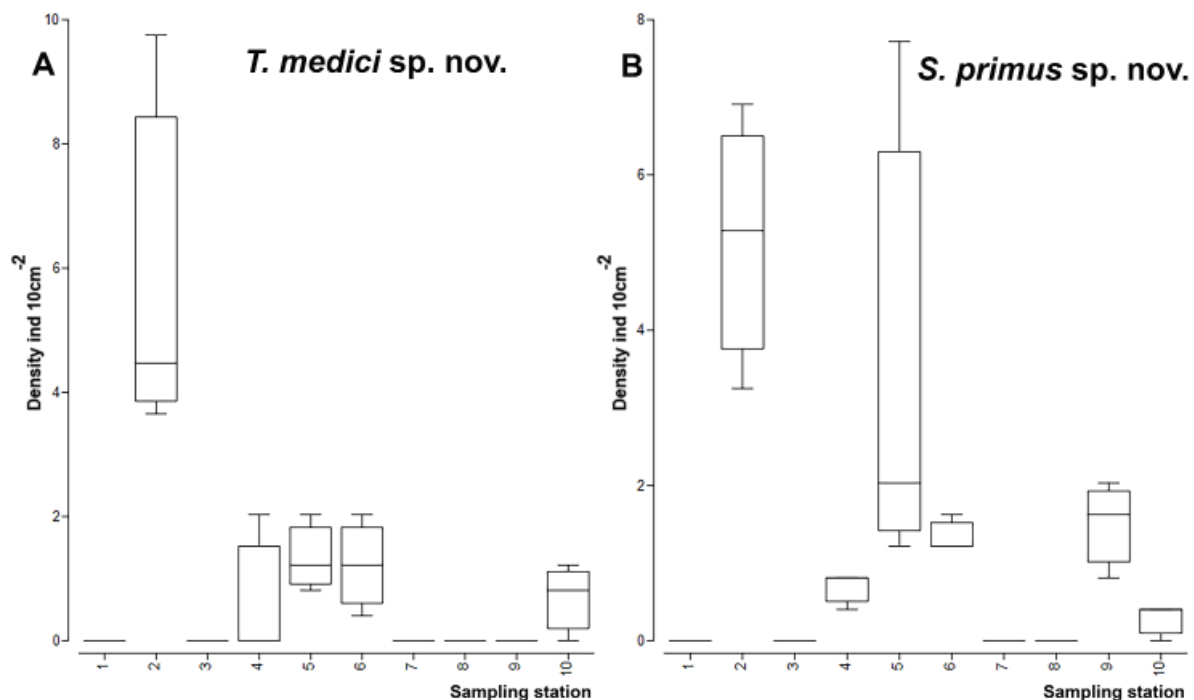
**Table 5.** Mean density values (ind. 10 cm<sup>-2</sup>) of *T. medici* sp. nov. and *S. primus* gen. et sp. nov. at the sampling stations along the Urías system recorded on 18 Jan. 2019. See also Gómez (2020a: 43, fig. 1).

	Stn 1	Stn 2	Stn 3	Stn 4	Stn 5	Stn 6	Stn 7	Stn 8	Stn 9	Stn 10
<i>T. medici</i> sp. nov.	0	5.96	0	0.68	1.36	1.21	0	0	0	0.68
<i>S. primus</i> gen. et sp. nov.	0	5.15	0	0.67	3.66	1.36	0	0	1.49	0.27

middle inner seta of the female P5 EXP issuing from a setophore (character 42 in Table 3); this character evolved independently in *Paramphiascella*, *Robertgurneya*, *Schizoperoides*, *Pseudamphiascopsis* and *Rhyncholagena*. Interestingly, the clade *Monardius–Spinodiosaccus* is unique in the – synapomorphic – presence of a short distal inner seta on the P2–P3 EXP3.

Although not recovered in our analyses, the *Antiboreodiosaccus–Pseudodiosaccus* clade could be basal to the *Amonardia–Psammotopa* clade. These two clades share character 43 (the middle – or the third seta from inner to outer margin – of the female P5 EXP not issuing from a setophore and arising directly from the ramus; a character reversion within the Diosaccinae). The loss of the inner armature of the P1 EXP2 (character 6 in Table 3) in the *Antiboreodiosaccus–Pseudodiosaccus* clade and at the base of the *Amonardia–Psammotopa* clade (in *Pholenota–Psammotopa*) is a potential piece of evidence for merging them.

Briefly, our preliminary data support the split of *Bulbamphiascus* into different genera, clearly showing that *Dinetia* gen. nov. does not belong to the *Typhlamphiascus–Spinodiosaccus* monophyletic clade. Our data also show that the Diosaccinae are divided into at least two large monophyletic units, but more work is needed to prove the monophyly of several genera and their phylogenetic relationships.

