



## Description of a new species of *Nannopus* Brady, 1880 (Copepoda: Harpacticoida: Nannopodidae) from Argentinean waters, including an updated key to species

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### Abstract

Both sexes of a new brackish-water species, *Nannopus sinusalbi* **sp. nov.** (Nannopodidae) are described from the Bahía Blanca estuary (38°53'S, 62°07'W) in Buenos Aires Province, Argentina. The only previous record of the genus in the study area was identified as the type species, *Nannopus palustris* Brady, 1880, with no description or illustrations, hence its authenticity cannot be confirmed. *Nannopus brasiliensis* Jakobi, 1956 is relegated to *species inquirenda* in the genus rather than being considered a junior synonym of the type species. Nomenclatural issues related to the usage of the alternative spellings *Iliophilus* Lilljeborg, 1902 and *Ilyophilus* sensu Sars (1909) and the unavailability of *Ilyophilus canui* Kim, Choi & Yoon, 2017 are discussed. An updated key to the 18 identifiable species of *Nannopus* (excluding the type species *N. palustris*) is presented. The harpacticoid assemblage at the type locality showed a distinct seasonality with *N. sinusalbi* **sp. nov.** representing about 8% of the community. The new species showed densities below 5 ind.cm<sup>-2</sup> during most of the year, reaching an abrupt peak of 40.17 ind.cm<sup>-2</sup> towards the end of the summer, when the maximum proportion of ovigerous females was recorded.

**Key words:** Argentina, Nannopodidae, meiofauna, taxonomy, *Nannopus canui* **sp. nov.**

### Introduction

Like many other estuaries, the Bahía Blanca estuary accommodates a benthic community with a high taxonomic diversity. However, the taxonomic literature on marine harpacticoid copepods from this region is remarkably scarce (Sciberras *et al.* 2014, 2017) and it is conceivable that several new species await discovery. During an ecological survey of the meiobenthos in the Bahía Blanca estuary, an as yet undescribed species of the cosmopolitan genus *Nannopus* Brady, 1880 (Nannopodidae) was discovered.

The genus *Nannopus* was established to accommodate the new species *N. palustris* Brady, 1880 collected from brackish water pools in a salt marsh at Seaton Sluice, Northumberland, England. Brady's (1880) text description and illustrations were based on only one or possibly two specimens but proved inadequate for identification purposes, causing considerable taxonomic confusion in post-1880 systematic accounts of the genus *Nannopus* (Fiers & Kotwicki 2013; Kim *et al.* 2017). Despite showing major differences with the original description, the specimens described and identified as *N. palustris* by Canu (1892) and Scott (1902) have generally been accepted as appropriate standards for comparison (Wells 1971; Fiers & Kotwicki 2013; Kim *et al.* 2017). Unfortunately the discrepancies with Brady's (1880) description created the false impression that *N. palustris* was a highly variable cosmopolitan species (Fiers & Kotwicki 2013), despite its limited dispersal ability due to the lack of long-standing pelagic forms (Giere 2009; Garlitska *et al.* 2012). *Nannopus palustris* has been recorded in different habitats, from marine to estuarine and freshwater habitats, and from several locations around the world (Fiers & Kotwicki 2013), including the Bahía Blanca estuary (Hoffmeyer 2004; Diodato *et al.* 2006; Dutto *et al.* 2012). Unfortunately, the Argentin-

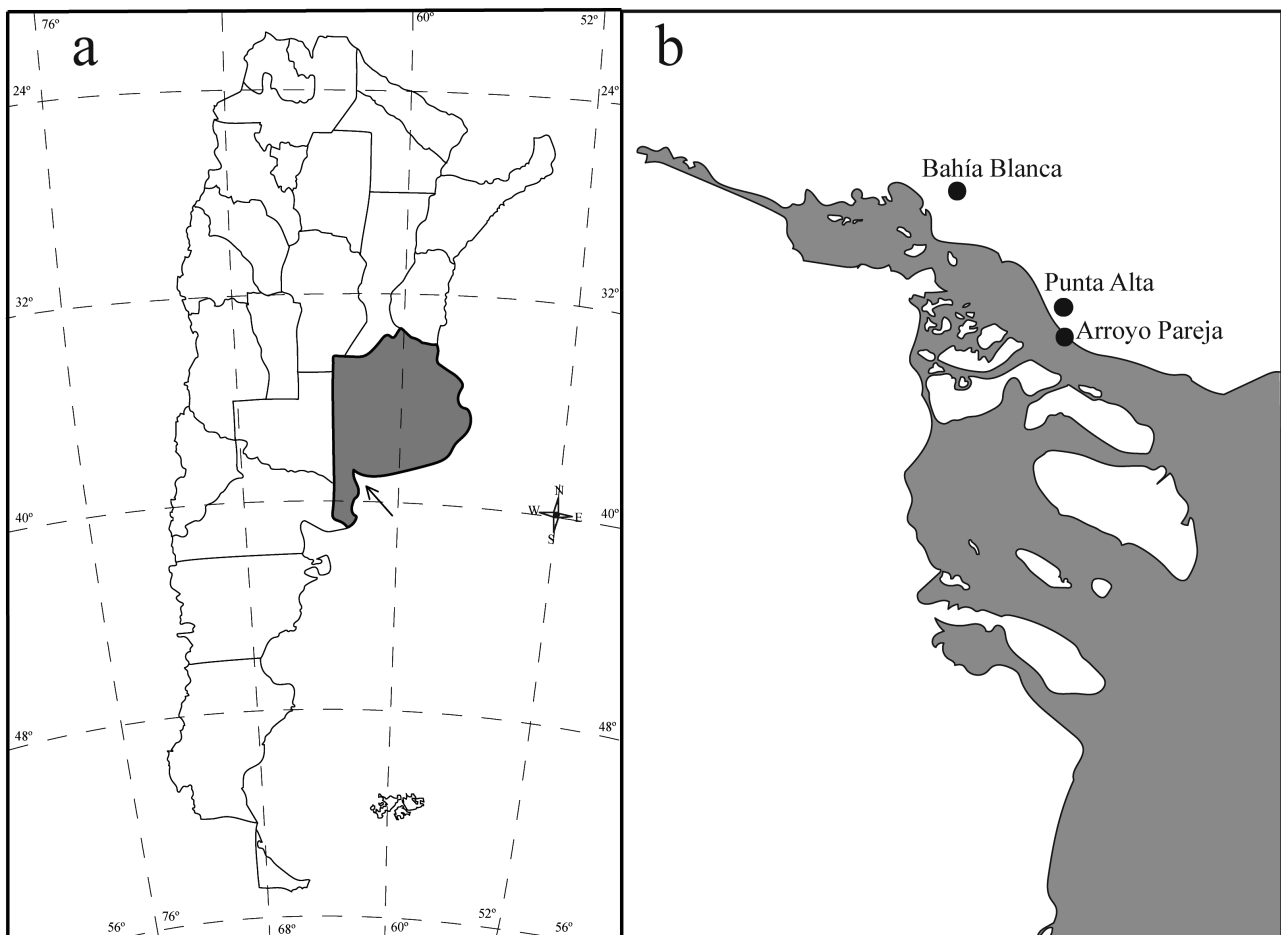
ean records were not accompanied by descriptions or illustrations and, considering that recent morphological and molecular studies have revealed that some previous reports of *N. palustris* were based on several pseudo-sibling species (Staton *et al.* 2005; Garlitska *et al.* 2012; Fiers & Kotwicki 2013), they should therefore be treated with caution. Brady (1880) proposed the subfamily Nannopinae [for the correct spelling of this name and its priority over Huntemanniidae Por, 1986 see Huys (2009: 30)] within the family Harpacticidae for *Nannopus* (type genus) and *Platychelipus* Brady, 1880 (now placed in the Laophontidae; *cf.* Sars 1908: 274). Lilljeborg (1902: 61) added the new genus *Iliophilus* Lilljeborg, 1902 for its type and only species *I. flexibilis*. Sars (1909a: 47) added a second species, *I. perplexus*, described from Lake Tanganyika, maintaining both *Nannopus* and *Iliophilus* (misspelled as *Ilyophilus*) as valid genera in the Cletodidae. In a subsequent paper Sars (1909b: 307) remarked that since *I. flexibilis* is identical to *Nannopus palustris* the generic name *Iliophilus* is to be considered a junior subjective synonym of *Nannopus*. Recently, Kim *et al.* (2017) suggested that the presence of a one-segmented endopod on the third swimming leg is a generic character of *Nannopus*, while a two-segmented endopod on the third swimming leg is diagnostic for *Iliophilus*. Based on this discrepancy in endopodal segmentation, Kim *et al.* (2017) reinstated *Iliophilus* as a valid genus and transferred to it several valid species from the genus *Nannopus*, leaving the latter to encompass only the type species, *N. palustris*, and *N. parvipilis* Kim, Choi & Yoon, 2017. However, according to the analysis of Vakati *et al.* (2019) which was based on four molecular markers, *N. parvipilis* is nested within the clade formed by *N. serratus* Vakati & Lee, 2017, *N. parvus* Vakati & Lee, 2017 and *N. bulbiseta* Vakati & Lee, 2017, all of which display a two-segmented endopod on the third swimming leg, casting doubt on the validity of the generic separation suggested by Kim *et al.* (2017). Although the latter morphology-based study has merit in recognizing the taxonomic problems within the group it has now become apparent that a consensus can only be reached by detailed re-examination of those species that had been incompletely described (*e.g.* *N. perplexus* (Sars, 1909a), *N. unisegmentatus* Shen & Tai, 1964), including the type species *N. palustris* (Vakati *et al.* 2019). Pending such a revision we concur with Vakati *et al.* (2019) and maintain *Nannopus* and *Iliophilus* as synonyms. At present, the genus *Nannopus* contains 18 valid species: *N. palustris*, *N. flexibilis* (Lilljeborg, 1902), *N. perplexus* (Sars, 1909a), *N. unisegmentatus* Shen & Tai, 1964, *N. didelphis* Fiers & Kotwicki, 2013, *N. hirsutus* Fiers & Kotwicki, 2013, *N. procerus* Fiers & Kotwicki, 2013, *N. scaldicola* Fiers & Kotwicki, 2013, *N. ganghwaensis* Vakati, Kihara & Lee, 2016, *N. camui* Kim, Choi & Yoo, 2017 (see below for the availability of this name), *N. parvipilis*, *N. bulbiseta*, *N. dimorphicus* Vakati & Lee, 2017, *N. minutus* Vakati & Lee, 2017, *N. parvus*, *N. serratus*, *N. cylindricus* Vakati & Lee, 2021 and *N. robustus* Vakati & Lee, 2021. In this paper, we describe both sexes of a new *Nannopus* species from the Bahía Blanca estuary in Argentina, provide some ecological data, collate armature formulae of all its congeners and present an updated key to the 18 identifiable species of the genus.

## Materials and methods

The study area is a recreational beach along the north coast of the Bahía Blanca estuary, one of the largest estuaries in Argentina. It extends over about 2,300 km<sup>2</sup> and comprises several tidal channels, extensive tidal flats (1,150 km<sup>2</sup>) with patches of low salt marshes, and islands (410 km<sup>2</sup>) (Piccolo *et al.* 2009). This shallow estuary (mean depth 10 m) is under anthropogenic impact due to human settlement, wastewater discharge, commercial harbour activities, and industries (Arias *et al.* 2010). Enrichment with inorganic nutrients and organic matter (Freije *et al.* 2008) and the hydrological dynamics bring on eutrophication and increase water turbidity (Piccolo & Perillo 1990; Piccolo *et al.* 2009).

