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A review of taxonomic concepts in the Nannoniscidae (Isopoda, Asellota), with a key to the genera and a description of *Nannoniscus oblongus* Sars

GEORGE D.F. WILSON
Australian Museum, 6 College Street, Sydney, NSW 2010 Australia. E-mail: buz.wilson@austmus.gov.au

Abstract

Owing to recent taxonomic changes to the Nannoniscidae Hansen, the concepts of the taxa within the family require clarification. Specimens of *Nannoniscus oblongus* Sars, putatively those examined by G.O. Sars, and specimens from Hjeltefjord, Norway were illustrated to clarify the concept of the type genus of the Nannoniscidae. Specimens used by Siebenaller and Hessler (1981) and several other recently-described taxa were evaluated. Standard views are argued to provide more consistent illustrations of morphology. The somite articulations of the posterior body were found to be variable and often inaccurately illustrated feature in nannoniscid taxonomy; this character complex is therefore unreliable for taxonomic concepts in the family. In replacement, new characters that distinguish this family from the Desmosomatidae Sars are described. These include the proximal segmentation of the antennal flagellum, a subdistal dorsal tooth on the left mandible incisor process and ventral pereonal insertions of the coxae. The composition and classification of the family is adjusted using this new information. Subfamilies recently proposed for the Nannoniscidae by George (2001) based on somite articulations are rejected. Diagnoses of several genera, including *Saetoniscus* Brandt, were reconsidered using this new information. This latter genus is found to be indistinguishable from *Nannoniscus* Sars and is placed in junior synonymy. A new diagnosis and a new key to the genera of the Nannoniscidae use the new character information, omitting somite articulations as a primary descriptor. New diagnoses for *Nannoniscus* Sars and *Nannonisconus* Schultz, and revised compositions for these genera are proposed. *Nannoniscus intermedius* Siebenaller & Hessler is transferred to *Nannonisconus*. *Rapaniscus* Siebenaller & Hessler is diagnosed and pereopods I–II of its type species, *R. dewdneyi* are illustrated.

Key words: Nannoniscidae, sexual dimorphism, terminal male, *Nannoniscus*, *Nannonisconus*, *Rapaniscus*, *Exiliniscus*, systematics, standard views, somite articulation, mandible incisor process

Introduction

Although the asellotan isopod family Nannoniscidae Hansen, 1916 has not received a complete revision since Siebenaller and Hessler (1977, 1981), this taxon has reasonably well-defined generic concepts. These authors nevertheless indicated that the generic classification required further study, especially with regard to the type genus *Nannoniscus* Sars, 1870. In addition, their concept depended on just a single, possibly variable character to establish family membership, the position of a robust seta on the anterolateral margin of pereonites 1–4. Several changes to nannoniscid classification have been introduced since their study that brings some of their conceptual framework into question. Svavarsson (1984) transferred *Micromesus* to the Nannoniscidae. Wägele (1989) proposed a return of *Thaumastosoma* Hessler, 1970 to the Desmosomatidae and made other proposals regarding the placement of related taxa. George (2001) proposed new subfamily and genus-level names, and revised generic compositions.

Fully mature males ("terminal male", cf. Just & Wilson 2004) of Nannoniscidae are not known in many species, and indeed some characters states of *Nannoniscus oblongus* Sars, 1870 (the type species) have

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remained uncertain because Sars (1870, 1897a) did not illustrate a male from Norway. Possibly as a result of this lack of information, Brandt (2002) added another genus, *Saetoniscus* from the Angola Basin (south eastern Atlantic Ocean), based on a male holotype. This taxon, if tested against the key in Siebenaller and Hessler (1981), would be identified as *Nannoniscus*. Because Brandt (2002) based the new genus on male features, information from the male of *N. oblongus* is needed to clarify the concept of the type genus of the family. To clarify the taxonomic concepts of *Nannoniscus* and the family, a fully mature male of *N. oblongus* Sars, 1870 from Hjeltefjord, Norway and female specimens from G.O. Sars's collection are illustrated. The generic concept of *Saetoniscus* Brandt, 2002 is evaluated in light of this new information.

The relative degree of articulation of the posterior somites has been a central character in nannoniscid taxonomy (Wolff, 1962; Siebenaller & Hessler, 1981; Kussakin, 1999); some genera have been defined solely on the state of these articulations, and indeed the subfamilies of George (2001) use only this feature. My survey of described species in the Nannoniscidae (Table 1) has shown that some taxa need re-evaluation once variability in somite articulation is taken into account. Although this feature remains useful for defining some taxa in the Nannoniscidae, other characters are introduced to define clades within this family, and indeed to define the family itself. Several taxa in George (2001) are assessed and assigned to relevant groups within a more conservative classification for the Nannoniscidae.

In the process of illustrating *N. oblongus* and reviewing the taxa described by Siebenaller and Hessler (1977, 1981), several characters were discovered that supplement the definition of the Nannoniscidae: dorsal cusps on the incisor process of the mandible and a conjoint antennal article 7 (compound proximal flagellomere). These characters allow a clearer definition of the Nannoniscidae, especially with respect to the Desmosomatidae. The evidence provided below support Siebenaller and Hessler's (1981) taxonomic concepts for *Thaumastosoma*. Proposals on the placement of this genus and other taxa in the Nannoniscidae and Desmosomatidae in a review of all isopods (Wägele 1989) are not considered further (see Wilson 1996). Using the new character evidence, a revised key to the genera of the Nannoniscidae is presented. Because the articulations between posterior somites were found to be ineffective for defining taxa within the family, *Nannoniscus intermedius* Siebenaller and Hessler, 1981 is transferred to the *Nannonisconus* Schultz, 1966, using improved information regarding articulations on the posterior pereonites. The study of specimens that were used by Siebenaller and Hessler (1977, 1981; Table 1) for their revision also uncovered a few deficiencies. In particular, the defining feature of their genus *Rapaniscus*, its enlarged first pereopod, was not illustrated in the type species, so this information is provided using topotypic specimens.

Methods

Standard views

Ramirez et al. (2007) argued for the use of "standard views" in taxonomic research, especially in digital taxonomic databases. Standard views are simply presentations of images that allow objective comparisons between and within taxa, i.e., ontology of the character data. Their arguments echo an earlier work on another group of deep-sea isopods (Wilson & Hessler 1980) where a series of standard views were illustrated for most limbs. A lack of consensus on what constitutes a standard view for many morphologies was a difficulty encountered in assessing nannoniscid morphology. Mandibles were the most problematic because authors have illustrated this limb in diverse orientations, and without regard to all features on the limb. Body shapes were often obfuscated by failure to illustrate specimens in precisely orthogonal positions, often with parts of the body substantially curving into the plane of view. As a result, interpretations of character distributions in the Nannoniscidae and Desmosomatidae have a degree of subjectivity. Standard views are needed in asellotan taxonomy, so a first step is taken in listing those used in this paper. Standard views can be achieved in practise by arranging specimens or parts of specimens in glycerine between a cover slip and the curving side of a concavity slide. By lightly contacting the upper and lower sides and gently moving the cover slip, any desired orientation can be achieved without crushing the specimen. Curved whole specimens become more flexible in glycerine and can be flexed if desired. For stiff but curved specimens (e.g., Ilyarachninae, Munnopsidae), the anterior and posterior parts of the body can be illustrated separately to achieve fully planar views of each tagma. Parts on museum slides, however, cannot be repositioned; if the mounting medium is sufficiently hardened (as in slides where Canada balsam has been used), the parts can be illustrated by placing the slide on the stage in an inverted position. Otherwise museum slides were illustrated as is.

Body illustrations

Whole specimens are oriented so that dorsal and lateral views are precisely orthogonal, similar to the illustrations in Hessler (1970) or Siebenaller and Hessler (1977, 1981). In these positions, the direction of view is perpendicular to either the frontal or horizontal plane of the specimen. In dorsal view, the specimen is arranged so that the lateral margins, front of the head and pleotelson are in approximately the same plane. Intact pleotelson illustrations are done in ventral view, again precisely orthogonal to the line of sight, and including pereonite 7 to show ventral structures and penes in the males. Enlargements of the uropods can be made from specimens in this position.

Mandibles: The dorsal side of the mandible (Fig. 1) shows the most information, especially if it is oriented so that the dorsal condyle, molar process (a small setose flap in Nannoniscidae), and the incisor process are in approximately the same plane. The shape of the incisor process can be shown by either an anterior or posterior view, which puts the distal part of the mandible in the plane of view.

Maxilliped, maxillula and maxilla: The ventral faces of these limbs have the most information, with varying setation found on ventral and distal margins, and full exposure of the maxillipedal palp, which emerges on the ventral face. The dorsal (internal) side of the maxilliped, although illustrated in several recent publications, is less informative because the setose dorsal ridge, which is the only complex feature visible on this side, occurs in most asellotans. The endite covers the palp in this orientation, obscuring potentially useful anatomy at its base. Most setae, denticles and other cuticular features occur on the external (ventral) side of the limb, which allows a richer context for defining taxonomically useful characters.

Pereopods are illustrated on the lateral face for the whole limb, with the direction of view perpendicular to a plane defined by the limb. The lateral face is the posterior side on pereopods I–IV and the anterior side on pereopods V–VII (anatomically determined if the limbs are projecting laterally). For the posterior limbs, enlargements of the dactylus should be done on the posterior side in order to show the articular plate on the distal margin of the propodus.

Specimens examined

The large collection of deep-sea isopods collected by the Woods Hole Oceanographic Institution was assembled by Robert R. Hessler, Scripps Institution of Oceanography, and is now housed at the Australian Museum. This collection contains some type and many non-type Nannoniscidae specimens of Siebenaller and Hessler (1977, 1981) and those of Hessler (1970; Table 1). Although those authors assigned types for each of their species that were deposited at the United States National Museum, their collection contained additional specimens that were not reported in the original publication, or were mentioned as "other material". Until recently, some lots were not explicitly labelled, so the collection was inspected to identify the relevant lots. In some cases, I determined that these unmentioned specimens may have been used in the description of the species, which is noted in Table 1. Although these specimens have no nomenclatural relevance, their taxonomic value is considerable because of their topotypic provenance, which will allow further taxonomic research in this family. These specimens are now registered at the Australian Museum (AM), along with many lots of undescribed specimens of each genus. Other specimens borrowed from the Zoologisches Institut und Museum, Universität Hamburg (ZMH) and Zoological Museum of the Universitetet i Oslo (ZMO), were also studied as part of this research.

TABLE 1. Nannoniscidae: material of described species at the Australian Museum, with comments relating to original description in Siebenaller and Hessler (1977, 1981; indicated by "S&H" in table). Type localities are indicated by "*". See Table 2 for Locality data.