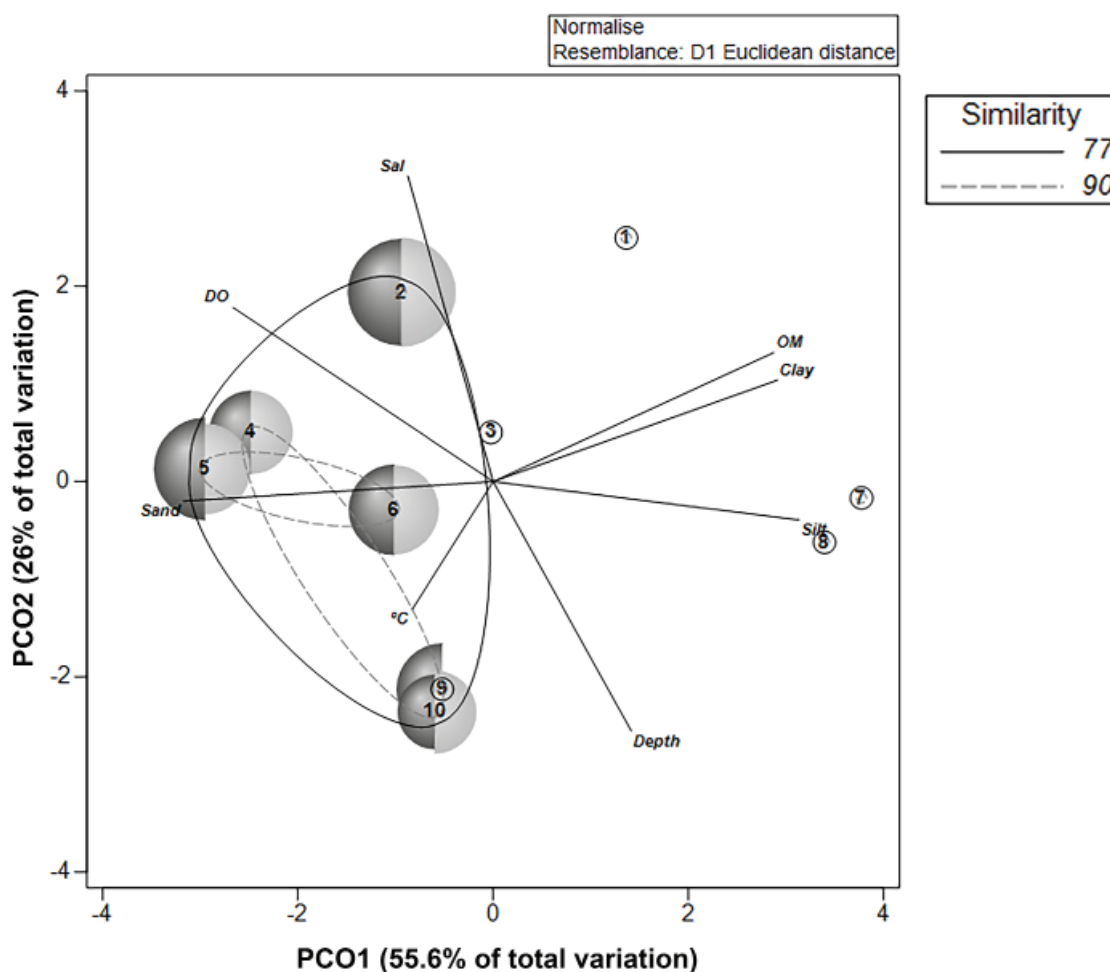


**Fig. 20.** Mean density values (ind. 10 cm<sup>-2</sup>) of *T. medici* sp. nov. and *S. primus* gen. et sp. nov. recorded on 18 Jan. 2019 at the sampling stations along the Urías system. See also Gómez (2020a: 43, fig. 1). **A.** *T. medici* sp. nov. **B.** *S. primus* gen. et sp. nov.



**Table 6.** Environmental variables at each sampling station along the Urías system recorded on 18 Jan. 2019. See also Gómez (2020a: 43, fig. 1).

Station	Depth (m)	Salinity (ups)	Temperature (°C)	Dissolved oxygen (mg L <sup>-1</sup> )	Organic matter (%)	Sand (%)	Silt (%)	Clay (%)
1	1.5	38.9	22.9	4.18	6.43	25.31	38.94	35.75
2	1.8	38.6	23.2	4.48	6.86	80.42	11.28	8.29
3	2.2	37.4	23.9	3.52	5.69	60.66	25.91	13.42
4	0.7	37.4	24.2	4.7	1.94	82.44	9.29	8.27
5	0.6	37.5	26.8	5.44	1.71	78.61	14.67	6.72
6	1.4	36.8	25	3.78	2.84	61.44	23.99	14.57
7	3.7	36.2	24.8	2.21	9.62	10.78	51.68	37.54
8	4	36.2	24.7	2.43	8.05	7.04	64.18	28.78
9	5.4	35.9	24.4	3.1	2.43	64.81	27.11	8.09
10	6	35.9	24.1	2.82	2.07	69.12	22.97	7.91

**Fig. 21.** Principal coordinates analysis between environmental variables (DO = dissolved oxygen; Sal = salinity; OM = organic matter content; temperature in °C; depth in m; grain size: sand, silt, clay), and mean density of *T. medici* sp. nov. (light grey semicircles) and *S. primus* gen. et sp. nov. (dark grey semicircles) at the sampling stations (Arabic numerals) along the Urías system.