The collecting locality is in the middle fringe of the mid-littoral beach at Arroyo Pareja (38°53'S, 62°07'W), three kilometres from Punta Alta city, in the southwestern part of Buenos Aires Province (Fig. 1a–b). The substrate is silt-clayey with average values of 87% mud and 13% sand, with no evidence of net sediment accumulation (Pratolongo *et al.* 2010). A mostly homogeneous landscape alternates with patches of the saltmarsh cordgrass *Spartina alterniflora* Loiseleur-Deslongchamps, 1807, which represents the dominant vegetation in the intertidal zone (Calvo-Marcilese & Pratolongo 2009). The macrobenthos is dominated by an association of *Laeonereis acuta* (Treadwell, 1923) (Annelida, Nereididae) and *Heleobia australis* (d'Orbigny, 1835) (Gastropoda, Cochliopidae) (Elías 1985; Elías & Bremec 1986). Five sediment samples were collected monthly during 2014 and 2015. Sediment was taken with 3 cm diameter plastic corers (7.07 cm<sup>2</sup>) during low tide, within patches dominated by *S. alterniflora*. The samples were fixed in 4% formalin. The specimens were separated by elutriation and sieved with 40, 225

and 500  $\mu\text{m}$  mesh size sieves (Giere 2009). Drawings of the habitus were prepared using the “sandwich mounting method” (Huys & Boxshall 1991). Specimens were dissected and mounted in glycerol. Preparations were sealed with transparent nail varnish. All drawings were prepared using a camera lucida mounted on an Olympus CH20 stereomicroscope. The descriptive terminology is adopted from Huys *et al.* (1996). Abbreviations used in the text are: *ae*, aesthetasc; *P1–P6*, first to sixth thoracopod; *exp*, exopod; *enp*, endopod; *exp (enp)-1 (2, 3)* to denote the proximal (middle, distal) segment of a ramus. The term ‘acrothek’ denotes the trifid setal structure typically found on the apical margin of the distal antennular segment (Huys & Iliffe 1998). Scale bars in the illustrations are in  $\mu\text{m}$ . The type series is deposited in the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN), Autonomous City of Buenos Aires, Argentina, and in the Museo de La Plata (MLP), La Plata, Argentina. Total number of adult specimens of all harpacticoid morphospecies were recorded, including the proportion of ovigerous females of *Nannopus sinusalbi* **sp. nov.** Water condition (temperature, salinity and pH), measured in the field with a Horiba multisensory U-10 Water Quality Checker, is shown in Table 1. Diversity of the harpacticoid assemblage was assessed by the Shannon-Wiener index using natural logarithms:  $H' = -\sum_{i=1}^s \left( \frac{n_i}{N} \ln \left( \frac{n_i}{N} \right) \right)$ , where *s* is the number of species in the sample, *n<sub>i</sub>* the number of specimens of species *i*, and *N* the total number of specimens in the sample. The effective number of species was defined as  $ENS = \exp(H')$ . Maximum diversity was calculated as  $H_{\text{max}} = \ln(sd)$ , where *sd* is the number of species recognized on each sampling date. Equitability was calculated as  $E = H'/H_{\text{max}}$ . All statistical analyses were made on whole sample counts, but density results are expressed in individuals per 10  $\text{cm}^2$ .



**FIGURE 1.** a, Map of Argentina with Buenos Aires Province in grey and sampling locality indicated by an arrow; b, Map of the Bahía Blanca estuary showing location of Arroyo Pareja (type locality); land area indicated in white.

**TABLE 1.** Water temperature, salinity and pH recorded at the study site (Arroyo Pareja, Argentina) during the various sampling periods.

	Water temperature (°C)	Salinity (%)	pH
April 2014	15.2	3.70	8.65
May 2014	15.4	3.56	7.00
June 2014	12.5	1.34	8.36
July 2014	9.8	2.80	7.48
August 2014	16.3	2.86	8.12
September 2014	17.6	3.15	8.52
October 2014	26.5	3.18	8.23
November 2014	19.8	3.35	7.69
December 2014	20.7	3.08	7.79
January 2015	26.0	3.60	7.55
February 2015	25.6	3.09	8.78
March 2015	26.6	3.43	8.40

## Results

### Order Harpacticoida Sars, 1903

#### Family Nannopodidae Brady, 1880

#### Genus *Nannopus* Brady, 1880

Type species: *Nannopus palustris* Brady, 1880 (by monotypy)

#### *Nannopus sinusalbi* sp. nov.

(Figs. 2–8)

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**Type locality.** Argentina, Buenos Aires Province; middle fringe of the mid littoral beach at Arroyo Pareja (38°53'S, 62°07'W); silt-clayey sediment with *Spartina alterniflora* (Fig. 1).

**Type material.** Holotype: adult ♀ dissected and mounted on four slides (MACN-In 42865), collected April 9, 2014. Paratypes deposited in MACN: three adult ♀♀ dissected, mounted on seven, four and five slides, respectively (MACN-In 42867), collected February 24, 2015; five ♀♀ preserved in ethanol (MACN-In 42868), collected March 19, 2015; one adult ♂ dissected and mounted on five slides (MACN-In 42866), collected February 24, 2015; two adult ♂♂ dissected and mounted on four slides each (MACN-In 42867), collected February 24, 2015; seven ♂♂ preserved in ethanol (MACN-In 42868), collected March 19, 2015. Paratypes deposited in MLP: five ♀♀ preserved in ethanol (MLP-Cr 27317), collected March 19, 2015; three ♂♂ preserved in ethanol (MLP-Cr 27318), collected February 24, 2015. All material was collected from the type locality by the senior author.

**Description of female (holotype).** Body length 562 µm. Habitus fusiform (Fig. 2a). Colour of preserved specimens pale yellowish to colourless. Rostrum prominent, fused to cephalothorax, recurved ventrally; anterior margin with long and slender setules and one pair of sensilla (Fig. 2b). Cephalothorax anteriorly attenuated in dorsal view, representing 28% of total body length; with one pair of dorsal pores; posterior margin serrate. Sensillar pattern on cephalothorax and body somites as illustrated (Figs. 2a, 3a–b). Posterodorsal margins of each somite serrate except for that of anal somite (Figs. 2a, 3a). Somite bearing P4 with one pair of dorsal pores (Fig. 2a). Genital and first abdominal somite fused forming genital double-somite; original segmentation marked by bilateral constriction and by transverse serrate ridge dorsally (Fig. 3a–b). Second abdominal somite with row of spinules on ventral posterior margin (Fig. 3b). Operculum well developed, with rows of setules (Fig. 3a). Anal somite cleft medially in ventral view; ventral posterior margin with row of spinules; dorsal surface with one pair of sensillae and three pairs of pores (Fig. 3a–b).

Caudal ramus (Fig. 3a–b) cylindrical and elongate, clearly separated from anal somite; with seven setae. Seta I naked, inserted closely to anterior margin of ramus. Seta II naked, as long as seta I; located dorsolaterally. Seta III bipinnate in distal half, inserted about halfway down outer margin. Seta IV naked, as long as ramus (in dorsal view); located at outer distal corner. Seta V strongest, bipinnate in middle section; slightly inflated proximally, with few spinules along outer margin; seven times as long as seta IV. Seta VI naked, as long as seta IV; located at inner distal corner. Dorsal seta VII bi-articulate at base; bipinnate; located close to inner margin. Ventral posterior margin of ramus with row of spinules; one pore on dorsal surface.

Antennule (Fig. 2c). Short, compact, 5-segmented. First and second segments strong and wide; first and third segments with row of spinules. Segment 2 with tri-articulate seta (marked by arrow). Segment 3 with aesthetasc (length 38  $\mu$ m) fused basally to short seta. Segment 5 with acrothek consisting of three setae, distinctly fused at base forming a minute pedestal. Armature as follows: 1-[1], 2-[4 + 5 bipinnate], 3-[5 + (1 + ae)], 4-[1], 5-[8 + acrothek].

Antenna (Fig. 2d). Relatively short, composed of allobasis, 1-segmented endopod and 1-segmented exopod; coxa not observed. Allobasis with row of setules and two pinnate setae on abexopodal margin. Endopod with transverse row of setules in proximal half; row of robust spinules near inner and outer corner; armed with five strong, naked spines and one naked setiform element. Exopod with four elements, one of them bipinnate.

Mandible (Fig. 4a). Gnathobase well developed; cutting edge provided with three rigid, multicuspidate teeth. Mandibular palp 1-segmented with rami completely incorporated into basis; outer margin with row of spinules; armed with four bipinnate setae, one of which (derived from the basis) originating from subcylindrical pedestal.

Maxillule (Fig. 4b). Praecoxal arthrite with two setae on anterior surface; distal margin with five stout spines and two slender elements. Coxal endite with two setae. Basis and rami fused; armed with five naked and two bipinnate setae (homology and origin of these elements unconfirmed).

Maxilla (Fig. 4c). Syncoxa bearing two endites, each with three elements, all of which confluent with segment. Allobasis with row of spinules, a strong claw with one long spinule along outer margin, and one accompanying seta. Endopod incorporated into basis, represented by two setae.

Maxilliped (Fig. 4d) subchelate, 3-segmented. Syncoxa shorter than basis with rows of spinules and one short seta (marked by arrow). Basis unarmed; with rows of spinules as illustrated. Endopod with strong, curved claw ornamented with spinules in distal half and two naked accessory setae.

Swimming legs (Figs. 5a–b, 6a–b) with 3-segmented exopods and 2- (P1–P3) or 1-segmented (P4) endopods; exopods longer than endopods. Coxae with a row of spinules on anterior surface and a row of strong spinules along outer margin (only illustrated for P2–P4; Figs. 5b, 6a–b). Bases with naked (P1–P2) or plumose (P3–P4) outer seta; with rows of spinules near insertion of exopod and endopod. First and second exopodal segments with anterior row of tiny spinules near inner distal corner; outer margins of exopodal and endopodal segments with spinular ornamentation, except for P4 endopod; inner margin of exp-2 with sparse setules; exp-3 with one anterior pore; inner seta of exp-2 plumose.

P1 (Fig. 5a) smaller than other legs. Basis with row of spinules near insertion of inner spine; inner basal spine naked. Outer exopodal spines of exp-1 and -2 naked; exp-3 with two outer spines, proximal one naked and distal one with few spinules, and two terminal elements, outer one bipinnate and inner one plumose. Enp-1 with anterior row of tiny spinules near inner distal corner; inner margin of enp-2 with few setules; outer element of enp-2 naked, terminal element bipinnate and inner seta short and plumose.

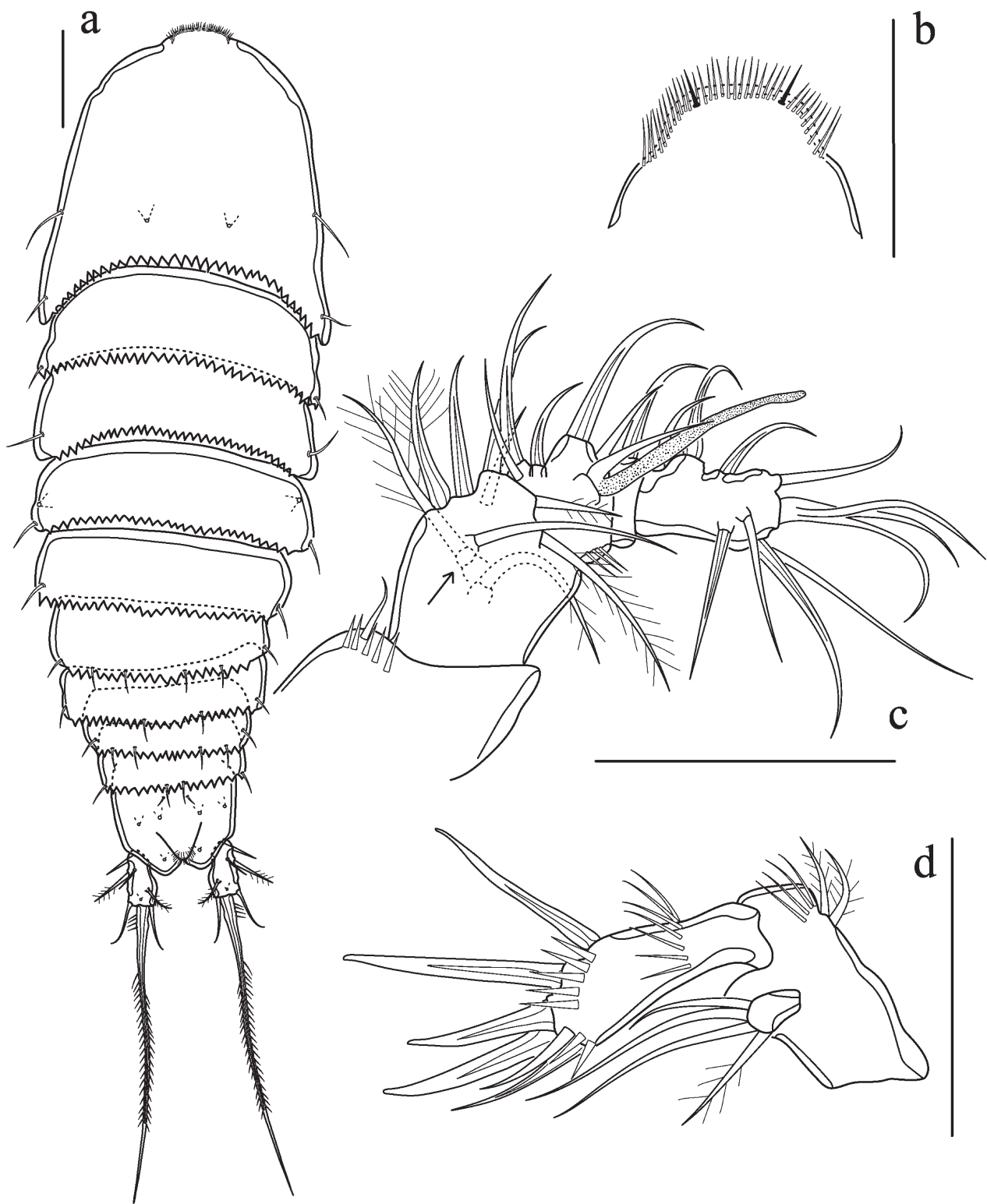
P2–P3 (Figs. 5b, 6a). Basis with a row of long setules along inner margin. Inner margins of all segments with setular row; outer exopodal spines of all segments naked, except for distal spine of exp-3 displaying few distal spinules. Outer terminal spine of exp-3 with outer spinules and inner setules; inner terminal element plumose; inner setae plumose. Inner margins of endopodal segments with setular row; outer element of enp-2 spiniform and naked, terminal and inner elements setiform and plumose.