Species	acc. no.	Inds	Sample	Comments
Austroniscus sp. "no.6"	P.76850	2	WHOI 195	"No. 6" in S&H fig.10E
Exiliniscus aculeatus Siebenaller & Hessler, 1981	P.76949	2	WHOI 201*	male & female; S&H "other material"
Exiliniscus aculeatus Siebenaller & Hessler, 1981	P.76948	1	WHOI 201*	S&H "other material"
Exiliniscus aculeatus Siebenaller & Hessler, 1981	P.76950	1	WHOI 201*	female, slide, S&H "other material", fig.2C–F,I,L
Exiliniscus aculeatus Siebenaller & Hessler, 1981	P.59590	3	WHOI 200	S&H "other material"
Exiliniscus clipeatus Siebenaller & Hessler, 1981	P.74560	5	WHOI 85*	2 females, 3 mancas; mandible illustrated herein
Exiliniscus clipeatus Siebenaller & Hessler, 1981	P.59562	1	WHOI 84	S&H "other material"
Exiliniscus clipeatus Siebenaller & Hessler, 1981	P.59564	1	WHOI 120	S&H "other material"
Exiliniscus clipeatus Siebenaller & Hessler, 1981	P.59565	2	WHOI 121	S&H "other material"
Exiliniscus clipeatus Siebenaller & Hessler, 1981	P.59566	5	WHOI 122	S&H "other material"
Exiliniscus clipeatus Siebenaller & Hessler, 1981	P.59573	1	WHOI 175	S&H "other material"
Hebefustis cornutus Siebenaller and Hessler, 1977	P.58991	2	WHOI 126*	paratypes
Hebefustis dispar Siebenaller and Hessler, 1977	P.58990	~90	WHOI 202B*	paratypes
Hebefustis hexadentium Siebenaller and Hessler, 1977	P.58988	1	WHOI 247A*	paratype
Hebefustis mollicellus Siebenaller and Hessler, 1977	P.58989	2	WHOI 167*	paratypes
Nannoniscoides biscutatus Siebenaller & Hessler, 1977	P.59007	2	WHOI 155*	paratypes
Nannoniscoides biscutatus Siebenaller & Hessler, 1977	P.59006	1	WHOI 156*	paratype
Nannoniscoides biscutatus Siebenaller & Hessler, 1977	P.59005	1	WHOI 156*	paratype
Nannoniscoides gigas Siebenaller & Hessler, 1977	P.59008	1	WHOI 256*	paratype
Nannoniscoides latediffusus Siebenaller & Hessler, 1977	P.59000	1	WHOI 122	S&H "other material"
Nannoniscoides latediffusus Siebenaller & Hessler, 1977	P.59001	1	WHOI 126	S&H "other material"
Nannoniscoides latediffusus Siebenaller & Hessler, 1977	P.59002	1	WHOI 159	S&H "other material"
Nannoniscoides latediffusus Siebenaller & Hessler, 1977	P.59003	2	WHOI 167	S&H "other material"
Nannoniscoides latediffusus Siebenaller & Hessler, 1977	P.59004	11	WHOI 169A*	paratypes
Nannoniscoides latediffusus Siebenaller & Hessler, 1977	P.58999	1	WHOI Chain 35 Dredge 12	S&H "other material"
Nannonisconus intermedius (Siebenaller & Hessler, 1981)	P.74558	7	WHOI 295	1 dissected; mandible illustrated herein
Nannonisconus intermedius (Siebenaller & Hessler, 1981)	P.74559	6	WHOI 297*	S&H "other material"
Nannoniscus oblongus Sars, 1870	P.74561	1	Hjeltefjord, 4vii1978	female, 1.6mm; illustrated herein, see text for site data
Nannoniscus oblongus Sars, 1870	P.74562	1	Hjeltefjord, 4vii1978	male, 1.4mm; illustrated herein, see text for site data
Nannoniscus oblongus Sars, 1870	P.76916	3	Hjeltefjord, 4vii1978	see text for site data
Nannoniscus oblongus Sars, 1870	P.76917	1	Hjeltefjord, 7–8vii1978	see text for site data
Nannoniscus teres Siebenaller & Hessler, 1981	P.76928	3	WHOI 328*	S&H "other material"

.....continued

TABLE 1 (continued).

Species	acc. no.	Inds	Sample	Comments
Nannoniscus teres Siebenaller & Hessler, 1981	P.76928	3	WHOI 328*	S&H "other material"
Panetela wolffi Siebenaller & Hessler, 1981	P.76932	2	WHOI 202B*	females, slide 10; S&H "other material": fig.5C,F–K
Panetela wolffi Siebenaller & Hessler, 1981	P.76933	2	WHOI 202B*	female, manca; S&H "other material"
Panetela wolffi Siebenaller & Hessler, 1981	P.76934	2	WHOI 202B*	females; S&H "other material"
Panetela wolffi Siebenaller & Hessler, 1981	P.76935	8	WHOI 201*	S&H "other material"
Panetela wolffi Siebenaller & Hessler, 1981	P.76936	1	WHOI 201*	dissected female, "other material"
Rapaniscus crassipes (Hansen, 1916)	P.76956	3	WHOI 209A	slide 15, S&H: fig.4C–H
Rapaniscus crassipes (Hansen, 1916)	P.76957	1	WHOI 209A	female, S&H: fig.4A,B,E
Rapaniscus crassipes (Hansen, 1916)	P.76958	1	WHOI 209B	female
Rapaniscus crassipes (Hansen, 1916)	P.76959	1	WHOI 200	female
Rapaniscus crassipes (Hansen, 1916)	P.59732	2	WHOI 73	
Rapaniscus crassipes (Hansen, 1916)	P.59733	3	WHOI 145	
Rapaniscus crassipes (Hansen, 1916)	P.59734	1	WHOI 200	
Rapaniscus crassipes (Hansen, 1916)	P.59731	2	WHOI G1	
Rapaniscus crassipes (Hansen, 1916)	P.59730	2	WHOI G1	
Rapaniscus dewdneyi Siebenaller & Hessler, 1981	P.59736	4	WHOI 61	S&H "other material"
Rapaniscus dewdneyi Siebenaller & Hessler, 1981	P.59737	1	WHOI 119	S&H "other material"
Rapaniscus dewdneyi Siebenaller & Hessler, 1981	P.59738	4	WHOI 128	S&H "other material"
Rapaniscus dewdneyi Siebenaller & Hessler, 1981	P.59739	3	WHOI 131	S&H "other material"
Rapaniscus dewdneyi Siebenaller & Hessler, 1981	P.59735	1	WHOI G9	S&H "other material"
Rapaniscus dewneyi Siebenaller & Hessler, 1981	P.74555	8	WHOI 209A*	male illustrated herein; non-types
Rapaniscus dewneyi Siebenaller & Hessler, 1981	P.74556	2	WHOI 209A*	female, S&H: fig.3E–G,I–J,N
Rapaniscus dewneyi Siebenaller & Hessler, 1981	P.74557	1	WHOI 209B*	female illustrated herein; non-type
Regabellator armatus (Hansen, 1916)	P.59749	8	ALLEN S50	
Regabellator armatus (Hansen, 1916)	P.59750	6	WHOI 85	
Regabellator armatus (Hansen, 1916)	P.59754	6	WHOI 149	
Regabellator armatus (Hansen, 1916)	P.59751	2	WHOI 328	
Regabellator profugus Siebenaller & Hessler, 1981	P.76918	19	WHOI 201*	non-types
Regabellator profugus Siebenaller & Hessler, 1981	P.76919	1	WHOI 201*	female, parts on slide; S&H: figs.6E–F, 7
Regabellator profugus Siebenaller & Hessler, 1981	P.59755	1	WHOI 195	S&H "other material"
Regabellator profugus Siebenaller & Hessler, 1981	P.59756	1	WHOI 200	S&H "other material"
Thaumastosoma platycarpus Hessler, 1970	P.59254	7	WHOI 64*	paratypes
Thaumastosoma platycarpus Hessler, 1970	P.65517	3	WHOI 66	
Thaumastosoma platycarpus Hessler, 1970	P.58793	1	WHOI 122	
Thaumastosoma tenue Hessler, 1970	P.59255	1	WHOI 64*	paratype
Thaumastosoma tenue Hessler, 1970	P.59256	1	WHOI 95*	paratype

TABLE 2. Locality data for Nannoniscidae listed in Table 1.

Locality	Sample	Midpoint Position	Depth m	Date
Off Cork Ireland, N. Atlantic Ocean	WHOI 328	50°04.70'N 15°44.80'W	4431	23/08/1972
Bay of Biscay, North Atlantic Ocean	ALLEN S50	43°46.70'N 3°38.00'W	2379	18/07/1967
Gay Head-Bermuda transect, North Atlantic Ocean	WHOI 61	39°43.20'N 70°37.80'W	2000	20/08/1964
	WHOI 64	38°46.00'N 70°06.00'W	2886	21/08/1964
	WHOI 66	38°46.70'N 70°08.80'W	2802	21/08/1964
	WHOI 73	39°46.50'N 70°43.30'W	1400	25/08/1964
	WHOI 84	36°24.40'N 67°56.00'W	4749	04/07/1965
	WHOI 85	37°59.20'N 69°26.20'W	3834	05/07/1965
	WHOI 95	38°33.00'N 68°32.00'W	3753	17/12/1965
	WHOI 119	32°15.80'N 64°31.60'W	2159	19/08/1966
	WHOI 120	34°43.00'N 66°32.80'W	5021	20/08/1966
	WHOI 121	35°50.00'N 65°11.00'W	4800	21/08/1966
	WHOI 122	35°50.00'N 64°57.50'W	4833	21/08/1966
	WHOI 126	39°37.00'N 66°47.00'W	3806	24/08/1966
	WHOI 128	39°46.50'N 70°45.20'W	1254	16/12/1966
	WHOI 131	36°28.90'N 67°58.20'W	2178	18/12/1966
	WHOI 175	36°36.00'N 68°29.00'W	4680	29/11/1967
	WHOI G1	39°42.00'N 70°39.00'W	2000	24/05/1961
	WHOI G9	39°44.70'N 70°38.30'W	2021	09/09/1962
West of North Africa, N. Atlantic Ocean	WHOI 145	10°36.00'N 17°49.00'W	2185	06/02/1967
	WHOI 149	10°30.00'N 18°18.00'W	3861	07/02/1967
off Suriname, South America	WHOI 295	8°04.20'N 54°21.30'W	1011	28/02/1972
	WHOI 297	7°45.30'N 54°24.00'W	516	28/02/1972
Equatorial Atlantic Ocean	WHOI 155	0°03.00'S 27°48.00'W	3757	13/02/1967
	WHOI 156	0°46.00'S 29°28.00'W	3459	14/02/1967
off Brazil, Equatorial Atlantic Ocean	WHOI 159	7°58.00'S 34°22.00'W	887	18/02/1967
	WHOI 167	7°58.00'S 34°17.00'W	975	20/02/1967
	WHOI 169	8°03.00'S 34°23.00'W	587	21/02/1967
	WHOI Chain 35 Dredge 12	7°09.00'S 34°23.50'W	788	06/04/1963
off Luanda, South Africa, S. Atlantic Ocean	WHOI 195	14°49.00'S 9°56.00'E	3797	19/05/1968
	WHOI 200	9°41.00'S 10°55.00'E	2699	22/05/1968
	WHOI 201	9°29.00'S 11°34.00'E	1998	23/05/1968
	WHOI 202	9°05.00'S 12°17.00'E	1535	23/05/1968
Argentine Basin, S. Atlantic Ocean	WHOI 247	43°33.00'S 48°58.10'W	5216	17/03/1971
	WHOI 256	37°40.90'S 52°19.30'W	3912	24/03/1971

Illustrations

Pencil drawings of specimens were made using a compound microscope fitted with interference contrast optics and a camera lucida. The pencil drawings were scanned into bitmap images, which were used as background templates in a vector graphics program (*Inkscape* version 0.45.1). Each separate drawing was traced into layer in a vector graphic digital file using a graphics tablet. For the final plates, the vector images assembled into plates and exported to bitmap images.