**Table 7.** Spearman's correlation coefficient between density of *Typhlamphiascus medici* sp. nov. and environmental variables. Sal = salinity; °C = temperature; DO = dissolved oxygen; OM = organic matter content.

	Density	Depth	Sal	°C	DO	OM	Sand	Silt
Depth	-0.513							
Sal	0.347	-0.752						
°C	0.169	-0.212	-0.367					
DO	0.655	-0.842	0.752	-0.091				
OM	-0.428	0.358	0.018	-0.212	-0.588			
Sand	0.753	-0.394	0.226	-0.091	0.721	-0.709		
Silt	-0.817	0.503	-0.330	0.091	-0.758	0.673	-0.964	
Clay	-0.525	0.067	0.135	-0.127	-0.455	0.855	-0.770	0.685

### Ecology

*Typhlamphiascus medici* sp. nov. and *S. primus* gen. et sp. nov. were present at sampling stations 2, 4, 5, 7 and 10, and *S. primus* gen. et sp. nov. was also recorded at station 9 (Table 5, Fig. 20). Spearman's correlation coefficient ( $p \leq 0.05$ ) revealed a strong positive correlation between the density of both *T. medici* sp. nov. and *S. primus* gen. et sp. nov., and sand and dissolved oxygen (see also Table 6 for environmental variables). Similarly, Spearman's correlation coefficient showed a strong negative correlation between the density of these two species and silt and clay contents (Tables 7–8).

The non-parametric analysis of variance revealed statistical differences ( $F = 5.09$ ,  $p < 0.05$ ) in the density values of *T. medici* sp. nov. and *S. primus* gen. et sp. nov. between stations along the Uriás system.

The PCoA (Fig. 21) showed that principal component 1 (PCO1) accounts for 55.6% of total variation and principal component 2 (PCO2) explains 26% of total variation. Stations 1, 7 and 8 with silty sediments and station 3 with comparatively coarser sediments are considered as atypical due to the absence of both *T. medici* sp. nov. and *S. primus* gen. et sp. nov. Stations 2, 4, 5, 6 and 10 are 77% similar in terms of mean density of both species, and station 9 is excluded from this group due to the absence of *T. medici* sp. nov. Stations 5 and 6 are 90% similar, as are stations 4 and 10 in terms of mean density of both species. Station 2 seems to be different from all the other stations where *T. medici* sp. nov. and *S. primus* gen. et sp. nov. were found. On the other hand, higher mean density values of *T. medici* sp. nov. and *S. primus* gen. et sp. nov. were recorded at stations characterized by well-oxygenated sandy sediments at the shallower upper and middle-upper region of the Uriás system with comparatively higher salinity values (stations 2, 5, 4 and 6). Comparatively lower mean density values of these two species were recorded at the comparatively deeper station 10 with sandy sediments, where a comparatively lower salinity and dissolved oxygen values were also observed. *Typhlamphiascus medici* sp. nov. was not found at station 9, where only *S. primus* gen. et sp. nov. was present. See Gómez (2020a: 43, fig. 1) for a map with the location of the sampling stations.

Briefly, grain size and dissolved oxygen content are the main proxies for the distribution of *T. medici* sp. nov. and *S. primus* gen. et sp. nov. in the Uriás system. High levels of organic matter content and low levels of dissolved oxygen are commonly associated with muddy sediments and are likely important factors for the distribution of these two species. Morales-Serna *et al.* (2006) showed similar results in their study on the spatial and temporal variation of species richness of benthic copepods from the same area. The analysis of the distribution of these two species and of the rest of the harpacticoids collected

**Table 8.** Spearman's correlation coefficient between density of *Spinodiosaccus primus* gen. et sp. nov. and environmental variables. Sal = salinity; °C = temperature; DO = dissolved oxygen; OM = organic matter content.

	Density	Depth	Sal	°C	DO	OM	Sand	Silt
Depth	-0.325							
Sal	0.148	-0.752						
°C	0.200	-0.212	-0.367					
DO	0.600	-0.842	0.752	-0.091				
OM	-0.494	0.358	0.018	-0.212	-0.588			
Sand	0.782	-0.394	0.226	-0.091	0.721	-0.709		
Silt	-0.700	0.503	-0.330	0.091	-0.758	0.673	-0.964	
Clay	-0.700	0.503	-0.330	0.091	-0.758	0.673	-0.964	1.000

during four sampling campaigns in the year 2019 is still pending, but a similar trend is expected at least for other genera of the family Miraciidae.

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**Supplementary File 1.** Twelve most parsimonious cladograms of the possible generic relationships within the Diosaccinae Sars, 1906. 126 steps, CI of 42 and RI of 77. Empty circle = homoplasy; dark circle = apomorphy. <https://doi.org/10.5852/ejt.2021.759.1433.4671>