P4 (Fig. 6b). Inner margins of exopodal segments with sparse setules. Outer spine of exp-1 with small apical setule; outer spine of exp-2 naked; outer spines of exp-3 naked, except for distal one having a few distal setules; outer terminal spine of exp-3 with outer spinules and inner setules; inner terminal element of exp-3 plumose; inner distal seta shortest and pectinate; inner proximal seta plumose. Endopod with long plumose apical seta and short, naked inner element.

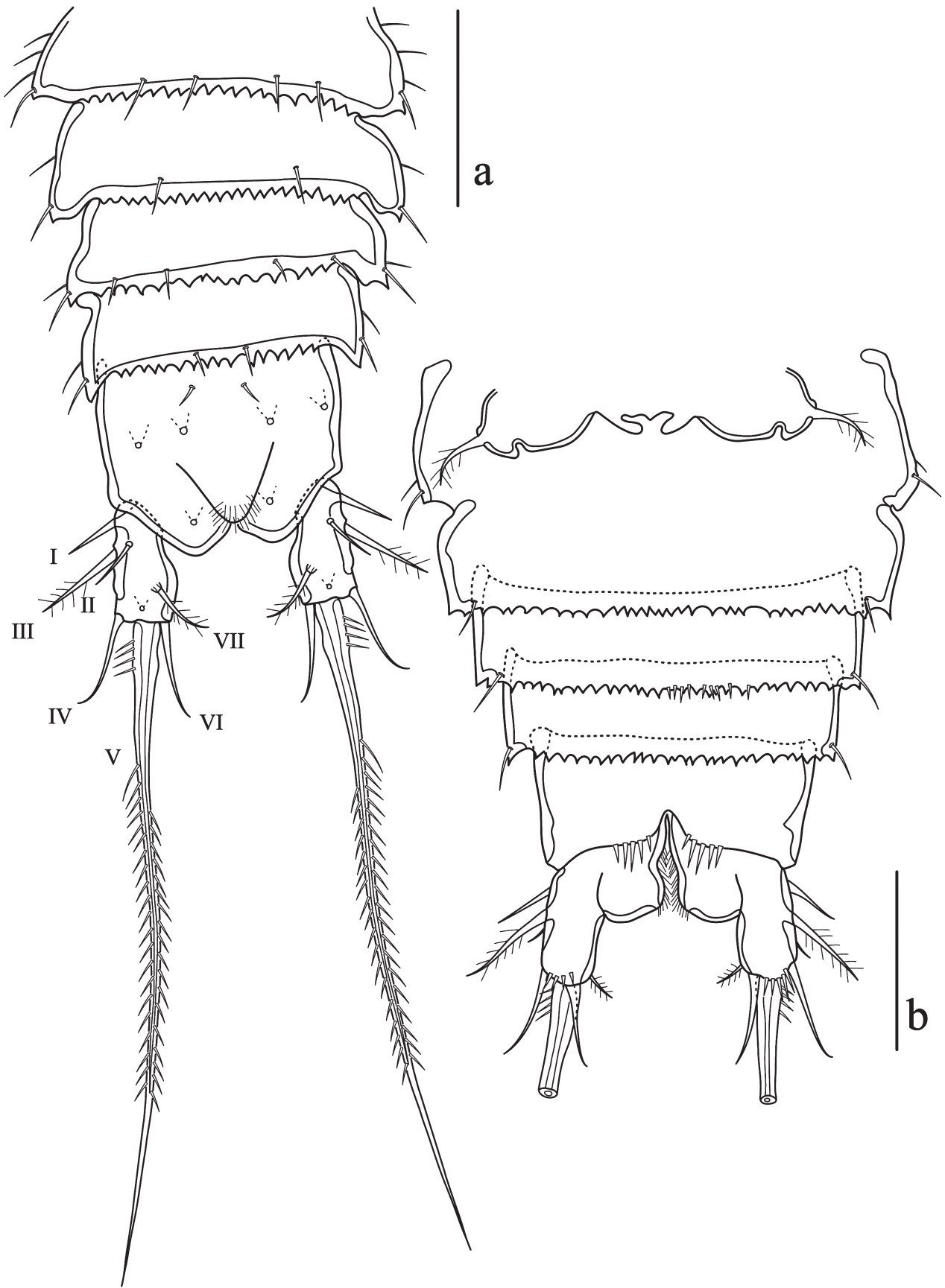
Armature formulae as follows:

Exopod	Endopod
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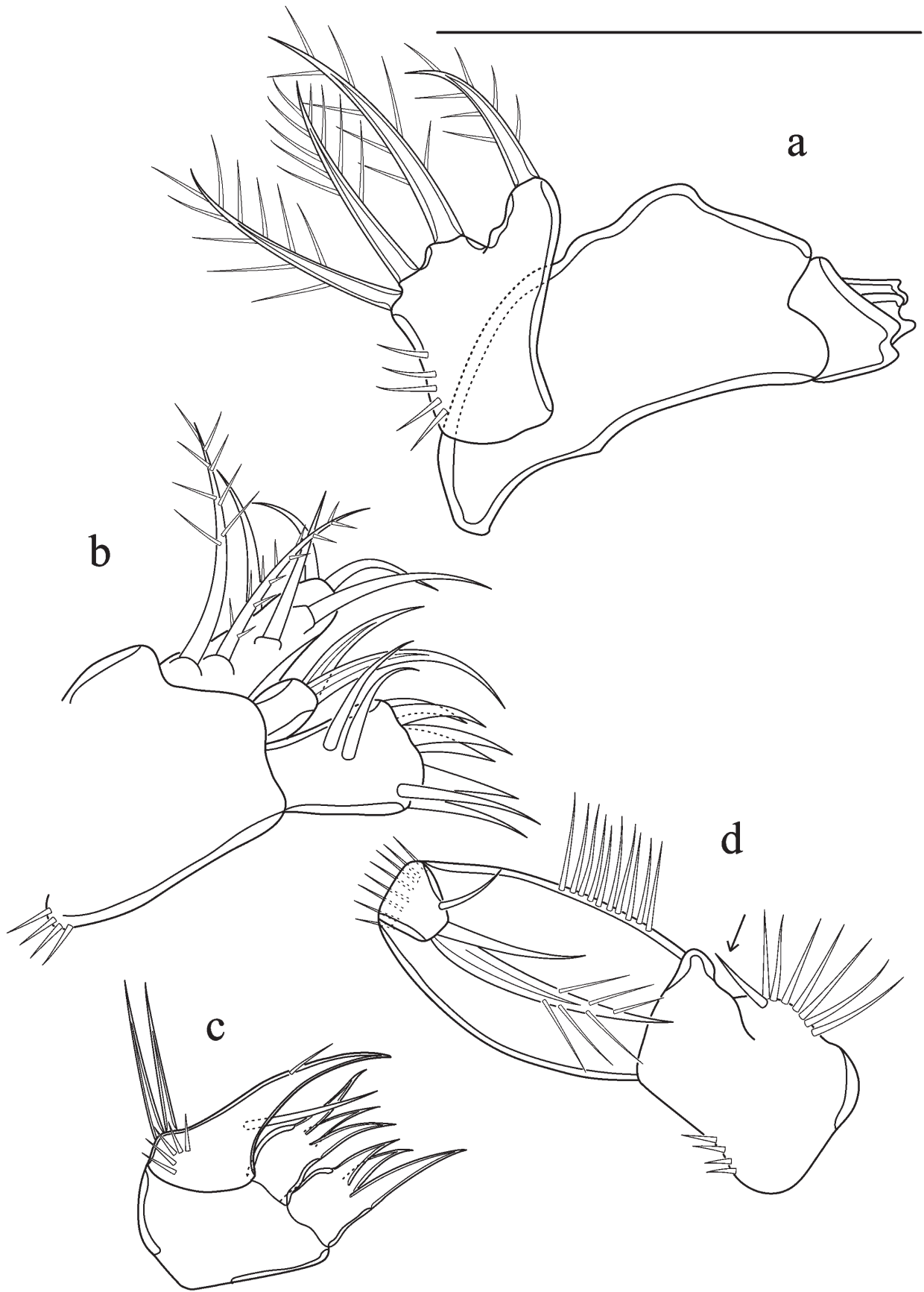
P1	0.1.022	0.111
P2	0.1.123	0.111
P3	0.1.223	0.111
P4	0.1.223	110



**FIGURE 2.** *Nannopus sinusalbi* sp. nov., female holotype. a, habitus, dorsal; b, rostrum, dorsal; c, antennule (triarticulate seta marked by an arrow), ventral; d, antenna. Scale bars: 50  $\mu$ m.



**FIGURE 3.** *Nannopus sinusalbi* sp. nov., female holotype. a, urosome, dorsal; b, urosome, ventral. Scale bars: 50  $\mu$ m.

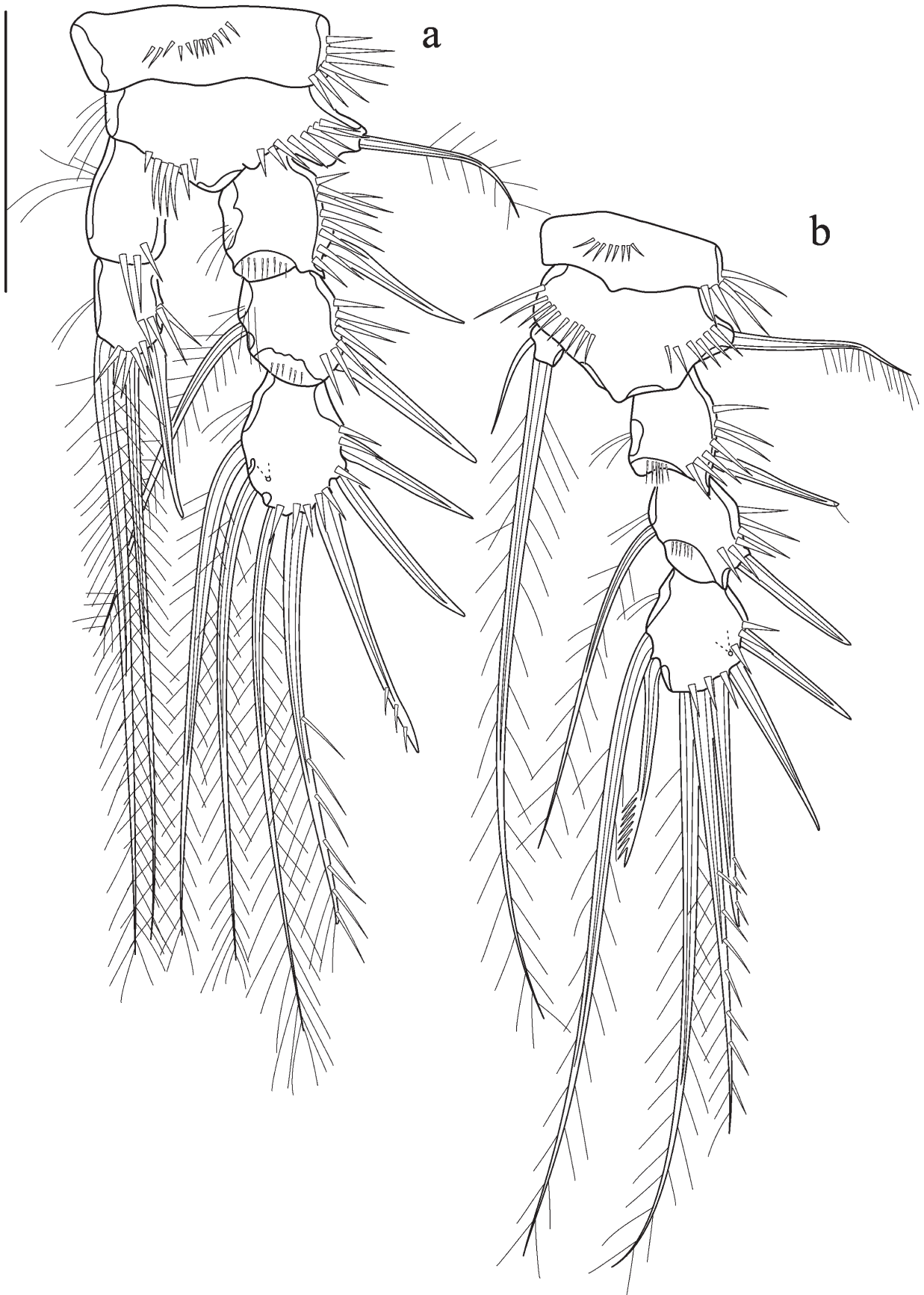


**FIGURE 4.** *Nannopus sinusalbi* **sp. nov.**, female holotype. a, mandible; b, maxillule; c, maxilla; d, maxilliped. Scale bar: 50  $\mu$ m.