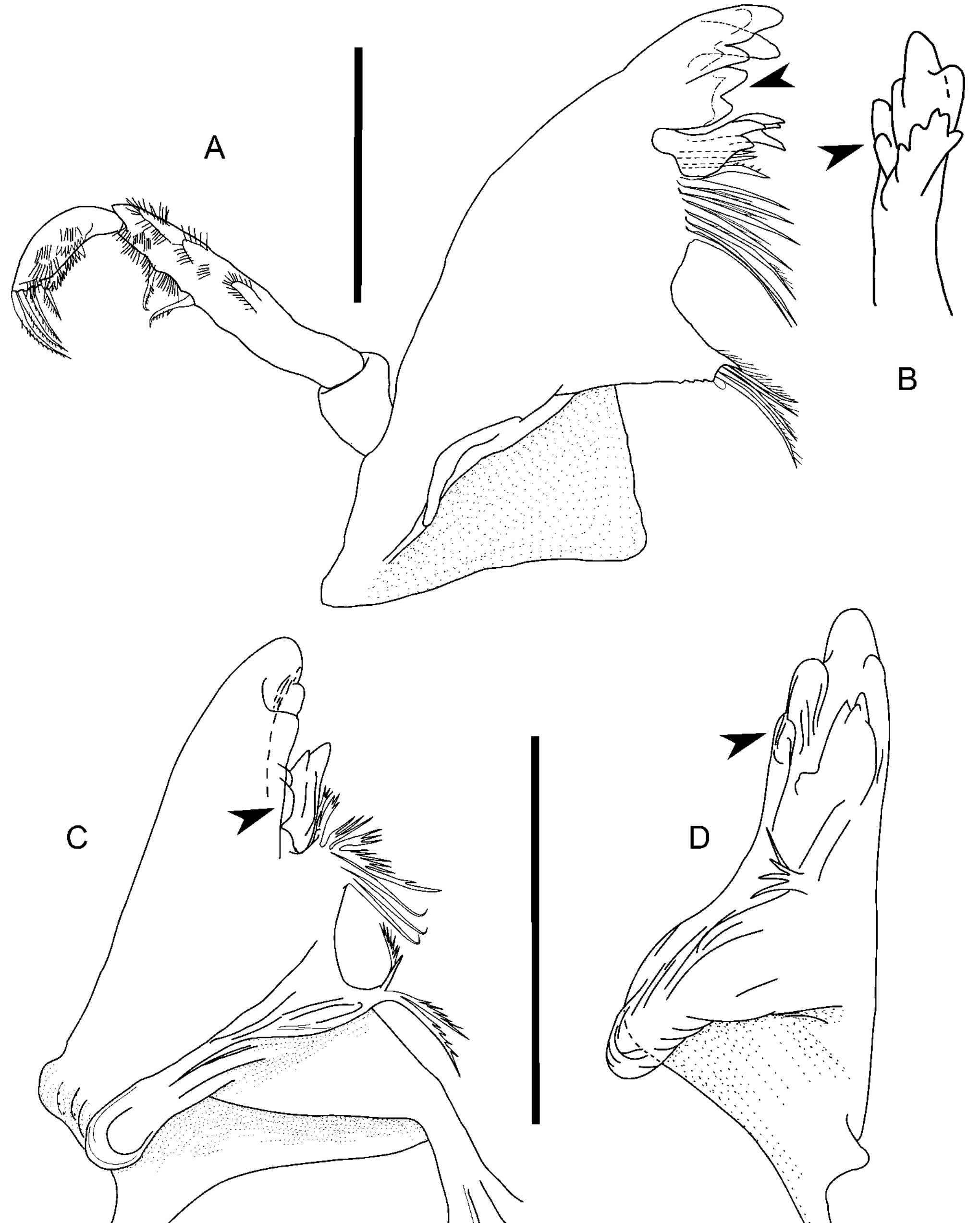

FIGURE 1. Left mandibles, dorsal and medial view respectively; arrowheads indicate position of dorsal tooth. A–B, *Nannonisconus intermedius* Siebenaller & Hessler, 1981 (WHOI 295, AM P.74558). C–D, *Exiliniscus clipeatus* Siebenaller & Hessler, 1981) (WHOI 85, AM P.74560). Scale bar 0.1 mm.

Characters of the Nannoniscidae

The complex expression of posterior somite articular margins in the Nannoniscidae is a variable trait and can be shown to be inadequate for defining clades within the family. This character complex varies considerably in nannoniscid species, both as morphological variability and as misinterpretation. In their definition of *Nannoniscoides* Hansen, 1916, Siebenaller and Hessler (1977) included variability in the pereonite 6–7 articular margins of *Nannoniscoides* Hansen, 1916, already laying doubt on whether this feature was fundamentally useful in nannoniscid taxonomy. On the posterior ventral surface (e.g., *Nannoniscus reticulatus* Hansen, in

Svavarsson 1988: fig. 3), the somite articulations are often absent ventrally. The articular margins are often illustrated incorrectly, as in *Nannoniscus antennaspinis* Brandt, 2002. Examination of what remains of the dissected holotype of *N. antennaspinis* (ZMH 40110: a section of the posterior part of the body) shows that the pereonites 6–7 lack articulation, although Brandt (2002: fig. 17) clearly drew a well-defined articulation between the pereonites. Even Sars (1897a: pl. 50) showed articulations between pereonites 6–7 of *N. oblongus*, even though they are absent (Fig. 4A), something already pointed out by Hansen (1916: 89). Other deep-sea janiroidean families show considerable variation in the expression of somite articulation, e.g., the Ischnomesidae (Kavanagh & Wilson 2007) or the Munnopsidae (Wilson 1989; Malyutina & Brandt 2006). Although these correspondences are only analogous to character transformations within the Nannoniscidae, they nevertheless demonstrate an evolutionary propensity within Janiroidea as a whole, particularly in deep-sea taxa. Because the phylogenetic structure of the Nannoniscidae is not fully understood, divisions of the family based on only this feature are at least premature, and not supportable given the available evidence. To replace this character complex, several new derived (putatively apomorphic) characters can be used to define the Nannoniscidae, in conjunction with other features.

The first character derives from Siebenaller & Hessler's (1977, 1981) original defining character relating to the position of a robust setae on the anterior pereonites. In most janiroideans, the anterolateral margins of the body typically bear robust setae, regardless of whether the margin is coxal or tergal. Siebenaller & Hessler (1977: 19) comment "… the positioning of this seta may reflect the general development of the coxal epimere." They referred to whether the tergite or the coxa projects into the anterolateral margin, so that a coxal seta diagnosed Desmosomatidae and a tergal seta diagnosed Nannoniscidae. The position of a robust seta seems like a weak feature on which to base family membership, particularly because robust setae can occur anywhere on the tergites and the coxae.

An understanding the anatomical differences between the families suggests a different approach, of which the seta is only a subsidiary element. The pereopodal coxae insert ventrally in the Nannoniscidae, so that they are not ordinarily visible in dorsal view, except in a few taxa with anteriorly or anterolaterally projecting coxae, e.g., *Nannoniscus perunis, N. muscarius*, or in narrow taxa like *Exiliniscus* or *Panetela* that lack projecting tergites. As a result, the tergite has an anterolateral robust seta in the majority of Nannoniscidae. Conversely, taxa in the Desmosomatidae have laterally-placed pereopods, to the extent that the anterior pereopods assume a dorsolaterally projecting position similar to that seen in Macrostylidae. Thus, desmosomatids have the definitive robust seta on the anterior coxae, which are well exposed on the lateral margin.

A further observation may be made on the coxal positions. In the Nannoniscidae, posterior pereopods V–VII coxae insert increasingly closer to the midline, and are positioned distinctly medially, especially for the last pereopods (Figs 3A, 4D, 6B). This complex feature is related to the presence of laterally projecting tergal plates in most Nannoniscidae, with the exception of narrow, worm-like taxa, *Exiliniscus* and *Panetela*. Species in these latter two genera lack tergal plates or projections lateral to the coxae, so the coxae are near the lateral margin, although in ventral orientation. Coxa VII of both genera, however, is close to the midline rather on the lateral margin. In exceptionally broad species of *Austroniscus*, this medial-ward trend in the coxa VII position involves an additional transformation of the associated tergite. In *Austroniscus* "No. 6" (Siebenaller & Hessler 1981: 244, fig. 10E; AM P.76850), tergite 7 does not participate in the lateral margin and the ventral pereonal articulation is lost on the midline. The medial positioning of the posterior coxae is also seen in other families, such as the Ischnomesidae and Haploniscidae, although as discussed above, this may be analogy, rather than homology. Some Desmosomatidae have especially narrow posterior pereonites (e.g., *Mirabilicoxa* species); these taxa are easily distinguished on other grounds, such as the form of the antennula, but still have clearly lateral, dorsally visible coxae on the posterior pereonites. Specimens in either family with broader bodies are easily distinguished using the position of the coxae. Notably, *Pseudomesus* species are desmosomatids using this criterion, corroborating Svavarsson's (1984) transfer of this genus and elimination of the family Pseudomesidae.

The nannoniscid left mandible incisor process has a large, subdistal tooth or cusp that is positioned dorsally, forming nearly a right angle to the terminal cusps (arrows in Figs 1, 5A). Although the mandible is not illustrated well in most species, this feature appears in the taxa where the left mandible has been drawn in dorsal view. *Austroniscus*, *Exiliniscus* (Fig. 1C–D) and *Thaumastosoma* (Hessler 1970: fig. 52d) species have this tooth, but it is reduced compared to other nannoniscid genera owing to further transformation of their mandibles. This possibly apomorphic character is not an exclusive feature of the Nannoniscidae because taxa in the Macrostylidae have a well-developed dorsal tooth (e.g., *Macrostylis polaris* Malyutina & Kussakin, 1996). Desmosomatidae have a more typical mandible that lacks the subdistal dorsal tooth.

In all Nannoniscidae, the antennal proximal flagellar article (Figs 2A–B, 4B) is consistently much longer than more distal articles. In all cases that I have examined, this flagellomere has multiple setal positions and apparently degenerate segmentation. Thus the nannoniscid first flagellar article is conjoint, with annular margins failing to express in the first few articles. In terminal males (Fig. 2A–B), this compound annulus is enlarged or inflated and is more setose. The antenna of *Nannoniscus antennaspinis* Brandt, 2002 (holotype ZMH K40110) although illustrated with a short proximal article (Brandt 2002: fig. 17), proves to have an elongate article that is nearly as long as the next 3 articles. Species of Desmosomatidae (multiple examples in Hessler 1970) and Macrostylidae (e.g., *Macrostylis belyaevi* Mezhov, 1989: fig. 1) may have a proximal flagellomere that is longer than the subsequent articles, as is common in many isopods, but it does not have multiple rows of setae and derives from only the one article.

Composition of the Nannoniscidae

The Nannoniscidae has received recent changes to its classification, some of which destabilise the conceptual structure of the family. Several recently proposed genera appear to lack supporting evidence. The following section reviews these changes and proposes adjustments that will allow a clearer path to further revisions of superspecific taxa in the family.

George (2001) introduced three subfamily names to the Nannoniscidae, of which two were incorrectly constructed or are unavailable under ICZN articles 13.1 or 16.2; these names are not repeated for this reason. These subfamilies were defined using the degree of articulation between the last two pereonites and the pleotelson. This character complex, as currently understood, does not allow a well-supported division of the family. Therefore, the proposed subfamilies of George (2001) are rejected in the classification of the Nannoniscidae.

The generic composition follows Siebenaller and Hessler (1977, 1981) with the addition of *Micromesus* Birstein, 1963 that was included by Svavarsson (1984). Menzies & George (1972) did not provide valid arguments for including *Sugoniscus parasitus* in the Nannoniscidae. Species of this genus occur in the North Pacific (Thistle & Wilson 1996) so this taxon seems to represent a widespread clade in that ocean. The mouthparts, head capsule and body form of *Sugoniscus* are unlike any member of the Nannoniscidae. Currently *Sugoniscus* is classified as family *incertae sedis* (Siebenaller & Hessler 1977: 21).

The revised family concept allows an objective assignment of the unusual genus *Thaumastosoma* Hessler, 1970 to this family, corroborating Siebenaller & Hessler's (1981) original placement. In particular, *T. platycarpus* Hessler, 1970 (fig. 50) clearly shows various features identifying this genus as a nannoniscid: the antennal proximal flagellar article is conjoint and expanded, the coxae of pereopods VII are ventral and displaced toward the midline, and pereonites 1–4 each has a robust seta on the anterolateral margin, which was the original character provided by Siebenaller & Hessler (1981). Although not apparent in *T. platycarpus* owing to the reduction of the incisor process of the prognathous mandibles, the mandibular dorsal tooth is present in *T. tenue* Hessler, 1970 (his fig. 52d); this condition is similar to that seen in *Exiliniscus* species (Fig. 1C–D).

The proposed division of *Nannoniscoides* Siebenaller & Hessler, 1977 with the introduction of *Nannoniscella* George, 2001 is invalid because this name is a junior homonym of available name *Nannoniscella*

Hansen, 1916, which itself is a junior synonym of *Austroniscus* Vanhöffen, 1914. *Nannoniscella* George was created with little justification, other than the different patterns of articulation between pereonites 6–7 in species of *Nannoniscoides*.

The genus *Leutziniscus* George, 2001 is poorly supported by evidence. The subfamily named to contain this genus is invalid under ICZN article 16.2; no type genus was cited and the subfamily as proposed contained more than one genus. Although the genus *Leutziniscus* did not have an explicit type designation, it is automatically available owing to implicit monotypy (ICZN Art. 68.3). *Leutziniscus jebamoni* George, 2001, however, is a *nomen dubium* because the holotype of the species is missing and the original illustrations are inconclusive. No types of this species are deposited at the US National Museum of Natural History (M. Schotte, pers. comm.); a specific enquiry (in litt.) to George regarding the whereabouts of the type was not answered. The catalogue number given for the holotype by George (2001), "USNM 138733", is identical to the number given for another species (*Mirabilicoxa alberti*) in the same paper. The species, as far as can be determined from the distorted illustrations of George (2001: fig. 9), appears to be a species of *Thaumastosoma*. George (2001: 1847) even mentions that the posterolateral spines on the pleotelson were the only difference between his genus and *Thaumastosoma*. Although Hessler (1970: 26) in his diagnosis writes that *Thaumastosoma* lacks posterolateral spines, all species of this genus have "acute posterolateral angles", which are essentially broad posterolateral spines. Therefore, no objective difference exists between *Thaumastosoma* and *Leutziniscus*, based on the information in George (2001). The absence of the type specimen means that new characters cannot be found, and existing features cannot be verified. Consequently, *Leutziniscus* George, 2001 is referred to junior synonymy with *Thaumastosoma* Hessler, 1970, and *L. jebamoni* is assigned to *Thaumastosoma*, but only as a *nomen dubium*.

Exiliniscus chandravoli George, 2001 was presented without an explicit fixation of the type specimen, although the "Material examined" (George 2001: 1848) mentions a "Holotype female with marsupium containing four eggs". This species is unlikely to be a member of *Exiliniscus*: the illustrated specimen (George 2001: fig.10) shows a broad anterior pereon and head. Nevertheless, the type specimen is not held at the US National Museum of Natural History (M. Schotte, pers. comm.). The lack of a type specimen and lack of any mention of depository for this specimen requires that the species name "*E. chandravoli* George, 2001" is unavailable under ICZN article 16.4.2.

Brandt's (2002: 12) discussion of relationships of *Saetoniscus* mentioned most genera in the Nannoniscidae but did not mention *Nannoniscus* itself. *S. meteori*, nevertheless, has the diagnostic characters of *Nannoniscus* as defined by Siebenaller & Hessler (1981). Brandt (2002) provided the following diagnostic characters for the genus, each of which is assessed here for evidence that *Saetoniscus* is distinct from *Nannoniscus*. The diagnostic state will be deemed uninformative if it is found elsewhere among the family, especially if found in *N. oblongus*. "Pereonites 6 and 7 dorsomedially fused." This is identical to *Nannoniscus*. "Body length about 5.5 times width of pereonite 2. Fine setules dispersed over dorsum,…" These are variable traits and not suitable for a generic diagnosis. "…female with anteroventral spine on operculum. A1 [*antennula*] 5-segmented, peduncular [*sic*] article 4 with long lateral projection." These characters are found in many *Nannoniscus* species, including *N. oblongus* (Fig.4D, 6A–B). "A2 [*antenna*] flagellar article 1 longer than last peduncular one, swollen." The use of "peduncular" is somewhat confusing, but apparently article 7 is being referred to. As discussed above, this character state is found in the family, not particular to any genus. "Mandible with palp." Most species of nannoniscids have a mandibular palp. "Mxp [*maxilliped*] epipod very long and slender, reaching distal margin of palp article 3." The maxilliped has a reasonably common form across the Nannoniscidae (Fig. 5E), and the relative length of the epipod is sufficiently variable to be suitable only as a species-level character. "P 1–4 [*pereopods I–IV*] with stout sensory setae on ventral margins of carpus and propodus, dorsal margins with stout setae." This is a general janiroidean feature of little consequence for defining genera. "P 5–7 [*pereopods V–VII*] with very long and slender setae ventrally; propodus with long natatory setae dorsally and tiny setules." Among nannoniscids and desmosomatids, especially on males of *N.*

oblongus, long distally setulate can be found on the carpus and propodus (Fig. 2B, E; see also Svavarsson 1984). "Urp [*uropod*] with short, slender exopod; approximately 1/4 length of endopod; exopod 1/3 width of endopod." These details are variable among species of Nannoniscidae, although an exopod that is shorter and narrower than the endopod would be typical for most janiroidean species that have both rami. Indeed, the uropod of *S. meteori* is similar to that of *N. oblongus*, except that its exopod seems to be shorter; similar variation is found among species in *Nannoniscus*. Thus, Brandt's diagnosis has no characters that distinguish her genus from *Nannoniscus*. Therefore, *Saetoniscus* is relegated to junior synonymy, and a new combination is proposed for the species, *Nannoniscus meteori* (Brandt, 2002). Because *Nannoniscus* includes substantial morphological diversity, the apomorphic features of *N. meteori* may define a clade of species within this diversity.

The species *Panetela compacta* Malyutina & Kussakin, 1996, based on a single female specimen, is problematic for the family-level concept of the Nannoniscidae as proposed here. This species is clearly not a member of the genus *Panetela* Siebenaller & Hessler, 1981, because it has distinct tergal plates, which are absent in the type species *P. wolffi*. In fact, the broad flat body with a projecting rostral crest and sternal keels of *P. compacta* is more reminiscent of Joeropsidae or Acanthaspidiidae. More significantly, the antenna, as illustrated (Malyutina & Kussakin 1996: fig. 33), is plesiomorphic with the proximal flagellar article being non-conjoint. The elongate, narrow and biarticulate exopod on pleopod III is not found in any member of the large desmosomatid-macrostylid-nannoniscid clade; members of this group have a small subtriangular or rounded uniarticulate exopod that is distinctly shorter than the endopod. The elongate biarticulate exopod is similar to that on the pleopods of the Ischnomesidae. Nevertheless, the antennula with an inflated distal article 5 and mandible with a reduced molar process supports the assignment to the Nannoniscidae as proposed by Malyutina & Kussakin (1996). More information about the head capsule of this species is needed to assess its affinities, but the holotype was dissected so the type specimen may not be informative.

Taxonomy

Nannoniscidae Hansen, 1916

Desmosomidae Sars, 1897a: 118 (part)
Nannoniscini.—Hansen, 1916: 83; Nordenstam, 1933: 251–252.
Nannoniscidae.—Gurjanova, 1932: 50, 1933: 413; Menzies, 1962a: 29, 1962b: 133; Wolff, 1962: 31; Birstein, 1963: 78; Menzies & George, 1972: 95; Siebenaller & Hessler, 1977: 18, 1981: 229; Svavarsson, 1982: 179; Kussakin, 1999: 28; George, 2001: 1843.
Type genus. *Nannoniscus* Sars, 1870.

Composition. *Austroniscus* Vanhöffen, 1914 (= *Nannoniscella* Hansen, 1916); *Exiliniscus* Siebenaller & Hessler, 1981; *Hebefustis* Siebenaller & Hessler, 1977; *Micromesus* Birstein, 1963; *Nannoniscoides* Hansen, 1916 (= *Nannoniscella* George, 2001, junior homonym of *Nannoniscella* Hansen, 1916); *Nannonisconus* Schultz, 1966; *Nannoniscus* Sars, 1870 (type genus); *Panetela* Siebenaller & Hessler, 1981; *Rapaniscus* Siebenaller & Hessler, 1981; *Regabellator* Siebenaller & Hessler, 1981; *Thaumastosoma* Hessler, 1970 (= *Leutziniscus* George, 2001).

Excluded. *Sugoniscus* Menzies & George, 1972 (family *incertae sedis*).

Diagnosis. Head longer than deep, frons broad, antennulae and antennae well separated, insertions recessed into broad posterolateral margins of head; eyes absent. Pereonites approximately parallel sided; pereonites 2–4 anterolateral margin with robust seta. Pleonite 1 posterior articulation absent (except in *Thaumastosoma*), pleon articular margin reduced to single suture, if present. Pleotelson with ventral anus, separated from pleopodal chamber. Antennulae shorter than head, with 5–9 articles; distal article with a single aesthetasc, often enlarged and bulbous in taxa with 5 articles. Antenna article 7 (first flagellar article) distinctly longer than more distal articles, conjoint. Mandible left incisor with dorsal subdistal cusp, distinctly separated from distal cusps; molar process triangular flattened spinose lobe with dentate or spinulate spines on distal margin. Pereopods length less than body length; dactyli with ventral claw shorter than major dorsal claw; coxae II–IV without robust seta; coxae insert ventrally on body, coxae V–VII insertions converging to midline posteriorly. Pleopod III exopod uniarticulate, subtriangular or ovoid, shorter than endopod. Uropods inserting posteroventrally, adjacent to anus.

Sexual dimorphism, males compared to females. Head rostral crest enlarged, more projecting or thickened. Pereonites and pleotelson lateral margins more projecting and flattened, occasionally indurate and narrower. Antenna flagellum basally enlarged often with many curled setae. Pereopods V–VII propodus dorsal margins with more elongate distally setulate setae.

Remarks. The diagnosis is substantially revised from Siebenaller and Hessler (1977: 18), including information on sexual dimorphism and some new characters. Variable features, such as that of the ventral keels and spination were omitted. The apomorphic bulbous antennular article 5, which characterises many, but not all species, is retained in the diagnosis because it is easily recognisable and, if present, unequivocally diagnoses a specimen as a nannoniscid. Variable articulation of the posterior somites is removed, but this is replaced with the absence (in most species) of pleonite 1. The mandibular palp presence has been removed from the diagnosis, because it is absent in *Exiliniscus* and *Micromesus*. The shape of the maxillipedal palp articles 4–5 is seen in many deep-sea Asellota so this character state is not particularly diagnostic. The inclusion of *Micromesus* into the Nannoniscidae by Svavarsson (1984) requires the removal of the free head and biramous uropod characters, both of which are putative plesiomorphies anyway, from the diagnosis. As discussed above, the ventral insertion of the coxae with laterally extended tergites in most species, a conjoint article 7 on the antenna and the dorsal subproximal cusp on the mandibular incisor process are added as new defining features of the Nannoniscidae. Several characters are apomorphies of larger clades of isopods, but are included for completeness, in the absence of a useful division of the Janiroidea. The ventral anus separate from the pleopodal chamber is common in many but not all deep-sea asellotans. The flattened, triangular mandibular molar and the pleopod III exopod shape are synapomorphies of the Nannoniscidae, Desmosomatidae and Macrostylidae.