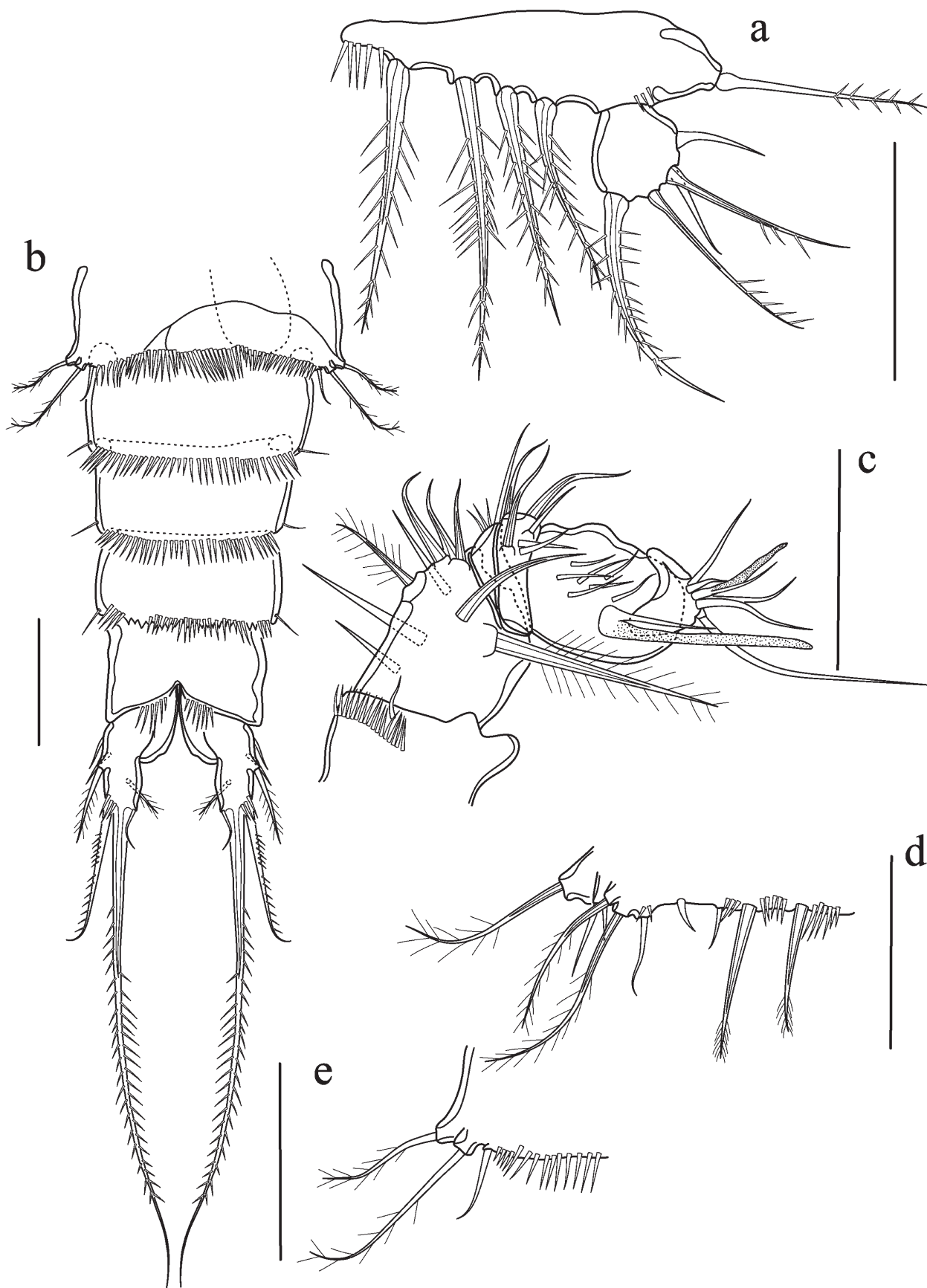




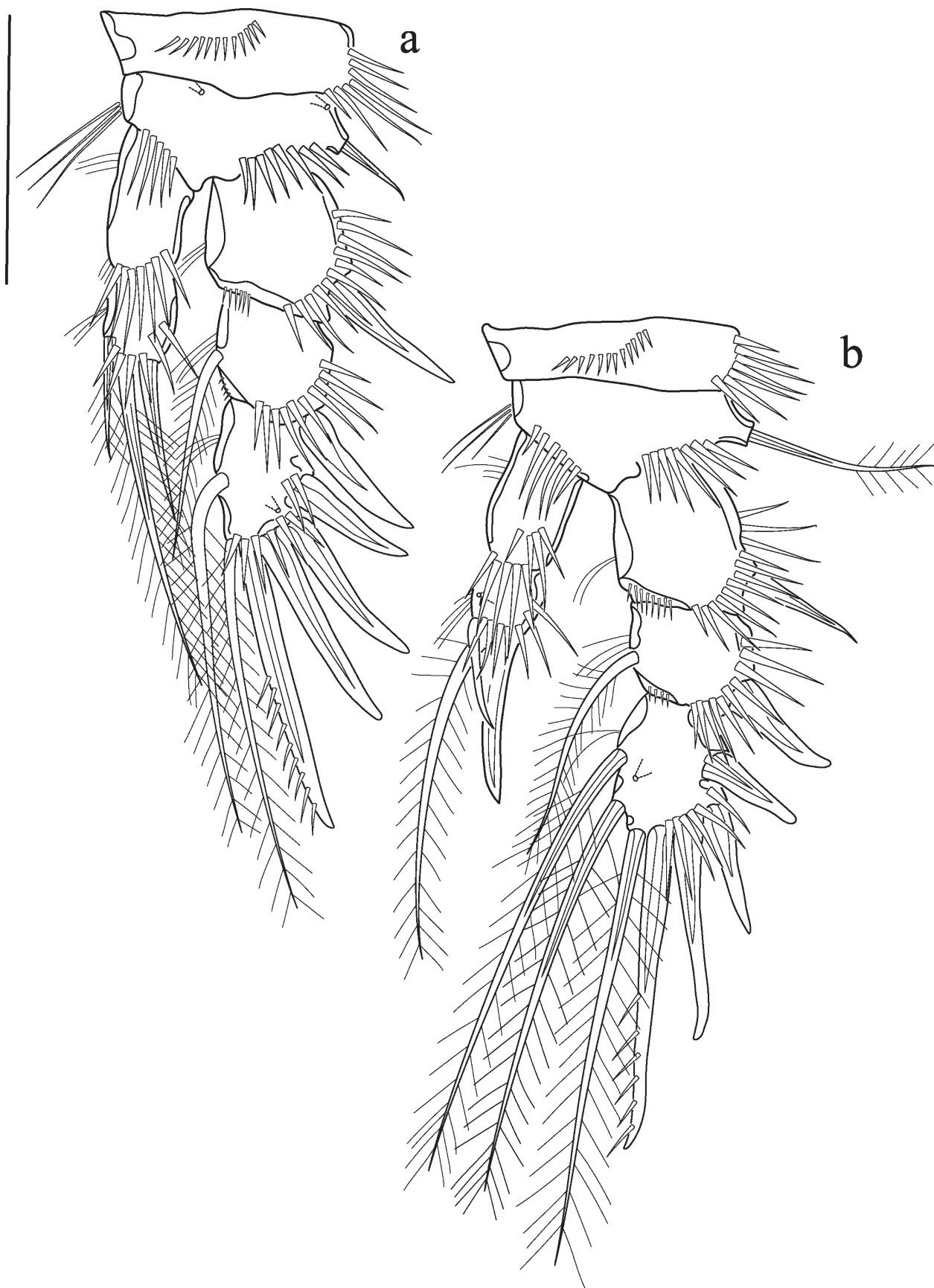
**FIGURE 5.** *Nannopus sinusalbi* sp. nov., female holotype. a, P1, anterior; b, P2, anterior. Scale bar: 50  $\mu$ m.



**FIGURE 6.** *Nannopus sinusalbi* sp. nov., female holotype. a, P3, anterior; b, P4, anterior. Scale bar: 50  $\mu$ m.



**FIGURE 7.** *Nannopus sinusalbi* sp. nov., female holotype (a), male paratype (b–e). a, P5, anterior; b, urosome, ventral; c, antennule, ventral; d, P5, anterior; e, P6, anterior. Scale bars: 50  $\mu$ m.



**FIGURE 8.** *Nannopus sinusalbi* sp. nov., male paratype. a, P2, anterior; b, P3, anterior. Scale bar: 50  $\mu$ m.

P5 (Fig. 7a). Baseoendopod represented by transversely elongate plate with spinules along inner distal corner and near articulation with exopod; endopodal lobe with four bipinnate elements; outer expansion with bipinnate basal seta. Exopod articulating with baseoendopod; semicircular and about as long as wide; with five elements: innermost bipinnate element strongest and articulating at base; next two elements pinnate; two outermost elements naked.

P6 (Fig. 3b) closing off paired genital apertures, semi-triangular with protruding outer distal edge bearing one short bipinnate element.

**Description of male.** Body length 537  $\mu\text{m}$ . Sexual dimorphism expressed in antennule, P2, P3, P5, P6, urosomal segmentation and caudal ramus setae.

Ornamentation of body generally as in female, except for minor differences such as the presence of a ventral row of long spinules on the genital and three abdominal somites (Fig. 7b).

Armature of caudal ramus almost as in female except for seta IV being twice as long and seta VI being shorter (Fig. 7b).

Antennule (Fig. 7c) short, 6-segmented; geniculation located between segments 5 and 6. All segments strongly chitinized. First and third segments with a row of spinules. Segment 5 and 6 with aesthetasc fused basally to a short seta. Armature formula as follows: 1-[1], 2-[7 + 2 bipinnate], 3-[1], 4-[6], 5-[7 + (1 + ae)], 6-[5 + (1 + ae)].

P2–P3 (Figs. 8a–b). Exp-2 and -3 with outer spines stronger than in female; outer terminal spine of exp-3 with inner spinules and stronger than in female. P3 exp-2 (Fig. 8b) with outer spine forming basally fused, robust apophysis; terminal and inner element shorter than in female; inner element naked.

P5 (Fig. 7d). Baseoendopod and exopod fused forming basally fused common plate with four rows of spinules. Endopodal lobe armed with two pinnate elements and two shorter naked elements. Outer setophore with plumose basal seta. Exopodal lobe with three naked and two plumose elements.

P6 (Fig. 7e). Sixth pair of legs asymmetrical with functional left leg forming a simple flap; confluent with somite; with spinules along distal margin and armed with one naked and two plumose elements. Single spermatophore observed underneath left flap.

**Variability.** Female body length varied between 552 and 643  $\mu\text{m}$  ( $n = 10$ ; mean = 597.4  $\mu\text{m}$ ; standard deviation = 33.81  $\mu\text{m}$ ), while males measured 546 to 611  $\mu\text{m}$  ( $n = 10$ ; mean = 577.7  $\mu\text{m}$ ; standard deviation = 22.72  $\mu\text{m}$ ).

**Etymology.** The specific name *sinusalbi* is the genitive form of the Latin compound translating the name of the type locality (*Bahía Blanca*, i.e., White Bay): *sinus*, *us* (4<sup>th</sup> declension, masculine: bay) and *albus* (white).

## Discussion

With the description of *Nannopus sinusalbi* **sp. nov.** the number of valid species in the genus has risen to 19. Only one valid species has its type locality in the Southern Hemisphere: *Nannopus perplexus* from the southwestern shores of Lake Tanganyika (Zambia) (Sars 1909a). *Nannopus brasiliensis* Jakobi, 1956 was originally described from mangal habitats in Cananéia, southeastern Brazil but has subsequently been considered conspecific with *N. palustris* (Wells 1971; Reid 1998). Jakobi's (1956) text description is confusing and his illustrations are grossly inadequate for morphological comparison. The species was differentiated from "*N. palustris*" collected from the mangroves of Rio Nanáu and Baía de Guaratuba, although morphological information of those specimens was not presented by Jakobi (1956). *Nannopus brasiliensis* differs from all its congeners, including its geographically closest relative *N. sinusalbi* **sp. nov.**, in the structure of the outer distal element on P3 exp-3, i.e. being long and distinctly pinnate instead of short, naked and spiniform. The Brazilian morphs ("*N. palustris*" and *N. brasiliensis*) reported by Jakobi (1956, 1959) and other authors (Gerlach 1958; Por 1984, Por *et al.* 1984) should be re-examined in order to elucidate their taxonomic status; pending this, *N. brasiliensis* is here relegated to *species inquirenda* in the genus rather than being considered a junior synonym of the type species.

The genus *Nannopus* can be subdivided in two artificial species groups based on the presence or absence of the inner seta on P1 exp-2 (Table 2). Symptomatic for the taxonomic confusion surrounding the genus is the fact that this character state is unknown for *N. palustris* [Brady's (1880: Fig. 19) illustration of P1 in reality refers to P3] and hence the type species cannot be assigned to either Group I or II. The armature formula of P1–P4 displayed by *N. sinusalbi* **sp. nov.** is shared by most members of Group II except for *N. flexibilis*, *N. procerus* and *N. scaldicola*. The new species can be differentiated from the remaining seven species of this group [*N. palustris* *sensu* Scott (1902) and *N. brasiliensis* are not considered here] by the characters below.

*Nannopus didelphis* differs from *N. sinusalbi* **sp. nov.** in the length of caudal ramus seta IV (about three times as long as VI *vs* almost equal in length) and the ornamentation of the inner seta of the ♀ P4 endopod (plumose *vs* smooth). Males of *N. didelphis* differ from those of the new species in the paired genital system (*vs* unpaired with dextral and sinistral configurations), the symmetrical sixth legs (*vs* asymmetrical with only one functional P6), and differences in setal length on P2 enp-2 (inner seta as long as apical one *vs* only 1/3 the length).

Females of *N. hirsutus* (♂ unknown) are characterized by the conspicuous body ornamentation, particularly the setular clusters on the pleurotergites of the urosomites and the outer margins of the caudal rami, and by the morphology of caudal seta V which displays a long cylindrical and heavily ornamented proximal region. Both characters are absent in the new species.

*Nannopus ganghwaensis* can readily be differentiated from *N. sinusalbi* **sp. nov.** by the dense setular ornamentation of the cephalothorax and body somites, the disproportionate difference in length between caudal ramus setae IV and VI, and the relative length of caudal ramus seta V (distinctly shorter in *N. ganghwaensis*). Females of both species also differ in the length of the setae on P3 enp-2 (inner distinctly shorter than apical *vs* of approximately equal length), the basal fusion of the innermost seta of P5 exopod (*vs* free at base), and the relative lengths of the endopodal setation elements of P5.

*Nannopus dimorphicus* differs from *N. sinusalbi* **sp. nov.** in the presence of a large dorsal integumental window on the cephalothorax of both sexes. In addition, females of both species can be distinguished by the morphology of caudal ramus setae IV (pinnate and swollen at base *vs* naked and not basally dilated) and V (characteristically inflated in proximal part in *N. dimorphicus*), the basal fusion of the innermost seta of P5 exopod (*vs* free at base), and the ornamentation of the two innermost endopodal setae of P5.

Females of *N. minutus* can be differentiated from those of *N. sinusalbi* **sp. nov.** by the presence of three integumental windows on the cephalothorax (absent in the ♂ and in both sexes of the new species), the spinular ornamentation around the ventral posterior margin of the genital double-somite and free abdominal somites, the shape of caudal setae IV (spiniiform and hirsute *vs* setiform and naked) and V (distinctly shorter in *N. minutus*), the inner seta of P3 enp-2 being distinctly shorter than the apical one (*vs* both setae being equally long), and the basal fusion of the innermost seta of P5 exopod (*vs* free at base). Males of both species can be distinguished by caudal ramus morphology (distinctly shorter and with projection along inner margin in *N. minutus*), sexual length dimorphism of inner seta of P2 exp-2 (not expressed in *N. sinusalbi* **sp. nov.**), length of the distal inner seta on P3 enp-2, and ornamentation of setation elements on P5–P6.

*Nannopus cylindricus* (♂ unknown) primarily differs from *N. sinusalbi* **sp. nov.** by the distinctly shorter caudal rami and the conspicuous cylindrical shape of the base of the inflated caudal seta V.

*Nannopus canui* **sp. nov.** (♂ unknown) is morphologically very close to *N. sinusalbi* **sp. nov.**, differing in the larger body size (♀: 870 *vs* 562.5 µm), the spacing of the endopodal setae of the ♀ P5 baseoendopod (but note that substantial variability has been observed in other species: *e.g.* *N. didelphis*, *cf.* Fiers & Kotwicki 2013, Fig. 9), the absence of a pectinate distal inner seta on P4 exp-3 (it is as long and pinnate as the proximal inner seta; note that this could be an aberrant condition), and the length of ♀ caudal ramus seta IV (longer than the ramus and almost half the size of seta V *vs* shorter than the ramus and about 1/6 the length of seta V).

## Nomenclatural issues

Lilljeborg (1902: 61) proposed the genus *Iliophilus* for a new species *I. flexibilis* (type species by monotypy) collected from the Ekoln gulf in the freshwater Lake Malar (Mälaren) near Stockholm, Sweden. Most early 20<sup>th</sup>-century workers such as Zykoff (1905: 281), Berg (1908: 432), Meissner (1907: 589, 597, 601; 1908: 39, Plate II, Fig. 5 a–d), Brehm (1908: 451; 1913: 580; 1916: 450–451) and Chugunov (1921: 124) followed Lilljeborg's spelling of the generic name until Sars (1909a: 47–48, 68–71, 74, Plate XIII, figs 93–104) introduced the alternative spelling *Ilyophilus* for a new species, *I. perplexus*, from Lake Tanganyika. This incorrect subsequent spelling was also adopted by Sars (1909b: 306) when he synonymized the genus with *Nannopus* and by Cunnington (1920: 560) and Plotnikov (2016: 87), however most authors continued using the original spelling *Iliophilus* when referring to Lilljeborg's generic name, including Klie (1913: 34; 1925: 134), Haberbosch (1917: 598), Gurney (1932: 326), Kiefer (1956: 265) and Dussart & Defaye (1990: 272). Fiers & Kotwicki (2013) used both alternative spellings *Iliophilus* (p. 60) and *Ilyophilus* (pp. 59, 64) in their discussion and suggested that the genus should probably be

**TABLE 2.** Swimming leg armature formulae of female *Nannopus* species. Differences with *Nannopus simusalbi* sp. nov. indicated in **boldface**.

Species	P1		P2		P3		P4	
	exp	enp	exp	enp	exp	enp	exp	enp <sup>a</sup>
<i>N. parvus</i> Vakati & Lee, 2017	0.0.022	0.111	0.1.122	0.111	0.1.222	0.111	0.1.222	110
<i>N. bulbiseta</i> Vakati & Lee, 2017	0.0.022	0.111	0.1.022	0.111	0.1.122	0.111	0.1.122	110
<i>N. perplexus</i> (Sars, 1909a)	0.0.022	0.010	unknown <sup>b</sup>	unknown <sup>b</sup>	0.1.222	0.111	0.1.222	<b>010</b>
<i>N. serratus</i> Vakati & Lee, 2017	0.0.022	<b>110</b>	0.1.122 <sup>c</sup>	0.011 <sup>d</sup>	0.1.222	0.111	0.0.222	110
<i>N. robustus</i> Vakati & Lee, 2021	0.0.022	<b>110</b>	0.0.122 <sup>c</sup>	0.011 <sup>d</sup>	0.1.222	0.111	0.0.222	110
<i>N. parvipilis</i> Kim, Choi & Yoon, 2017	0.0.022	<b>110</b>	0.1.122	0.011	0.1.222	<b>010</b>	0.1.122	<b>010</b>
<i>N. unisegmentatus</i> Shen & Tai, 1964	0.0.022	<b>010</b>	0.1.122	0.011	0.1.222	0.111	0.0.222	110
<i>N. palustris</i> Brady, 1880 <sup>e</sup>	unknown	unknown	0.1.123	0.111	unknown	unknown	0.1.222	110
<i>N. palustris</i> Brady, 1880 sensu Scott (1902) <sup>f</sup>	0.1.022	0.111	unknown	unknown	0.1.223	0.111	0.1.223	110
<sup>g</sup> <i>N. brasiliensis</i> Jakobi, 1956 <sup>g</sup>	0.1.022	0.111	0.1.123	0.111	0.1.223	0.111	0.1.223	110
<i>N. didelphis</i> Fiers & Kotwicki, 2013	0.1.022	0.111	0.1.123	0.111	0.1.223	0.111	0.1.223	110
<i>N. hirsutus</i> Fiers & Kotwicki, 2013	0.1.022 <sup>h</sup>	0.111	0.1.123	0.111	0.1.223	0.111	0.1.223	110
<i>N. ganghwaensis</i> Vakati, Kihara & Lee, 2016	0.1.022 <sup>i</sup>	0.111	0.1.123	0.111	0.1.223	0.111	0.1.223	110
<i>N. dimorphicus</i> Vakati & Lee, 2017	0.1.022 <sup>i</sup>	0.111	0.1.123	0.111	0.1.223	0.111	0.1.223	110
<i>N. minutus</i> Vakati & Lee, 2017	0.1.022 <sup>i</sup>	0.111	0.1.123	0.111	0.1.223	0.111	0.1.223	110
<i>N. cylindricus</i> Vakati & Lee, 2021	0.1.022 <sup>i</sup>	0.111	0.1.123	0.111	0.1.223	0.111	0.1.223	110
<i>N. canui</i> sp. nov.	0.1.022	0.111	0.1.123	0.111	0.1.223	0.111	0.1.223 <sup>j</sup>	110
<i>N. simusalbi</i> sp. nov.	0.1.022	0.111	0.1.123	0.111	0.1.223	0.111	0.1.223	110
<i>N. scaldicola</i> Fiers & Kotwicki, 2013	0.1.022	0.111	0.1.123	0.111	0.1.223	0.111	0.1.123	110
<i>N. procerus</i> Fiers & Kotwicki, 2013	0.1.022	0.111	0.1.123	0.111	0.1.123	0.111	0.1.123	110
<i>N. flexibilis</i> (Lilljeborg, 1902)	0.1.022	0.111	<b>0.1.122<sup>k</sup></b>	0.111	0.1.223	0.111	0.1.223	110

<sup>a</sup> Various authors (e.g. Vakati *et al.* 2016; Vakati & Lee 2021) describe the armature pattern of the P4 endopod as 020. Based on most recent detailed descriptions it is clear that this pattern should be interpreted as 110 with the inner element typically being reduced in the majority of the species.

<sup>b</sup> Sars (1909a) did not illustrate P2 but stated that the distal exopod segment of P2–P3 is “... somewhat broader [than in P1] and provided with one or two additional setae”. No information was provided for the P2 endopod.

<sup>c</sup> Vakati & Lee (2017, 2021) described the pattern of P2 exp-3 as 212.

<sup>d</sup> Vakati & Lee (2017, 2021) described the pattern of P2 exp-2 as 110.

<sup>e</sup> Brady (1880: Plate LXXVII, Figs 19–20) erroneously labelled P2 as P1 and P4 as P3, respectively (cf. Canu 1892: 167; Fiers & Kotwicki 2013: 58) — but see Kim *et al.* (2017) for a dissenting opinion. The distal exopod segment of P4 was illustrated with only two outer spines; whether this is the typical condition has to be confirmed since variation in the number of outer spines has been observed in other species (Fiers & Kotwicki 2013).

<sup>f</sup> Scott's (1902: Plate XXIII, Fig. 20) illustration of P2 in reality refers to P3. Based on the presence of a pectinate inner distal element on P4 exp-3 and differences in caudal rami armature Fiers & Kotwicki (2013: 60) claimed that Scott's material is not conspecific with *N. palustris*.

<sup>g</sup> Wells (1971) considered this species as conspecific with *N. palustris*, however given the complex taxonomy and cryptic diversity of *Nannopus* (Garlitska *et al.* 2012; Fiers & Kotwicki 2013; Vakati *et al.* 2019) it is more prudent to consider it *species inquirenda* in the genus.

<sup>h</sup> Fiers & Kotwicki (2013: Fig. 6H) illustrate the male P2 exopod without an inner seta on exp-2 but make no comment on this in the text (p. 43). It is therefore not clear whether the seta was accidentally omitted during the drawing process, the exopod was damaged, or the P2 genuinely displays a sexually dimorphic armature formula.

Vakati *et al.* (2016) used this character to differentiate males of *N.ganghwaensis* and *N. didelphis*.

<sup>i</sup> Vakati *et al.* (2016) and Vakati & Lee (2017, 2021) described the pattern as 0.1.013.

<sup>j</sup> Canu (1892: Plate IV, fig. 18) illustrates three inner setae on P4 exp-3. This pattern has been considered the normal condition by Wells (1971: 515) while the more common 2-setae condition was regarded as variation. Fiers & Kotwicki (2013: 53) questioned this interpretation, claiming that Canu's (1892) female was aberrant. Their interpretation is adopted here.