Key to the genera of the Nannoniscidae

Because the posterior somite articulation is an unreliable character but nevertheless is used in previous keys (Siebenaller & Hessler 1981; Kussakin 1999), this key uses different characters, and recognises useful features such as the form of the pleotelson. *Micromesus*, added to the family by Svavarsson (1984), is included. This key is also designed to be used without dissection; although the mandibular palp is used, this character can be determined on intact specimens. The composition of some genera, like *Panetela* (discussed above) and *Austroniscus*, need to be reconsidered as some species differ from the generic concepts established by Siebenaller & Hessler (1981) and may not key out properly here. For example, the narrow-bodied species *A. coronatus* Schiecke & Modigh-Tota, 1976, although accepted to be *Austroniscus* by Kaiser & Brandt (2007), probably needs to be placed elsewhere. This species may key out as *Nannoniscoides*.

1. Antennula with 5 articles, distal article bulbous 2
\- Antennula with 6 or more articles, distal article tubular or rounded 3
2. Antennula article 4 distomedial margin with shelf-like process..5
\- Antennula article 4 distomedial margin unmodified, lacking projections..10
3. Pereonites and pleon broadly expanded laterally (distance from midline to posterior coxae subequal or less than distance from coxae to lateral margin); pleopodal operculum (pleopods I–II) in ventral view width less than half pleotelson width... *Austroniscus*
\- Pereonites and pleon not broadly expanded laterally (distance from midline to posterior coxae greater than distance from coxae to lateral margin); pleopodal operculum (pleopods I–II) in ventral view more than half pleotelson width...4

4. Head anterolateral margin rounded, not projecting; mandibles prognathous, often projecting anteriorly in dorsal view; pleopod II of female with ventromedial spines or projections....................... *Thaumastosoma*
- Head anterolateral margin projecting and angular; mandibles projecting anteroventrally, not prognathous, not visible in dorsal view; pleopod II of female smooth, without ventromedial spines or projections.......... .... *Nannoniscoides*

5. Body narrow—pereonal margins rounded in cross-section, tergites curving ventrally, pereonites 4–5 longer than wide; ventral surfaces never with spines 6
- Body moderately broad—tergites projecting laterally, especially in pereonites 5–7; pereonites 4–5 wider than long; ventral surfaces often with spines or keels 7

6. Head with projecting rostrum; antennula tiny, not projecting anteriorly; antenna short—article 5 and flagellum altogether near length of proximal articles, flagellum strongly tapering distally; mandible palp absent... *Exiliniscus*
- Head without projecting rostrum; antennula projecting beyond margin of head; antenna normal length—article 5 and flagellum altogether distinctly longer than proximal articles, flagellum weakly tapering; mandible palp present.. *Panetela*

7. Pleon broad and elongate—wider than head or pereonites 5–7, distinctly longer than pereonites 5–7; pleopods near length of pleotelson.. *Nannonisconus*
- Pleon small—less than or near width of head or pereonites 5–7, subequal or shorter than pereonites 5–7; pleopods distinctly shorter than pleotelson..8

8. Pereopod I robust, all podomeres distinctly wider than those of pereopod II, carpus and propodus with robust elongate ventral setae... *Rapaniscus*
- Pereopod I not robust, podomeres near width to those of pereopod II, carpus and propodus with simple ventral setae 9

9. Pereon or pleopodal surfaces with at most one ventromedial spine; pereopod I and II similar in setation and width of carpus and propodus.. *Nannoniscus*
- Pereon or pleopodal surfaces with 2 or more ventromedial spines; pereopod II carpus and propodus broader and with more robust setae than pereopod I..*Regabellator*

10. Uropod biramous, antennula article 2 distal margin without projections; pleotelson broad (length near width) and shield shaped, with distolateral spines..*Hebefustis*
- Uropod uniramous, antennula article 2 distal margin with flat dorsal spine; pleotelson narrow (much longer than wide) and ovoid, without distolateral spines .... *Micromesus*

Nannoniscus Sars, 1870

Nannoniscus Sars, 1870: 164; Hansen, 1916: 87–89; Gurjanova, 1932: 51; Menzies, 1962b: 133; Birstein, 1963: 78; Siebenaller & Hessler, 1981: 241; Kussakin, 1999: 68.
Saetoniscus Brandt, 2002: 11, figs. 6–13.
Type species. *Nannoniscus oblongus* Sars, 1870.

Composition. *N. acanthurus* Birstein, 1963; *N. aequiremus* Hansen, 1916; *N. affinis* Hansen, 1916; *N. analis* Hansen, 1916; *N. antennaspinis* Brandt, 2002; *N. arcticus* Hansen, 1916; *N. arctoabyssalis* Just, 1980; *N. australis* Vanhöffen, 1914; *N. bidens* Vanhöffen, 1914; *N. bidens* sensu Brandt, 1992; *N. camayae* Menzies, 1962; *N. caspius* G. O. Sars, 1897b; *N. cristatus* Mezhov, 1986; *N. coalescus* (Menzies & George, 1972); *N. detrimentus* Menzies & George, 1972; *N. inermis* Hansen, 1916; *N. laevis* Menzies, 1962; *N. laticeps* Hansen, 1916; *N. menziesi* Mezhov, 1986; *N. meteori* (Brandt, 2002), comb. nov.; *N. minutus* Hansen, 1916; *N. muscarius* Menzies & George, 1972; *N. oblongus* G. O. Sars, 1870; *N. ovatus* Menzies & George, 1972; *N. perunis* Menzies & George, 1972; *N. plebejus* Hansen, 1916; *N. profundus* Svavarsson, 1982; *N. reticulatus* Hansen, 1916; *N. robustus* Birstein, 1963; *N. simplex* Hansen, 1916; *N. spinicornis* Hansen, 1916; *N. teres* Siebenaller & Hessler, 1981.

Diagnosis **(modified from Siebenaller & Hessler 1981:241).** Pereonal tergites projecting laterally from pereopodal coxae; pereonites 6–7 dorsal articulation absent medially. Pleon distinctly shorter than pereonites 5–7. Antennula with 5 segments, distal article bulbous, article 4 distal margin with ventromedial often angular projection. Mandible with palp. Pereopods I–II equally robust. Uropods biramous.

Remarks. Siebenaller & Hessler (1981: 241) noted that further division of *Nannoniscus* was possible, and described several substantially different species that were retained in the genus under their concept. The pleotelson varies considerably within *Nannoniscus*, with species having posterolateral or posterior spines or substantially different widths to length ratios. The presence and position of ventral spines is also variable amongst the described species in the genus. All species, however, are broad bodied with distinct tergal plates extending over and laterally from the ventrally placed coxae. As discussed below, *N. intermedius* Siebenaller & Hessler, 1981 is transferred to *Nannonisconus* owing to its distinctly enlarged pleotelson, compared to all other species in the genus. *Hebefustis* Siebenaller & Hessler, 1977 is similar to some species of *Nannoniscus*, given the latter's variability in such features as ventral spination and posterolateral spines on the pleotelson. This variability leaves the absence of antennal article 4 projection as the only definitive character of *Hebefustis*. Siebenaller & Hessler (1981: 241) left this character out of the diagnosis of *Nannoniscus*.

A possibly new species was found among the published descriptions of species of *Nannoniscus*. Brandt (1992) did not provide evidence that specimens found in the eastern Weddell Sea were conspecific with *N. bidens* Vanhöffen, 1914 from Gauss-Station. Brandt's "redescription" is in fact a new record because Vanhöffen's type material was not newly described or illustrated. Brandt (1992: 147) mentions Vanhöffen's illustrations but does not discuss the appearance of his specimens, and states that specimens from the Weddell Sea were used for "redescription" (p.141). A comparison of Brandt's illustrations with those of Vanhöffen suggests that the two species are not conspecific. In particular, the antennular articles and the head shape differ substantially between the two descriptions. Because other asellote taxa in Antarctic oceans have proven to be narrow range endemics (e.g., Paramunnidae; Just & Wilson 2004), this identification should be tested by a study of Vanhöffen's 3 specimens. In the meantime, this record of *N. bidens*, and perhaps that of Amar & Roman (1974) should be considered as possibly new species.

Nannoniscus oblongus Sars, 1870

(Figs 2–6)

Nannoniscus oblongus Sars, 1870: 164; Sars, 1897a: 119, pl. 50 (partim); Hansen, 1916: 92–94, pl. VIII, fig. 4a–4f; Gurjanova, 1932: 53, table XVIII, 68; Wolff, 1962: 262.
Not *Nannoniscus oblongus*: Menzies, 1962: 136–137.

Material examined. Zoological Museum of Oslo "Ex Coll. G.O. Sars, *Nannoniscus oblongus* G.O. Sars", no indication of locality or collection date: ZMO #10107, intact female on slide, Fig. 4A–D; ZMO #10108, dissected parts on slide, Figs 4E, 5A–E. Hjeltefjord, coll. by R.R. Hessler, J.-O. Strömberg, near 60°40'N 4°54'E (position from gazetteer): 4. vii. 1978, Rothlisberg-Pearcy sled, 260 m, 3 females, 1 female (Fig. 6; AM P.74561), 1 male (Figs 2–3, AM P.74562); 7–8. vii. 1978, Beyer 1-net sled, 260 m, 1 female.

Remarks on material examined. Sars (1870; 1897a) did not establish types for his species, but Museum material exists that might have been used for his descriptions. Two female specimens were borrowed from the Zoological Museum of Oslo and are re-illustrated here. Although these specimens are listed as "Ex G.O. Sars collection", whether or not they were used in his description is uncertain. The ZMO specimens illustrated here (Figs 4–5) do not precisely match those of Sars (1897a: pl. 50, upper female), and they lack locality data. Consequently, no lectotype designation can be made using these specimens. Without any certainty that the "Sars collection" specimens are from the type locality, naming a neotype is also unwarranted.

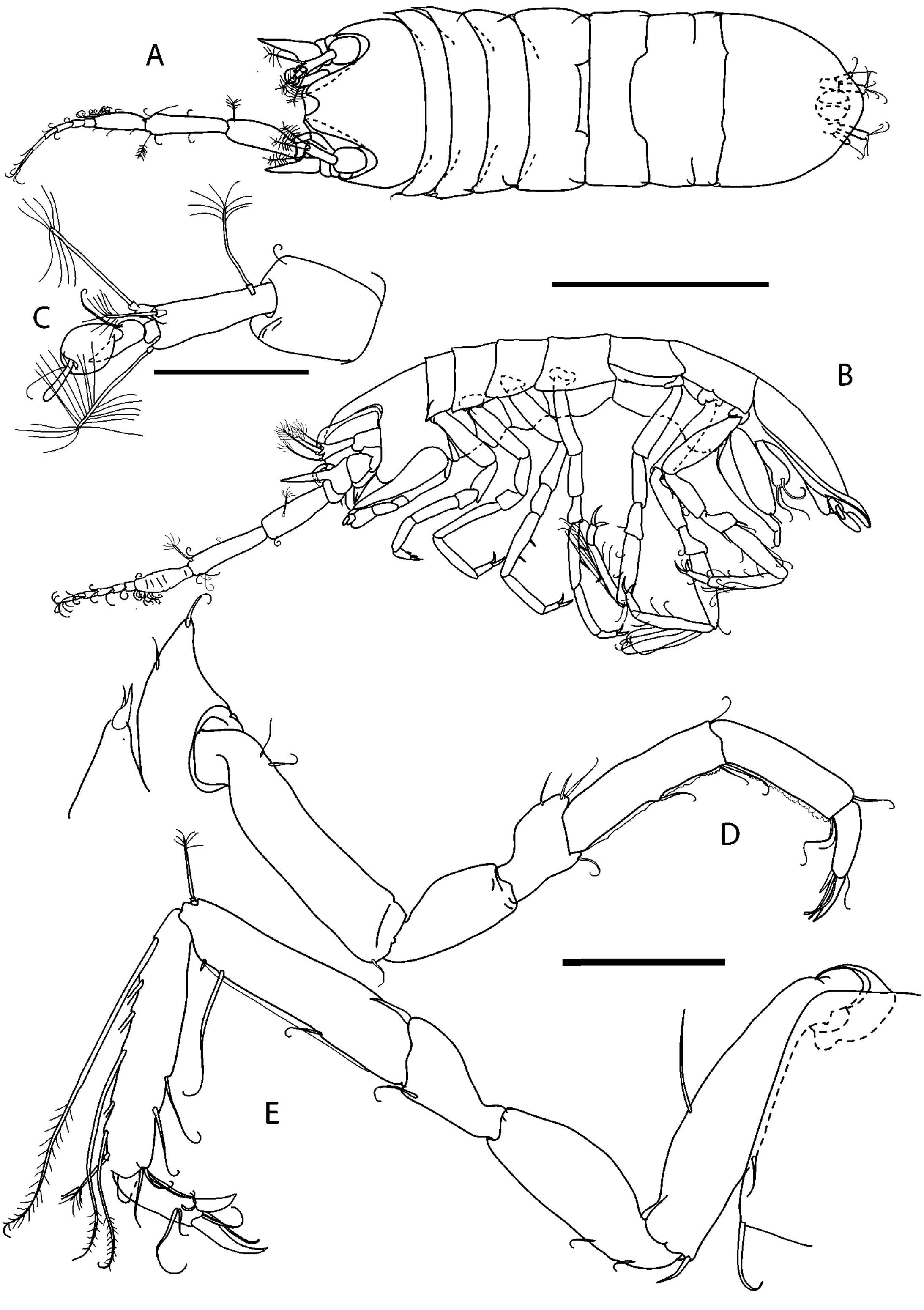

FIGURE 2. *Nannoniscus oblongus* Sars, 1870 (Hjeltefjord Norway, AM P.74562), adult male, all parts drawn in situ. A–B, body, dorsal and lateral view. C, left antennula, dorsal view. D, right pereopod I. E, right pereopod VII. Scale bars: A–B, 0.5 mm, C–E, 0.1 mm.

Diagnosis. Body broadly oval in dorsal view. Head lateral margins broadly curved and narrowing anteriorly, without projecting anterior spines. Pereonites 1–4 anterolateral angles with small setae, 2 with largest seta; 1 distinctly shorter that other pereonites, 1–4 increasing in length posteriorly; 4 lateral margin broadly convex, widest anteriorly; 5 lateral margin medially linear, not strongly angled to midline; 7 lateral margin distinctly shorter than 5–6 lateral margins; 6–7 ventral midline with rounded lobes in lateral view, posterior lobe largest. Pleotelson broader than head width; posteriorly rounded, without posterolateral spines, without indentation above uropods. Antennula article 2 distal margin with 3 blunt projections bearing penicillate setae. Antenna article 3 scale without basal articulation, spine-like, elongate, extending beyond distal margin of article 4; flagellum with 10 articles in female, 8 in male. Pereopods II–VII ventral dactylar ("accessory") claw robust, basally as wide as dorsal claw. Pleopod I of male lateral margin nearly straight, narrowing posteriorly; distal tip lateral lobes projecting beyond margin, angular, with narrower proximal neck, medial lobes broadly rounded, distally curving ventrally, margin with elongate fine setae increasing in length medially. Pleopod II of male endopod distal article length 0.85 protopod length. Pleopod II of female broadly rounded posteriorly, midline with posteroventrally-directed curved spine; midline posterior to spine concave in lateral view. Uropods inserting on ridge anterior to anus, adjacent to but not covering anus; exopod distinctly longer than protopod.

Remarks. The type species of *Nannoniscus* Sars, 1870, *N. oblongus* is distinctive in that it has a large anterolaterally directed spine on antennal article 3 in the position of antennal scale (Figs 2A–B, 4A). This spine is mentioned in Sars's (1870: 164) description. *Nannoniscus oblongus* is most similar to *N. caspius* Sars, 1897b; these two species share a broad body, the antennular article 3 spine and strong ventral claws on the pereopodal dactyli. *N. caspius*, however, has an angular tip to the pleotelson, a posteriorly curved ventral spine on pereonite 7 and a broader body than *N. oblongus*.

The concept of *N. oblongus* was confounded in Sars (1897a), in which a female of another species was shown as a male. Hansen (1916) corrected this by transferring Sars's "male" to *Nannoniscus crassipes*, which was subsequently assigned to *Rapaniscus* Siebenaller & Hessler (1981). Collections made in Hjeltefjord (Norway) by R.R. Hessler & J.-O. Strömberg included a fully mature male of *N. oblongus* that shows the essential features of a male *Nannoniscus* (Figs 2, 3).

Hansen (1916, pl. VIII, 4a–f) illustrated specimens from *Ingolf* samples, which agree with specimens illustrated here. The taxon *N. oblongus* appears to be widespread in the North Atlantic and Arctic Basins, ranging from coastal fjords of Norway and Spitzbergen to the Arctic Ocean and Iceland (Wolff 1962; Svavarsson et al, 1997). Subtle differences between the male illustrated here and those of Hansen (1916), e.g., tip of the pleopod I and shape of the pleotelson, may signal the presence of a species complex, of which *N. caspius* would be a member. Menzies (1962a: fig. 31I–K) records a female specimen from off Argentina, (LGO Biotrawl 212, 44°53.3'S, 51°26.5'W, 5843 m) but only copied Hansen's (1916) figures and didn't illustrate his specimen. Notably, Menzies (1962: 136) does not mention the distinctive antennal spine in his species diagnosis. This specimen from the South Atlantic is almost certainly not *N. oblongus*, although it should be checked.

The diagnosis above is based on the study of the Sars collection specimens (two females and the Hjeltefjord specimens). Given the detailed similarity between the females from the Sars collection and those from Hjeltefjord (Figs. 4, 6), I am confident that they all at least represent the same general taxon, *N. oblongus*. The diagnosis includes characters that were found to vary in *Nannoniscus* species. The male pleopods are illustrated only irregularly in the literature, but they almost certainly provide rich detail for distinguishing species. The male pleopod I presents two different lateral outlines in ventral view (Fig. 3A–B). When the pleopod is *in situ*, the medial margin of the second pleopod overlaps a thin lateral border of the first pleopod, so that the latter is convex-sided. The pleopod II of the mature male (Fig. 3C–D) has an elongate stylet so that the entire article is 85% the length of the protopod. Other species can be seen to have distinctly longer or shorter stylets, and the distal lateral and medial lobes of pleopod I vary considerably. As in the Desmosomatidae, nannoniscids vary in the setation and relative size of the pereopods, even within the genus *Nannoniscus* as currently defined. For example, some species, *N. oblongus* included, have a plesiomorphic form of the pereopod II–VII dactylar claws wherein the ventral claw is more robust although shorter than the dorsal claw. Deep-sea species, such as *N. meteori*, show a ventral claw reduced to practically a thin seta in species like *N. cristatus* Mezhov, 1986 or *N. inermis* Hansen, 1916, or a thin flat triangular plate (Fig.7B arrow) as in *Rapaniscus dew-*

dneyi Siebenaller & Hessler, 1981. The full range of variation is unknown so to define homologous states probably requires a synoptic survey of all species. Body shape and ventral spination also need to be thoroughly studied across *Nannoniscus* species to fully appreciate the phylogenetic patterns represented in this genus.

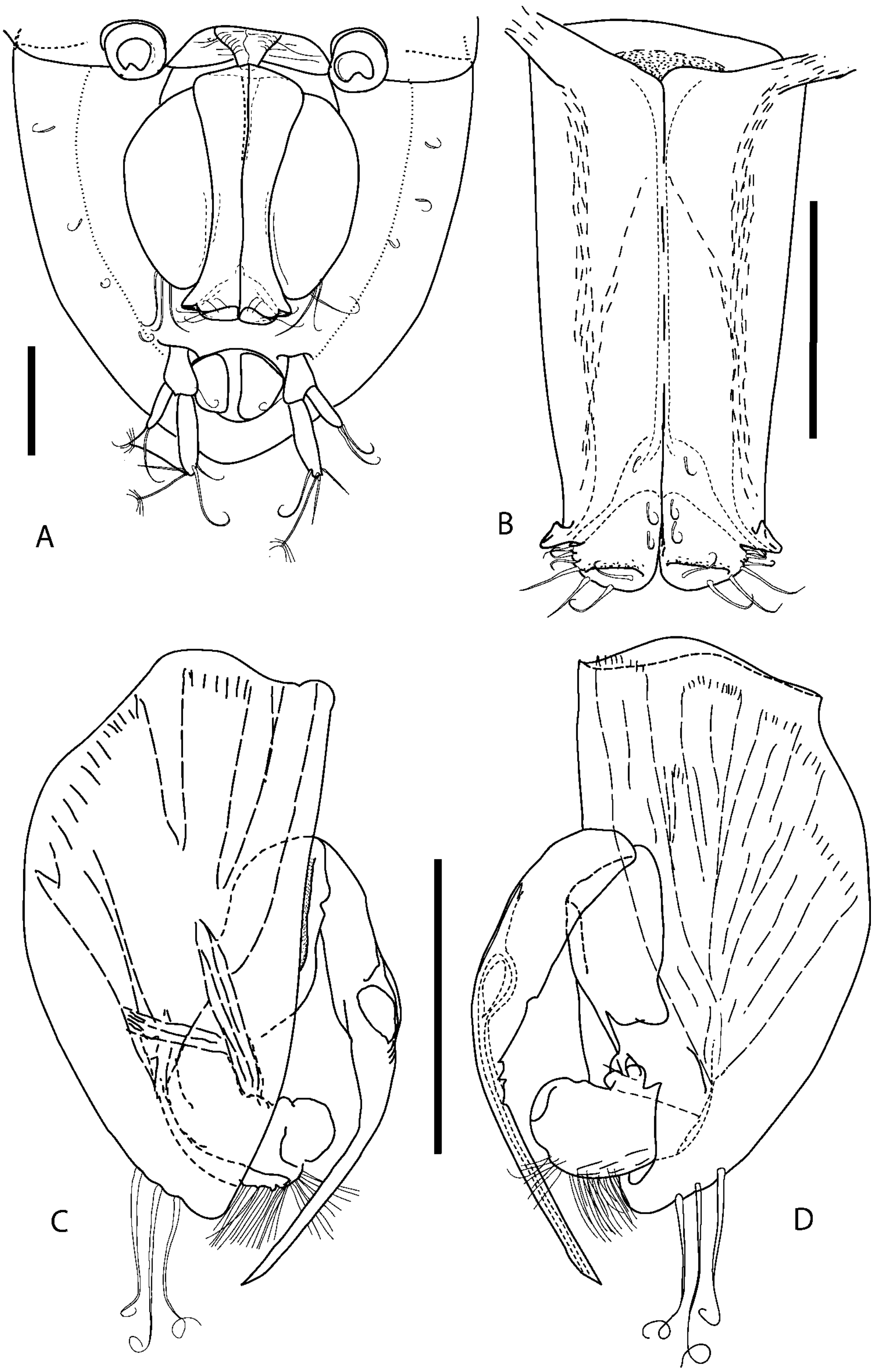

FIGURE 3. *Nannoniscus oblongus* Sars, 1870 (Hjeltefjord Norway, AM P.74562), adult male. A, pereonite 7 and pleotelson, ventral view. B, pleopod I, ventral view; dotted lines indicate medial sperm tube. C–D, pleopod II, ventral and dorsal views respectively; dotted lines in endopodal stylet indicate sperm tube. Scale bar 0.1 mm.