<sup>k</sup> The armature formula of P2 exp-3 was erroneously tabulated as III, I, 1 by Vakati *et al.* (2016: 228, Table 1) and Vakati & Lee (2017: 51, Table 1). Liljeborg (1902) does not illustrate P2 but mentions in the text (p. 63) that exp-3 has only two outer spines and one inner seta ("Fötterna af 2:dra paret likna i det allra närmaste dem af 1:sta paret, men afvika från dem därigenom, att yttergrenens 3:dje led har 1 ytterkanten nära nedre änden och i innerkanten nära nedre änden ett långt borst"). The endopod is described as being almost identical to that of P1 except that the apical seta of exp-2 is considerably longer.



reinstated under the latter spelling to accommodate *I. flexibilis* (type), *Nannopus perplexus*, *N. procerus*, *N. didelphis* and *N. hirsutus* while maintaining all other species in the genus *Nannopus*. Vakati *et al.* (2016: 231; 2019: 366, 376) and Vakati & Lee (2017: 50) argued quite forcefully against the recognition of two lineages while Kim *et al.* (2017) formally recognized both genera and their respective names as valid. All these authors consistently used the spelling *Ilyophilus*, overlooking that any subsequent spelling different from the correct original spelling *Iliophilus*, other than a mandatory change or an emendation, is an incorrect subsequent spelling. *Ilyophilus* is not an available name and, like an incorrect original spelling, does not enter into homonymy and cannot be used as a substitute name (ICZN Art. 33.3).

Fiers & Kotwicki (2013) expressed doubts about the identity of *Nannopus palustris* sensu Canu (1892), claiming that the slender fusiform body shape, the length of caudal ramus seta IV (twice as long as the ramus), and the position of the lateral caudal setae (II?) differ from Brady's (1880) type description and may indicate that Canu's specimens represent a different species, not conspecific with *N. palustris*. Kim *et al.* (2017) placed *Nannopus palustris* sensu Canu (1892) in *Iliophilus* and attributed distinct specific status to his material by naming it *I. canui* Kim, Choi & Yoon, 2017. In the absence of extant material, the authors refrained from explicitly fixing a holotype, but their course of action effectively makes the new name unavailable (ICZN Art. 16.4). The female specimen illustrated by Sars (1892: plate IV, figs 6–21) is here designated as the holotype of *Nannopus canui* **sp. nov.** (ICZN Art. 72.5.6) (urn:lsid:zoobank.org:act:83FA6D5C-1D75-4B05-8F46-E67B36BF87AF). The species can be differentiated by the characters listed and illustrated in Canu (1892: 166–167) (ICZN Art. 13.1) and Table 2. The specific epithet is named in honour of the French zoologist Eugène Canu (1864–1952) who worked extensively on the copepod fauna of northwestern France (La Manche). Type locality: France, Hauts-de-France region, Pas-de-Calais, Wimereux, estuarine mudflats.

## Updated key to species

In most recent keys (*e.g.* Vakati *et al.* 2016; Vakati & Lee 2017, 2021) the first couplet refers to the presence/absence of a pectinate inner distal seta on P4 exp-3. The absence of this element is traditionally used to split off early on in the key a group of three species, *i.e.* *N. palustris*, *N. canui* and *N. scaldicola*, however, only in the latter can this character state be confirmed with absolute certainty. Fiers & Kotwicki (2013: 64) attach considerable significance to its absence in this species group and go as far as to suggest that the presence of the pectinate seta in all other species may be a potential synapomorphy justifying the resurrection of *Iliophilus*. Fiers & Kotwicki also appear to indicate that the plesiomorphic condition (long bipinnate seta) was expressed in the ancestor of *N. scaldicola* before the armature element was eventually lost (the inner seta on P4 exp-3 is most likely the proximal inner one) but this statement remains hypothetical. Brady's (1880) description of *N. palustris* is fragmentary at best, showing only the body in dorsal aspect, and P2 and P4, both of which were erroneously labelled P1 and P3, respectively. Although the inner margin of P4 exp-3 shows two long non-pectinate setae (the proximal naked one uncharacteristically being distinctly shorter than the distal bipinnate one) it is disputable whether Canu's illustration is correct. Fiers & Kotwicki (2013: 60) assumed that Canu's (1892) drawing of the P4 of his French material of *N. palustris* (= *N. canui*) was based on an aberrant specimen since it shows three long inner bipinnate setae on exp-3. Given the dubious nature of both reports it would be prudent to disregard them until new evidence comes to light. Consequently, the pectinate seta presence/absence will not be used as a character in the key below and the type species *N. palustris* is omitted from it.

- |    |                                                                                                                                                                                                                                                          |                              |
|----|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------|
| 1. | P1 exp-2 without inner seta                                                                                                                                                                                                                              | .....2.                      |
| -  | P1 exp-2 with inner seta                                                                                                                                                                                                                                 | .....8.                      |
| 2. | P1 endopod 1-segmented                                                                                                                                                                                                                                   | .....3.                      |
| -  | P1 endopod 2-segmented                                                                                                                                                                                                                                   | .....6.                      |
| 3. | P3–P4 endopods very small, 1-segmented, bearing single short apical seta                                                                                                                                                                                 | ..... <i>N. parvipilis</i> . |
| -  | P3 endopod 2-segmented with armature formula [0.111]; P4 endopod 1-segmented, with small inner seta and very long apical seta                                                                                                                            | .....4.                      |
| 4. | P2 exp-2 without inner seta; distal outer spine of ♂ P2 exp-3 enlarged and robust, recurved, naked; caudal ramus seta V with inflated cylindrical proximal section in ♀                                                                                  | ..... <i>N. robustus</i> .   |
| -  | P2 exp-2 with inner seta; distal outer spine of ♂ P2 exp-3 not enlarged, relatively straight, bipinnate ( <i>N. serratus</i> ) or condition unknown ( <i>N. unisegmentatus</i> ); caudal ramus seta V without inflated cylindrical proximal section in ♀ | .....5.                      |
| 5. | Inner seta of P3 exp-2 and P4 endopod relatively well developed and bipinnate (♂ condition unknown); innermost seta of ♀ P5                                                                                                                              |                              |

- discrete at base ..... *N. unisegmentatus*.
- Inner seta of P3 exp-2 and P4 endopod very small and naked in both sexes; innermost seta of ♀ P5 fused at base ..... *N. serratus*.
6. P3–P4 exp-3 with five setae/spines ..... *N. bulbiseta*.
- P3–P4 exp-3 with six setae/spines ..... 7.
7. Caudal ramus seta V composite in ♀, consisting of spiniform naked proximal part and flagellate distal part; P1 endopod small, not reaching beyond distal margin of exp-1, with one apical seta; P4 exp-3 not markedly wider than other exopodal segments; P4 endopod minute, with one long apical seta ..... *N. perplexus*.
- Caudal ramus seta V not composite in ♀, bipinnate in distal part; P1 endopod reaching beyond distal margin of exp-2, with two bipinnate setae and one strong outer spine; P4 exp-3 markedly wider than other exopodal segments; P4 endopod small, with one long apical seta and one shorter inner seta ..... *N. parvus*.
8. P2 exp-3 with two outer spines ..... *N. flexibilis*.
- P2 exp-3 with three outer spines ..... 9.
9. P4 exp-3 with six setae/spines ..... 10.
- P4 exp-3 with seven setae/spines ..... 11.
10. Inner element of P4 exp-3 long, slender and bipinnate in both sexes; caudal ramus seta V of ♀ with dorsal spinous process in proximal part; sixth legs of ♂ asymmetrical with only one functional member ..... *N. scaldicola*.
- Inner element of P4 exp-3 pectinate in distal half in both sexes; caudal ramus seta V of ♀ without dorsal spinous process; sixth legs of ♂ symmetrical. .... *N. procerus*.
11. Pleurotergites of urosomites and outer margins of caudal rami with conspicuous setular clusters; caudal ramus seta V of ♀ with long, cylindrical and heavily ornamented proximal region ..... *N. hirsutus*.
- Urosome and caudal rami without conspicuous setular ornamentation; caudal ramus seta V of ♀ not heavily ornamented in proximal part ..... 12.
12. Inner seta of ♀ P4 endopod naked ..... 13.
- Inner seta of ♀ P4 endopod bipinnate ..... 15.
13. Seta IV of ♀ caudal ramus naked, about as long as seta VI; innermost seta of ♀ P5 defined at base; inner distal seta of ♂ P3 exp-2 about as long as endopod (measured from base of exp-1 to apex of apophysis) ..... *N. sinusalbi* **sp. nov.**
- Seta IV of ♀ caudal ramus pinnate, distinctly longer than seta VI; innermost seta of ♀ P5 fused at base; inner distal seta of ♂ P3 exp-2 1.6–2.0 times length of endopod. .... 14.
14. Cephalothorax without integumental windows in both sexes; P2 exp-2 ♀ inner seta longer than outer spine; P2–P3 exp-3 ♂ with four naked spines and two (P2) or three (P3) pinnate setae ..... *N. ganghwaensis*.
- Cephalothorax with three integumental windows in ♀, absent in ♂; P2 exp-2 ♀ inner seta shorter than outer spine; P2–P3 exp-3 ♂ with three sparsely pinnate spines and three (P2) or four (P3) pinnate setae. .... *N. minutus*.
15. Outer distal element of P1 exp-3 setiform and almost as long as inner distal seta; inner and distal setae of ♀ P3 exp-2 very long, about four times length of ramus ..... *N. canui* **sp. nov.**
- Outer distal element of P1 exp-3 spiniform and distinctly shorter than inner distal seta; inner and distal setae of ♀ P3 exp-2 much shorter. .... 16.
16. Cephalothorax of both sexes with dorsal integumental window; sixth legs of ♂ asymmetrical; caudal ramus seta V of ♀ with circlet of fine setules around basal globular expansion ..... *N. dimorphicus*.
- Cephalothorax of both sexes without dorsal integumental window; sixth legs of ♂ symmetrical; caudal ramus seta V of ♀ without ornamentation around basal expansion ..... *N. didelphis*.

## Ecology

A total of 13 putative species belonging to the order Harpacticoida were found at Arroyo Pareja, in the Bahía Blanca estuary. The harpacticoid community was dominated by five of them, collectively constituting 94% of the total number of obtained specimens (Fig. 9). *Halectinosoma parejae* Sciberras, Huys, Bulnes & Cazzaniga, 2017 was numerically dominant during most of the year, followed by *Nannopus sinusalbi* **sp. nov.**, *Quinquelaophonte aestuarii* Sciberras, Bulnes & Cazzaniga, 2014, and two species of the family Miraciidae which remain as yet unidentified. Descriptive statistics of abundance and indices for the interstitial harpacticoid copepod community are summarized in Table 3.

Harpacticoid density had a clear seasonality ( $F_{11,48} = 14,652$ ,  $p < 0.0001$ ), with significantly higher abundance in summer and autumn (Tukey HSD  $p < 0.0001$ ), and a smaller peak in winter (August) (Fig. 10a). Ovigerous females were recorded during nine months of the year and showed their highest abundance during spring and summer (Fig. 10a).

*Nannopus sinusalbi* **sp. nov.** represented about 8% of total harpacticoid abundance. Its density was below 5 ind.cm<sup>-2</sup> during most of the year, with an abrupt peak of 40.17 ind.cm<sup>-2</sup> towards the end of the summer (February–March), coinciding with the maximum relative abundance of ovigerous females (Fig. 10b).

**TABLE 3.** Quantitative data of the interstitial harpacticoid copepod assemblage at Arroyo Pareja, Bahía Blanca, Argentina. Density data expressed in ind.10 cm<sup>-2</sup>. Mean ± SE is shown where appropriate; number of samples by date = 5.