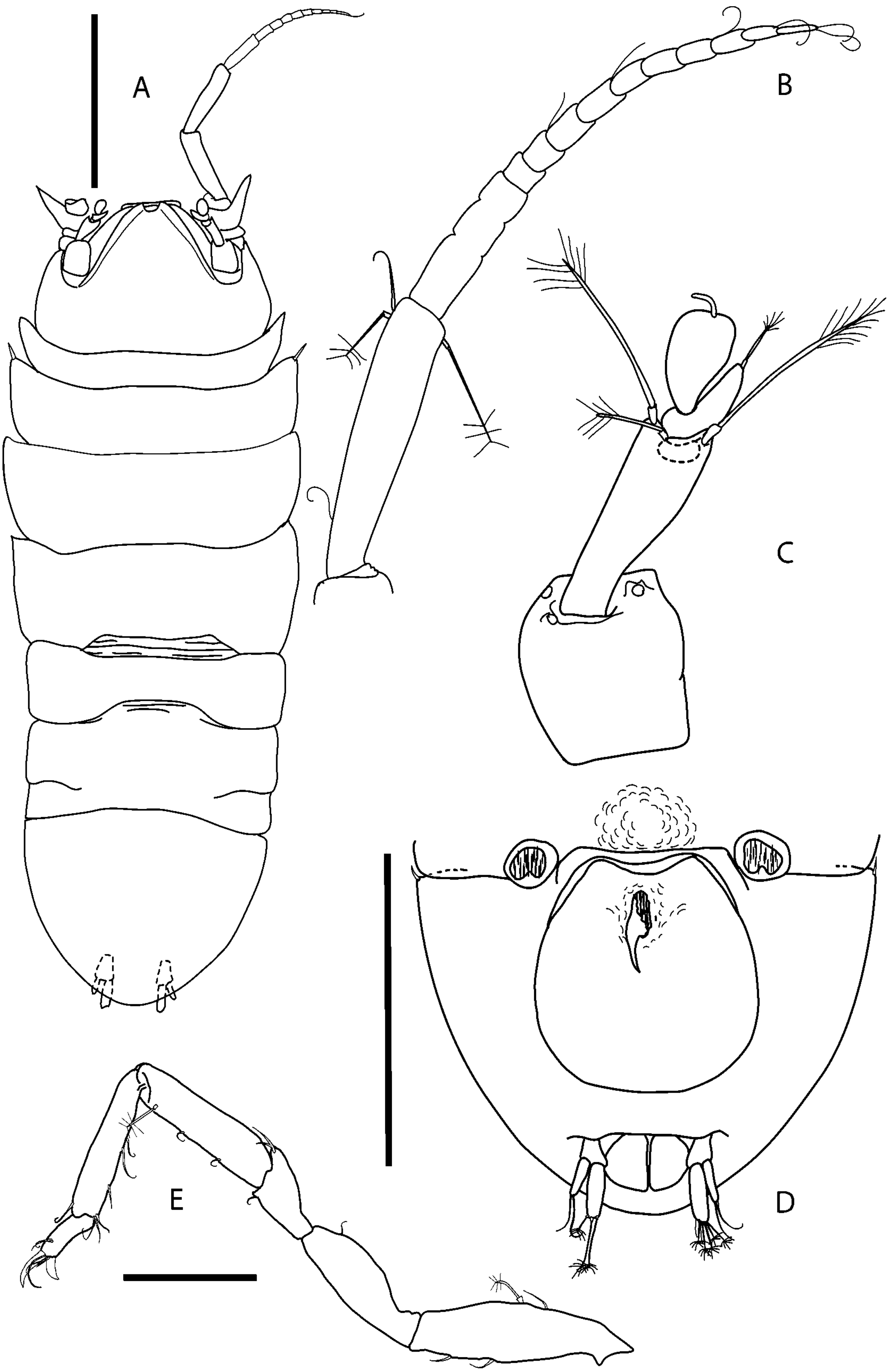

FIGURE 4. *Nannoniscus oblongus* Sars, 1870 (slides ex Sars Collection, Zoological Museum of Oslo). A–D, female, ZMO F10107. A, dorsal view. B–C, antenna and antennula, dorsal view. D, pereonite 7 and pleotelson, ventral view. E, pereopod, ZMO F10108. Scale bars: A, D, 0.5 mm; E, 0.1 mm.

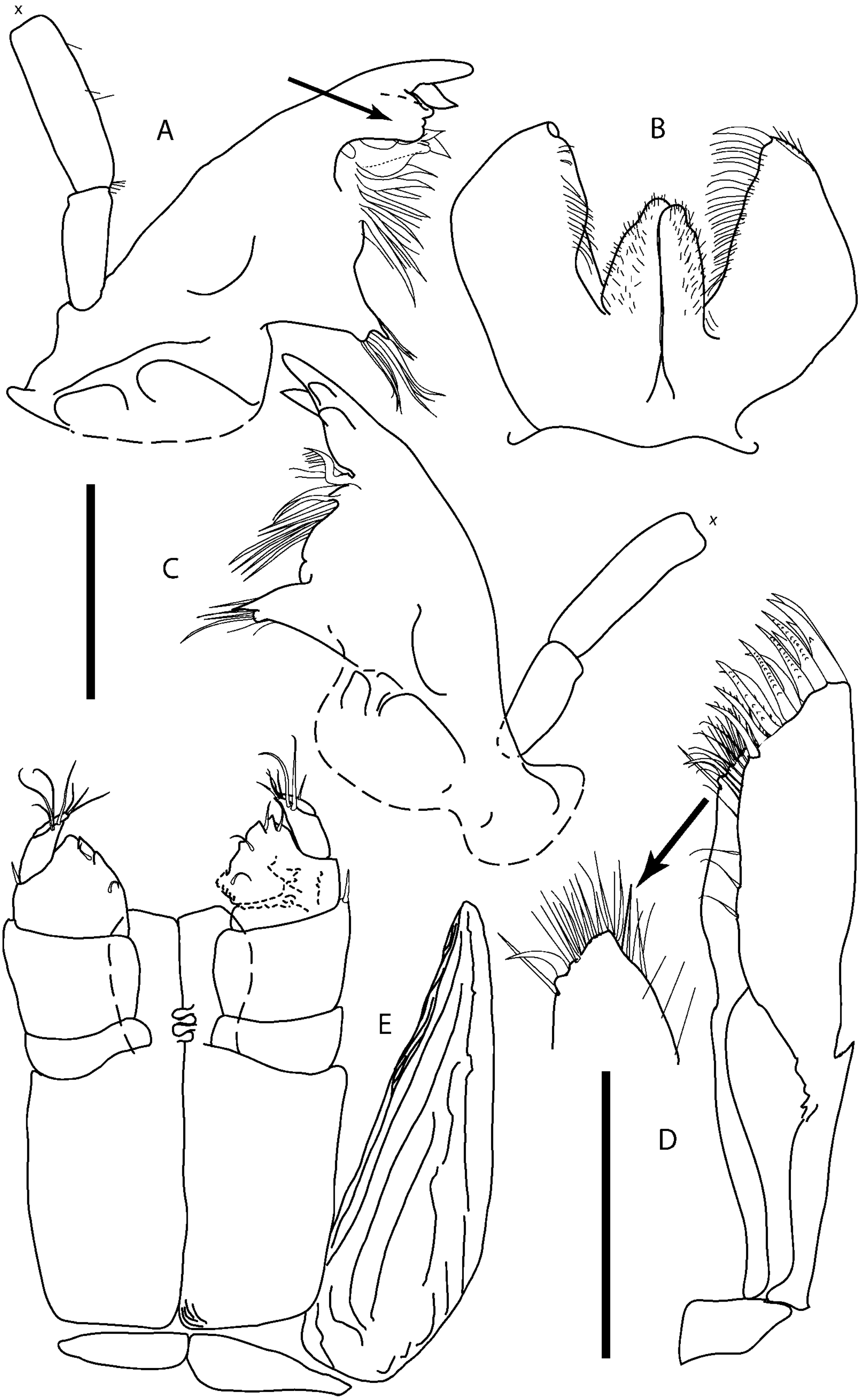

FIGURE 5. *Nannoniscus oblongus* Sars, 1870 (slide ex Sars Collection, Zoological Museum of Oslo). A–D, mouthparts from ZMO F10108. A, left mandible, dorsal view, arrow indicates dorsal tooth of incisor process. B, paragnaths, ventral view. C, right mandible, dorsal view. D, maxillula, ventral view. E, maxilliped, ventral view. Scale bars 0.1 mm (upper for A–C, lower for D–E).