	April 2014	May 2014	June 2014	July 2014	August 2014	September 2014
Density of adult harpacticoids	302,69 ± 75,633	63,08 ± 23,825	5,09 ± 3,572	4,24 ± 4,383	61,39 ± 26,221	7,07 ± 4,470
Density of <i>Halectinosoma parejae</i>	242,15 ± 58,825	33,95 ± 13,324	1,70 ± 1,358	0,00	2,83 ± 2,147	1,98 ± 2,075
Density of Miraciidae sp. 1	14,43 ± 6,925	7,92 ± 8,793	0,85 ± 1,109	0,28 ± 0,554	4,24 ± 4,639	1,13 ± 1,037
Density of <i>Nannopus sinusalbi</i> sp. nov.	5,37 ± 2,827	1,41 ± 1,240	0,28 ± 0,554	0,00	6,51 ± 3,112	0,85 ± 1,109
Total number of harpacticoid species by date (s <sub>d</sub> )	9	7	5	5	11	7
Mean number of harpacticoid species by sample	7,8	5,4	2,0	1,4	7,4	3,2
Maximum diversity (H <sub>max</sub> )	2,197	1,946	1,609	—	2,303	1,946
Harpacticoid diversity (H')	0,836	1,286	1,353	—	2,077	1,835
Effective number of species (ENS)	2,31	3,62	3,87	—	7,98	6,27
Equitability index (E)	0,381	0,661	0,841	—	0,866	0,943

**TABLE 3.** (Continued)

	October 2014	November 2014	December 2014	January 2015	February 2015	March 2015
Density of adult harpacticoids	18,39 ± 9,801	30,27 ± 11,144	10,75 ± 5,586	52,62 ± 35,518	200,57 ± 95,398	148,23 ± 101,419
Density of <i>Halectinosoma parejae</i>	7,07 ± 5,333	14,14 ± 4,295	5,66 ± 5,749	34,51 ± 26,498	174,26 ± 88,141	75,25 ± 41,947
Density of Miraciidae sp. 1	3,68 ± 2,854	10,18 ± 9,739	2,26 ± 2,252	0,85 ± 1,109	0,00	23,76 ± 17,932
Density of <i>Nannopus sinusalbi</i> sp. nov.	0,57 ± 0,679	1,98 ± 1,880	0,00	2,83 ± 3,507	0,00	40,17 ± 40,881
Total number of harpacticoid species by date (s <sub>d</sub> )	10	7	6	11	7	11
Mean number of harpacticoid species by sample	5,8	3,8	2,8	5,8	5,2	6,2
Maximum diversity (H <sub>max</sub> )	2,303	1,946	1,792	2,398	1,946	2,398
Harpacticoids diversity (H')	1,873	1,296	1,354	1,300	0,578	1,268
Effective number of species (ENS)	6,51	3,65	3,87	3,67	1,78	3,55
Equitability index (E)	0,814	0,666	0,756	0,542	0,297	0,529

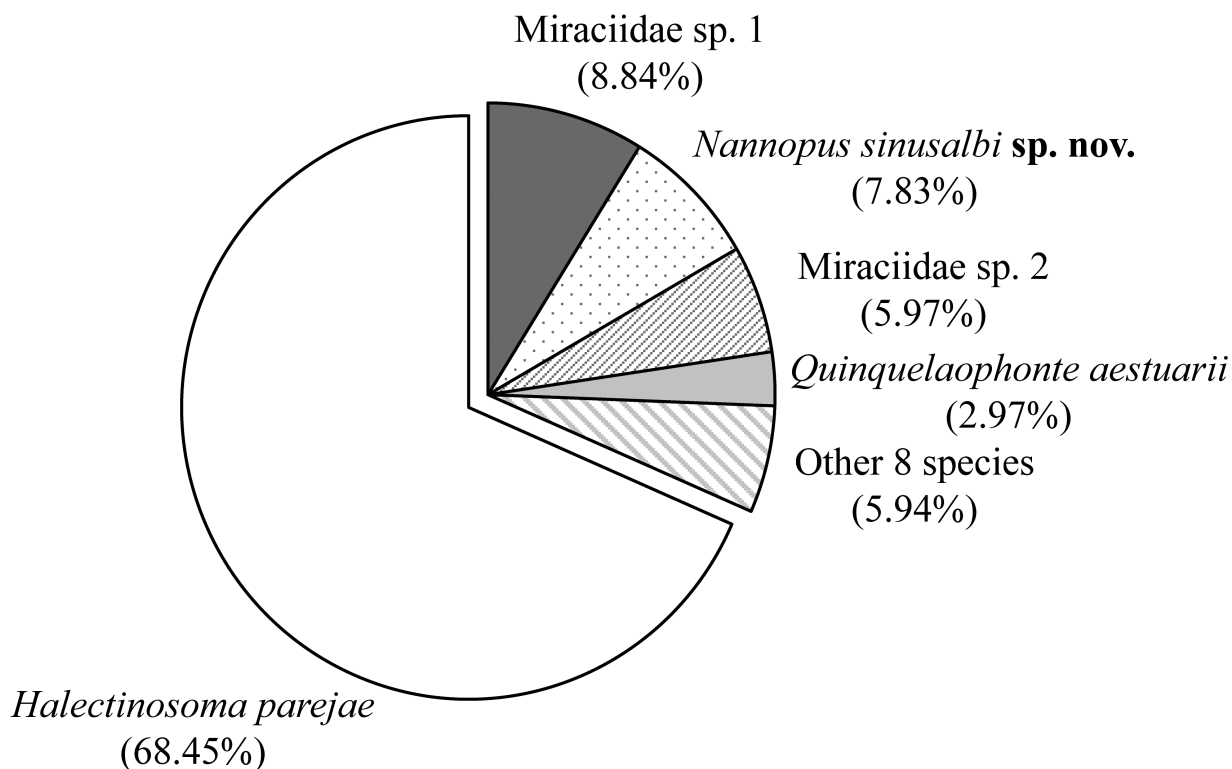


FIGURE 9. Specific composition of interstitial copepods collected in Arroyo Pareja (Bahía Blanca estuary) between April 2014 and March 2015 (N = 3068).

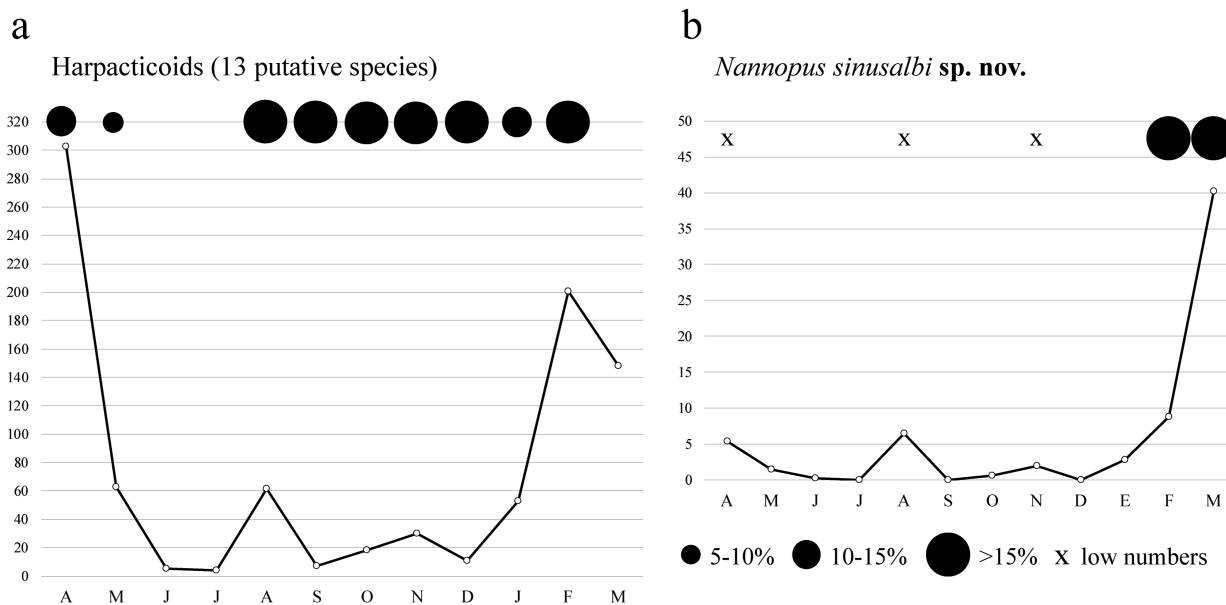


FIGURE 10. a, density of harpacticoids (ind.10 cm<sup>-2</sup>) in sediments of Arroyo Pareja (Bahía Blanca estuary) over a 1-year period; b, density of *Nannopus sinusalbi* sp. nov. (ind.10 cm<sup>-2</sup>) in sediments of Arroyo Pareja (Bahía Blanca estuary) over a 1-year period; filled circles and X indicate the proportion of ovigerous females in the population.

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## References

- Arias, A.H., Vázquez-Botello, A., Tombesi, N., Ponce-Vélez, G., Freije, R.H. & Marcovecchio, J.E. (2010) Presence, distribution, and origins of polycyclic aromatic hydrocarbons (PAHs) in sediments from Bahía Blanca estuary, Argentina. *Environmental Monitoring and Assessment*, 160, 301–314.  
<https://doi.org/10.1007/s10661-008-0696-5>
- Berg, L.S. (1908) Aral'skoe more. Opyt fiz.-geograf. monografii. Der Aral-See. Versuch einer physisch-geografischen Monografie. *Izvestiya Turkestanskogo Otdela imperatorskogo russkogo geograficheskogo Obshchestva*, 5, i–xiii + 1–580. [in Russian]
- Brady, G.S. (1880) *A Monograph of the Free and Semi-parasitic Copepoda of the British Islands. Vol. 2*. The Ray Society, London, 182 pp.
- Brehm, V. (1908) Die geographische Verbreitung der Copepoden und ihre Beziehung zur Eiszeit. *Internationale Revue der gesamten Hydrobiologie und Hydrographie*, 1, 447–462.  
<https://doi.org/10.1002/iroh.19080010308>
- Brehm, V. (1913) Über die Harpacticiden Mitteleuropas. *Archiv für Hydrobiologie*, 8, 313–318 + 575–588.
- Brehm, V. (1916) Brackwassercopepoden im Süßwasser der Mittelmeerländer. *Internationale Revue der gesamten Hydrobiologie und Hydrographie*, 7, 448–455.  
<https://doi.org/10.1002/iroh.19160070604>
- Calvo-Marcilese, L. & Pratolongo, P. (2009) Foraminíferos de marismas y llanuras de mareas del estuario de Bahía Blanca, Argentina: distribución e implicaciones ambientales. *Revista Española de Micropaleontología*, 41, 315–332.
- Canu, E. (1892) Les Copépodes du Boulonnais. Morphologie, embryologie, taxonomie. *Travaux de l'Institut zoologique de Lille et du Laboratoire de Zoologie maritime de Wimereux (Pas-de-Calais)*, 6, 1–292, pls. I–XXX.  
<https://doi.org/10.5962/bhl.title.58678>
- Chugunov, N.L. (1921) K izucheniyu planktona severnoi chasti Kaspiiskogo morya. Ueber das Plankton des nordlichen Teiles des Kaspisees. *Raboty Volzhskoi biologicheskoi Stantsii (Arbeiten der Biologischen Wolga-Station)*, 6 (3), 109–162, pl. 1.
- Cunnington, W.A. (1920) The fauna of the African lakes: A study in comparative limnology with special reference to Tanganyika. *Proceedings of the zoological Society of London*, 1920, 507–662.  
<https://doi.org/10.1111/j.1096-3642.1920.tb03243.x>
- Diodato, S.L., Berasategui, A.A. & Hoffmeyer, M.S. (2006) Morphological types and seasonal variation in eggs of zooplankton species from bottom sediments in Bahía Blanca estuary, Argentina. *Brazilian Journal of Oceanography*, 54, 161–167.  
<https://doi.org/10.1590/S1679-87592006000200007>
- Dussart, B.H. & Defaye, D. (1990) Répertoire mondial des Crustacés Copépodes des eaux intérieures. III. Harpacticoides. *Crustaceana*, Supplement 16, i–vii + 1–384.
- Dutto, M.S., López Abbate, M.C., Biancalana, F., Berasategui, A.A. & Hoffmeyer, M.S. (2012) The impact of sewage on environmental quality and the mesozooplankton community in a highly eutrophic estuary in Argentina. *ICES Journal of marine Science*, 69, 399–409.  
<https://doi.org/10.1093/icesjms/fsr204>
- Elías, R. (1985) Macrobentos del estuario de la Bahía Blanca. I: Mesolitoral. *Spheniscus*, 1, 1–33
- Elías, R. & Bremec, C.S. (1986) Macrobentos del área de Bahía Blanca (Argentina). II. Relaciones entre asociaciones de fondos blandos. *Spheniscus*, 3, 51–52.
- Fiers, F. & Kotwicki, L. (2013) The multiple faces of *Nannopus palustris* auct. reconsidered: a morphological approach (Copepoda: Harpacticoida: Nannopodidae). *Zoologischer Anzeiger*, 253, 36–65.  
<https://doi.org/10.1016/j.jcz.2013.08.001>
- Freije, R.H., Spetter, C., Marcovecchio, J.E., Popovich, C., Botté, S., Negrín, V., Arias, A., Delucchi, F. & Asteasuain, R.O. (2008) Water chemistry and nutrients of the Bahía Blanca estuary. In: Neves, R., Baretta, J. & Mateus, M. (Eds.), *Perspectives on Integrated Coastal Zone Management in South America*. IST Press, Lisbon, pp. 243–256
- Garlitska, L., Neritina, T., Schepetov, D., Mugue, N., De Troch, M., Baguley, J.G. & Azovsky, A. (2012) Cryptic diversity of the “cosmopolitan” harpacticoid copepod *Nannopus palustris*: genetic and morphological evidence. *Molecular Ecology*, 21, 5336–5347.  
<https://doi.org/10.1111/mec.12016>
- Gerlach, S.A. (1958) Die Mangroveregion tropischer Küsten als Lebensraum. *Zeitschrift für Morphologie und Ökologie der Tiere*, 46, 636–730.  
<https://doi.org/10.1007/BF00407459>
- Giere, O. (2009) *Meiobenthology. The microscopic motile fauna of aquatic sediments. 2<sup>nd</sup> Edition*. Springer, Berlin, xvii + 527 pp.
- Gurney, R. (1932) *British Fresh-water Copepoda. Vol. 2*. The Ray Society, London, ix + 336 pp.  
<https://doi.org/10.5962/bhl.title.82138>
- Haberbosh, P. (1917) Über Süßwasser Harpacticiden. *Archiv für Hydrobiologie*, 11, 593–605.
- Hoffmeyer, M.S. (2004) Decadal change in zooplankton seasonal succession in the Bahía Blanca estuary, Argentina, following introduction of two zooplankton species. *Journal of Plankton Research*, 26, 181–189.  
<https://doi.org/10.1093/plankt/fbh023>