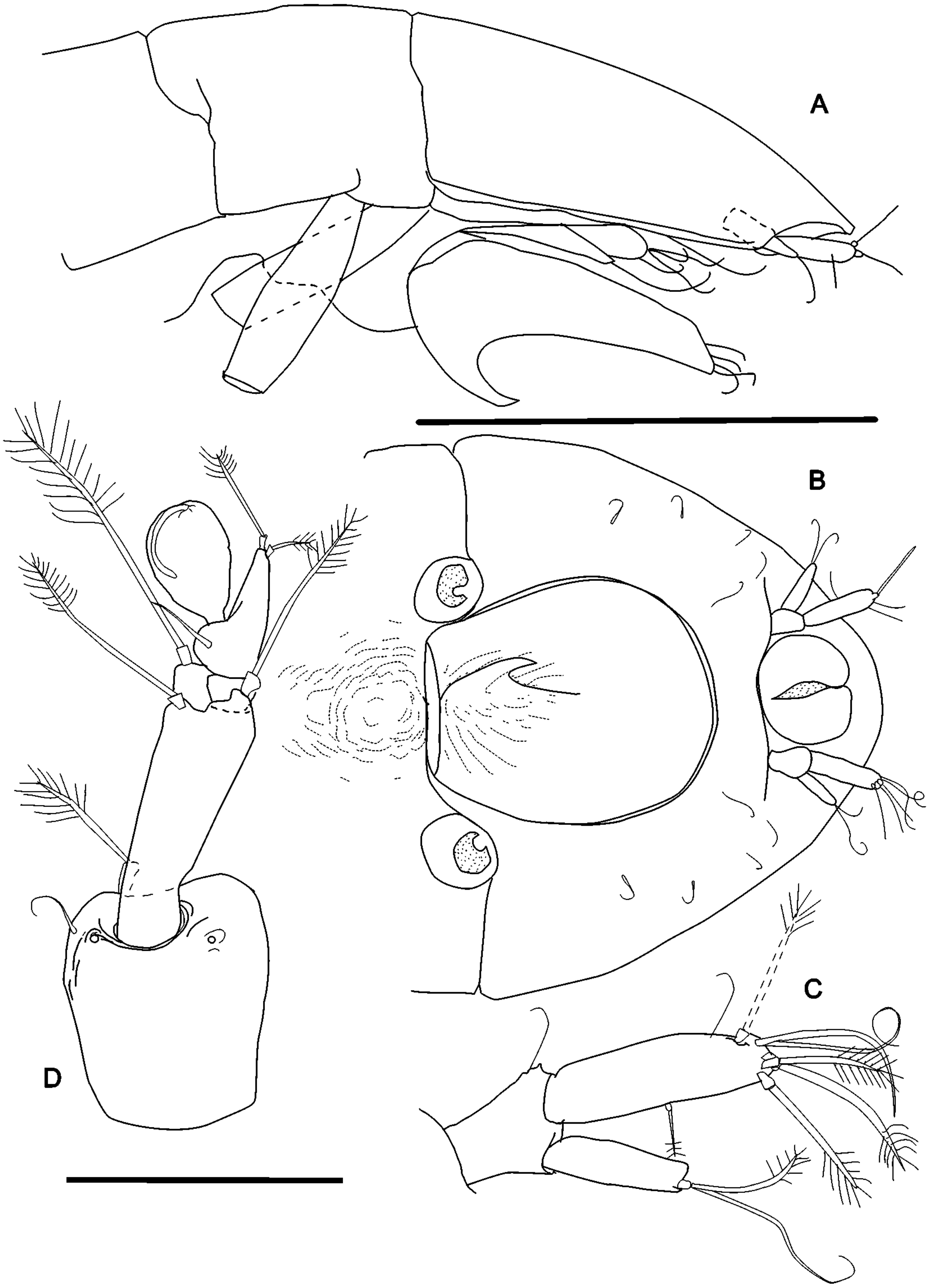

FIGURE 6. *Nannoniscus oblongus* Sars, 1870 (Hjeltefjord Norway, AM P.74561), adult female. A–B, pereonite 7 and pleotelson, lateral and ventral views respectively. C, right uropod, enlargement. D, left antennula, dorsal view. Scale bars: A, B, 0.5mm, C–D, 0.1 mm.

Nannonisconus Schultz, 1966

Nannonisconus Schultz, 1966: 24. Siebenaller & Hessler, 1977: 22; 1981: 249; Wilson, 1997: 102; Kussakin, 1999: 65.
Type species. *Nannonisconus latipleonus* Schultz, 1966.

Composition. *N. carinatus* Mezhov, 1986; *N. intermedius* (Siebenaller & Hessler, 1981), **comb. nov**.; *N. latipleonus* Schultz, 1966.

Diagnosis. Body with concave lateral outline in dorsal view. Pereonal tergites projecting laterally from pereopodal coxae; pereonite 6–7 and pleon articulations absent medially. Pleon broad and elongate, wider than head or pereon, distinctly longer than pereonites 5–7, posterolateral spines angled medially, posterior margin blunt, not projecting. Antennula extending beyond margin of head, with 5 segments, distal article bulbous, article 4 distal margin with ventromedial projection. Opercular pleopods elongate and broad, covering pleon ventral surface.

Remarks. The variability of the posterior body somite articulation, a central theme of this paper, necessitates a reconsideration of the genus *Nannonisconus* Schultz, 1966. A survey of the published descriptions of *Nannoniscus* and specimens in the Australian Museum's collection (Table 1) showed several species with an absent ventral articulation between the pleon and pereonite 7, as mentioned above. *N. oblongus*, however, does have a suture between the pleon and pereonite 7 (Figs 2A, 4A, 6A–B), suggesting that the absent pleonal suture on the dorsal surface in *Nannonisconus*, previously the only definitive character of this genus, is only an endpoint in a continuum. My inspection of *N. intermedius* Siebenaller & Hessler, 1981 (nontype specimens from the type locality WHOI 297; AM P.74558) showed that, although the suture is present dorsally between the pleon and pereonite 7, it is only a groove in the surface, which appeared to be absent in some specimens. *Nannonisconus*, however, does define a distinctive clade within the Nannoniscidae. Although the absence of pleonal articulation is a weak character, the genus can still be recognised by its unique pleotelson shape (Siebenaller & Hessler 1981: 242). Consequently, the species *N. intermedius* is moved to *Nannonisconus* and the generic diagnosis modified to reflect these changes. The genus may also be characterised by pleopods I–II covering entire ventral surface of pleotelson, although this feature is only incompletely known in some species. Additionally, the terminal article 5 of the antennula appears to have two segments but without an interannular margin (e.g., Wilson, 1997: fig. 1.42; Mezhov, 1986: fig.36), which may be significant once the full detail on this structure is known.

Rapaniscus Siebenaller & Hessler, 1981

Rapaniscus Siebenaller & Hessler, 1981: 234; Kussakin, 1999: 117.
Type species. *Rapaniscus dewdneyi* Siebenaller & Hessler, 1981.

Composition. *R. crassipes* (Hansen, 1916) [not "*R. crassipes* Siebenaller & Hessler, 1981" as written by Brandt, 2002: 88], *R. dewdneyi* Siebenaller & Hessler, 1981, *R. multisetosus* Brandt, 2002.

Diagnosis. Pereonal tergites projecting laterally from pereopodal coxae; pereonites 6–7 dorsal articulation absent medially. Pleon shorter than pereonites 5–7. Antennula with 5 articles, article 4 distal margin with ventromedial shelf-like process, article 5 bulbous. Mandible with palp. Pereopod I robust, podomeres distinctly broader than pereopod II; carpus with 2 or more robust sensillate setae on ventral margin; propodus with robust sensillate setae on ventral margin. Pereopods II–VII slender, distinctly narrower than pereopod I. Ventromedial posteriorly curved spines on pleopod II of female or on pereonite 7 sternite.

Rapaniscus dewdneyi Siebenaller & Hessler, 1981
(Fig. 7)

Rapaniscus dewdneyi Siebenaller & Hessler, 1981: 234; Kussakin, 1999: 117.

Remarks. This species does not require a new diagnosis, but was found to lack a critical piece of evidence

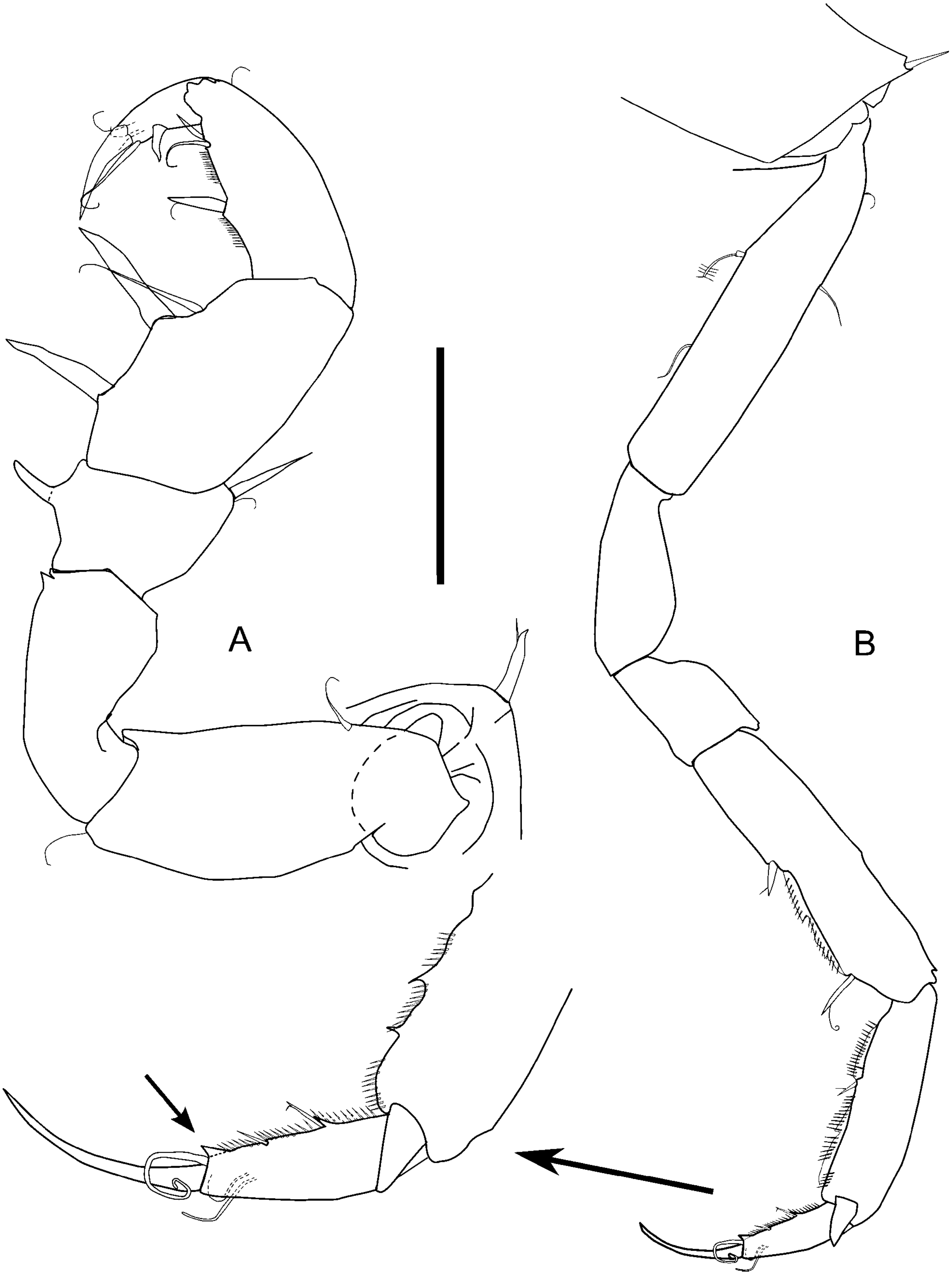

FIGURE 7. *Rapaniscus dewdneyi* Siebenaller and Hessler, 1981, Male, AM P.74555, WHOI 209 (type locality). A, left, pereopod I. B, right pereopod II, arrow indicates small triangular plate. Scales bar, 0.1 mm.

relating to the definition of the genus. While reviewing specimens described by Siebenaller and Hessler (1981; Table 1), the original publication of the type species, *Rapaniscus dewdneyi* was found to lack illustrations of pereopod I. Non-type specimens from the type locality (WHOI 209; AM P.74555–P.74557) were illustrated to correct this oversight. Pereopod I of both sexes are nearly identical (Fig. 7, male shown), perhaps with the male being slightly more robust; these limbs are also similar to *R. crassipes*. The second pereopod of *R. dewdneyi* (Fig. 7B) is much less robust than the first. *R. multisetosus* shows more robust setae on the first two pereopods than either *R. dewdneyi* or *R. crassipes*.

Pereopod I of *R. dewdneyi* in both sexes had a blunt curved spine on the merus that has not been previously reported in nannoniscids. This spine was extremely fragile and broke at the base with even the slightest touch. The spine was discovered when observing specimens at high power in the dissection microscope. Mounting the specimen for illustration caused the spine to break in several cases. This feature may be missing from many species descriptions where it was present, owing to its fragility.

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