- Huys, R. (2009) Unresolved cases of type fixation, synonymy and homonymy in harpacticoid copepod nomenclature (Crustacea: Copepoda). *Zootaxa*, 2183 (1), 1–99.  
<https://doi.org/10.11646/zootaxa.2183.1.1>
- Huys, R. & Boxshall, G.A. (1991) *Copepod Evolution*. The Ray Society, London, 468 pp.
- Huys, R. & Iliffe, T.M. (1998) Novocriiniidae, a new family of harpacticoid copepods from anchihaline caves in Belize. *Zoologica Scripta*, 27, 1–15.  
<https://doi.org/10.1111/j.1463-6409.1998.tb00425.x>
- Huys, R., Gee, J.M., Moore, C.G. & Hamond, R. (1996) Marine and Brackish Water Harpacticoid Copepods. Part 1. In: Barnes, R.S.K. & Crothers, J.H. (Eds.), *Synopses of the British Fauna, New Series. Vol. 51*. Field Studies Council, Shrewsbury, pp. i–viii + 1–352.
- ICZN (International Commission on Zoological Nomenclature) (1999) *International Code of Zoological Nomenclature. 4th Edition*. The International Trust for Zoological Nomenclature, London, xxx + 306 pp.
- Jakobi, H. (1956) Novas espécies de Harpacticoida (Copepoda-Crustacea) provenientes de regiões salobras da costa São Paulo-Paraná. *Dusenía*, 7 (3), 159–161.
- Jakobi, H. (1959) Contribuição para a ecologia dos Harpacticoida (Cop. Crust.). I. Adaptação aos biotopos. *Revista brasileira de Biologia*, 19, 134–150.
- Kiefer, F. (1956) Ruderfusskrebse aus dem Tanganjikasee (Crustacea Copepoda). Ergebnisse der Mission J.J. Symoens (Institut pour la Recherche Scientifique en Afrique Centrale). *Revue de Zoologie et Botanique africaine*, 54, 241–266.
- Kim, J.G., Choi, H.K. & Yoon, S.M. (2017) A reappraisal of the genera *Nannopus* Brady, 1880 and *Ilyophilus* Lilljeborg, 1902 (Copepoda, Harpacticoida, Nannopodidae) with a description of *N. parvipilis* sp. nov. from South Korea. *Crustaceana*, 90, 1351–1365.  
<https://doi.org/10.1163/15685403-00003700>
- Klie, W. (1913) Die Copepoda Harpacticoida des Gebietes der Unter- und Aussenweser und der Jade. *Schriften des Vereins für Naturkunde an der Unterweser*, 3, 1–49.
- Klie, W. (1925) Die Entomostraken der Salzwässer von Oldensloe. In: Thienemann, E. (Ed.), *Das Salzwasser von Oldensloe. Biologische Untersuchungen unter Mitwirkung zahlreicher Fachgenossen herausgegeben von August Thienemann, Plön. Mitteilungen der Geographischen Gesellschaft und des Naturhistorischen Museums in Lübeck*, 30–31, 123–136.
- Lilljeborg, W. (1902) Synopsis specierum huc usque in aquis dulcibus Sueciae observatarum familiae Harpacticidarum. Sive Bidrag till en Öfersikt af de uti Sveriges färska vatten hittills iaktagna Arterna af Familjen Harpacticidae. *Kungliga svenska Vetenskaps-Akademiens Handlingar; ny följd*, 36 (1), 1–75, pls. I–IV.
- Loiseleur-Deslongchamps, J.L.A. (1807) *Flora gallica: seu enumeratio plantarum in Gallia spontè nascentium. Parte 2. Ex Typis Matthaei Migneret, Lutetiae* [Paris], iv + 406 pp., 21 pls. [pp. i–iv, 337–742]
- Meissner, W. (1907) Das Plankton des Aralsees und der einmündenden Flüsse und seine vergleichende Charakteristik. *Biologischen Zentralblatt*, 27 (18), 587–592, 593–604.
- Meissner, W. (1908) Mikroskopische Wassertiere des Aralsees und der einmündenden Flüsse, im Zusammenhang mit der Frage über deren Verbreitungsbedingungen. *Izvestiya Turkestanskogo Otdela imperatorskogo russkogo geograficheskogo Obshchestva*, 4 (8), 1–102, pls. I–IV. [in Russian]
- Piccolo, M.C. & Perillo, G.M.E. (1990) Physical characteristics of the Bahía Blanca estuary (Argentina). *Estuarine, coastal and Shelf Science*, 31, 303–317.  
[https://doi.org/10.1016/0272-7714\(90\)90106-2](https://doi.org/10.1016/0272-7714(90)90106-2)
- Piccolo, M.C., Perillo, G.M.E. & Melo, W.D. (2009) The Bahía Blanca estuary: An integrated overview of its geomorphology and dynamics. In: Neves, R., Baretta, J.W. & Mateus, M. (Eds.), *Perspectives on Integrated Coastal Zone Management in South America*. IST Press, Lisbon, pp. 219–229.
- Plotnikov, I.S. (2016) *Mnogoletniye izmeneniya fauny svobodnozhivushchikh vodnykh bespozvonochnykh Aral'skogo moray. Long-term changes in the fauna of free-living aquatic invertebrates of the Aral Sea*. Zoologicheskiy Institut, Rossiyskoy Akademii Nauk (Zoological Institute, Russian Academy of Sciences), Saint Petersburg, 168 pp. [in Russian]
- Por, F.D. (1984) Notes on the benthic Copepoda of the mangal ecosystem. In: Por, F.D. & Dor, I. (Eds.), *Hydrobiology of the Mangal, the Ecosystem of the Mangrove Forests*. Dr. W. Junk, The Hague, pp. 67–70 + 229–251 (references paged separately).
- Por, F.D. (1986) A re-evaluation of the family Cletodidae Sars, Lang (Copepoda, Harpacticoida). In: Schriever, G., Schminke, H.K. & Shih, C.-t. (Eds.), *Proceedings of the Second International Conference on Copepoda, Ottawa, Canada, 13–17 August, 1984. Syllogeus*, 58, 420–425.
- Por, F.D., Almeida Prado Por, M.S. & Oliveira, E.C. (1984) The mangal of the estuary and lagoon system of Cananea (Brazil). In: Por, F.D. & Dor, I. (Eds.), *Hydrobiology of the Mangal, the Ecosystem of the Mangrove Forests*. Dr. W. Junk, The Hague, pp. 67–70 + 211–228 (references paged separately).
- Pratolongo, P.D., Perillo, G.M.E. & Piccolo, M.C. (2010) Combined effects of waves and plants on a mud deposition event at a mud flat-saltmarsh edge in the Bahía Blanca estuary. *Estuarine, coastal and Shelf Science*, 87, 207–212.  
<https://doi.org/10.1016/j.ecss.2009.09.024>
- Reid, J.W. (1998) Maxillopoda-Copepoda, Harpacticoida. In: Young, P.S. (Ed.), *Catalogue of Crustacea of Brazil. Série Livros No. 6*. Museu Nacional, Rio de Janeiro, pp. 75–127
- Sars, G.O. (1903) Copepoda Harpacticoida. Parts I & II, Misophriidae, Longipediidae, Cerviniidae, Ectinosomidae (part). *An Ac-*

- count of the Crustacea of Norway, with short Descriptions and Figures of all the Species, 5, 1–28, pls. I–XVI.
- Sars, G.O. (1908) Copepoda Harpacticoida. Parts XXIII & XXIV. Laophontidæ (continued). *An Account of the Crustacea of Norway, with short Descriptions and Figures of all the Species*, 5, 257–276, pls. CLXXVII–CXCII.
- Sars, G.O. (1909a) Zoological Results of the Third Tanganyika Expedition, conducted by Dr. W.A. Cunnington, F.Z.S., 1904–1905.—Report on the Copepoda. *Proceedings of the zoological Society of London*, 1909, 31–77, pls. VI–XXIII.  
<https://doi.org/10.1111/j.1096-3642.1909.tb01855.x>
- Sars, G.O. (1909b) Copepoda Harpacticoida. Parts XXVII & XXVIII. Cletodidæ (concluded), Anchorabolidæ, Cylindropsyllidæ, Tachidiidæ (part). *An Account of the Crustacea of Norway, with short Descriptions and Figures of all the Species*, 5, 305–336, pls. CCIX–CCXXIV.
- Sciberras, M., Bulnes, V.N. & Cazzaniga, N.J. (2014) A new species of *Quinquelaophonte* (Copepoda: Harpacticoida) from Argentina. *Zoologia, Curitiba*, 31, 496–502.  
<https://doi.org/10.1590/S1984-46702014000500010>
- Sciberras, M., Huys, R., Bulnes, V.N. & Cazzaniga, N.J. (2018) A new species of *Halectinosoma* Vervoort, 1962 (Copepoda: Harpacticoida) from Argentina, including a key to species with unusual leg armature patterns, notes on wrongly assigned taxa and an updated key to ectinosomatid genera. *Marine Biodiversity*, 48, 407–422.  
<https://doi.org/10.1007/s12526-017-0806-0>
- Scott, T. (1902) Notes on gatherings of Crustacea collected by the fishery steamer “Garland”, and the steam trawlers “Star of Peace” and “Star of Hope”, of Aberdeen, during the year 1901. *Reports of the Fishery Board for Scotland, Edinburgh*, 20 (3), 447–485, pls. XXII–XXV.
- Shen, C.-j. & Tai, A.-y. (1964) Description of new species of freshwater Copepoda from Kwangtung Province, South China. *Acta zootaxonomica sinica*, 1, 367–396 [in Chinese with English summary]
- Staton, J.L., Wickliffe, L.C., Garlitska, L., Villanueva, S.M. & Coull, B.C. (2005) Genetic isolation discovered among previously described sympatric morphs of a meiobenthic copepod. *Journal of crustacean Biology*, 25, 551–557.  
<https://doi.org/10.1651/C-2600.1>
- Treadwell, A.L. (1923) Duas novas especies de Anelidos Polychetos do genero *Nereis*. *Revista do Museu Paulista*, 13, 1–10.
- Vakati, V., Eyun, S. & Lee, W. (2019) Unraveling the intricate biodiversity of the benthic harpacticoid genus *Nannopus* (Copepoda, Harpacticoida, Nannopodidae) in Korean waters. *Molecular Phylogenetics and Evolution*, 130, 366–379.  
<https://doi.org/10.1016/j.ympev.2018.10.004>
- Vakati, V., Kihara, T.C. & Lee, W. (2016) A new species of the genus *Nannopus* (Copepoda, Harpacticoida, Nannopodidae) from the mudflat of Ganghwa Island, Korea. *Proceedings of the biological Society of Washington*, 129, 212–233.  
<https://doi.org/10.2988/0006-324X-129.Q3.212>
- Vakati, V. & Lee, W. (2017) Five new species of the genus *Nannopus* (Copepoda: Harpacticoida: Nannopodidae) from intertidal mudflats of the Korean West Coast (Yellow Sea). *Zootaxa*, 4360 (1), 1–66.  
<https://doi.org/10.11646/zootaxa.4360.1.1>
- Vakati, V. & Lee, W. (2021) On two new species of *Nannopus* Brady, 1880 (Copepoda: Harpacticoida: Nannopodidae) from intertidal mudflats of the Korean West Coast (Yellow Sea). *Zootaxa*, 5051 (1), 529–549.  
<https://doi.org/10.11646/zootaxa.5051.1.21>
- Wells, J.B.J. (1971) The Harpacticoida (Crustacea: Copepoda) of two beaches in south-east India. *Journal of natural History*, 5, 507–520.  
<https://doi.org/10.1080/00222937100770381>
- Zykoff, W.P. (1905) Bemerkung über das Plankton des Wolgadeltas. *Zoologischer Anzeiger*, 29, 278–283.