



ELSEVIER

Deep-Sea Research II 51 (2004) 1629–1641

DEEP-SEA RESEARCH
PART II

www.elsevier.com/locate/dsr2

Kliopsyllus andeep sp. n. (Copepoda: Harpacticoida) from the Antarctic deep sea—a copepod closely related to certain shallow-water species

Gritta Veit-Köhler*

DZMB—German Centre for Marine Biodiversity Research, Senckenberg Research Institute, Südstrand 44,
D-26382 Wilhelmshaven, Germany

Received 31 January 2004; received in revised form 28 May 2004; accepted 27 June 2004
Available online 27 October 2004

Abstract

The international scientific deep-sea cruise ANDEEP-2 (ANT XIX/4) to the Scotia Arc and the northern Weddell Sea in 2002 revealed a new species of the family Paramesochridae (Copepoda: Harpacticoida). *Kliopsyllus andeep* sp. n. can be distinguished from its congeners by characteristics such as a two-segmented endopod on the fourth leg and an additional seta on the endopod of the third leg. The most striking feature is its strong, flexed, chitinous thorns on the telson. Only three species in the family have such appendages, all of them interstitial, shallow-water species. Because the new species lacks the strong abdominal muscle observed by Kunz in *Kliopsyllus furcavaricatus* Kunz, 1974, it cannot spread its furcal rami using the thorns on the telson as antagonists the way the shallow-water species does. The furcal-rami spreading system, which is an adaptation to interstitial living, for *K. andeep* sp. n. is irrelevant, because the species has been collected from muddy sediments. Therefore, the abdominal muscle might have been lost during the species' evolution.

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1. Introduction

Compared to the meiofauna of beaches, inshore regions, and coastal shelves, deep-sea meiofauna has received little attention. In much previous work, benthic deep-sea copepods have

been studied only on the level of higher taxon and are referred to as “harpacticoids” (see, for example, Alongi, 1992; Herman and Dahms, 1992; Vanhove et al., 1995). Only a few deep-sea families have been studied in detail (Becker et al., 1979; Itô, 1982, 1983; Moura and Pottek, 1998; Por, 1969). Although the number of species-level investigations (see, for example, Thistle, 1978, 1979; Thistle and Eckman, 1990; Thistle et al., 1993) and diversity analyses (Thistle, 1998) based

*Tel.: +49-4421-9475-102; fax: +49-4421-9475-1111.

E-mail address: gveit-koehler@senckenberg.de
(G. Veit-Köhler).

on working species are increasing, the taxonomy of deep-sea copepods remains little known. Further, recent results show that some of the smallest harpacticoids, such as Paramesochridae or Cylindropsyllidae, which had formerly been thought to be exclusively interstitial, have invaded the interstitium-lacking muds of the deep sea (Becker et al., 1979; Thistle, 1982; Veit-Köhler, in press).

The members of the meiobenthic family Paramesochridae are typically small, cylindrical, interstitial animals, that inhabit sandy-beach ground water, and intertidal and shallow-water sandy sediments. *Kliopsyllus andeep* sp. n. belongs to a genus with 29 species known from shallow areas and beaches. Recently, the first species from the deep sea was described: *Kliopsyllus diva* (Veit-Köhler, in press), which was collected during the DIVA-1 cruise (Meteor 48/1) to the deep Angola Basin. Becker et al. (1979) placed a deep-sea species in *Kliopsyllus*, but it was removed by Kunz (1981).

2. Materials and methods

The sampling area in the Weddell Sea is situated at the North Weddell Kosminski Fracture Zone. *K. andeep* sp. n. was found in two replicate multicorer (MUC) hauls at station 138. One female was found in PS 61/138-9 (corer 2) at 62°57,90'S and 27°54,13'W at a depth of 4540.8 m, which was sampled on 03-17-02. A second female was found in PS 61/138-11 (corer 2) at 62°58,03'S and 27°54,08'W at a depth of 4541.3 m, which was sampled on 03-18-02.

The formalin-preserved upper 5-cm sediment layer was washed with tap water through a 40- μ m mesh sieve. Meiofauna was extracted from remaining particles by centrifugation with a colloidal silica polymer (H.C. Stark, Levasil 200/40%, $\rho=1.17$) as flotation medium. Kaolin was used to cover the heavier particles in order to retain them at the bottom of the centrifuge beaker while decanting the supernatant containing the specimens (McIntyre and Warwick, 1984). The centrifugation was repeated three times at 4000 rpm for 6 minutes, each time. After each centrifugation,

the floating matter was decanted and rinsed with tap water. Meiofauna was sorted to the higher-taxon level, and copepods were subsequently transferred to glycerine. *Kliopsyllus* specimens were detected with the aid of a Leica MZ 12.5 stereomicroscope.

Before dissection, the holotype of *K. andeep* sp. n. was drawn from the dorsal side and detailed dorsal and lateral drawings of the abdomen were made. The paratype was dissected without preliminary drawings. The dissected parts were mounted on slides in glycerine. Drawings were made with the aid of a camera lucida on a Leica DMR microscope equipped with differential interference contrast (DIC) at 1000 \times magnification. All specimens are registered in the collection of the University of Oldenburg (=UNIOL-collection), Department of Zoosystematics and Morphology and kept at the German Centre for Marine Biodiversity Research (DZMB) in Wilhelmshaven, Germany.¹

3. Taxonomy

3.1. Material

The examined specimens are registered in the UNIOL-collection.

Female holotype: No. 2004.009/1–6 (6 slides), PS 61/138-11 (corer 2), 62°58,03'S 27°54,08'W, 03-18-02, depth 4541.3 m. Female paratype: No. 2004.010/1-7 (7 slides), PS 61/138-9 (corer 2), 62°57,90'S 27°54,13'W, 03-17-02, depth 4540.8 m.

3.2. Etymology

The species name *andeep* refers to the ANDEEP 1 + 2 campaigns of RV *Polarstern* (cruise PS 61) to the Weddell Sea, the Scotia Arc, and the Antarctic Peninsula in 2002. ANDEEP stands for ANtartic benthic DEEP-sea biodiversity—colonization history and recent community patterns.

¹Abbreviations used in the text: exp=exopod, enp=endopod, benp=baseendopod, P1–P6=swimming legs 1–6, “enp1 P2”=the first segment of the endopod of P2.

3.3. Description

3.3.1. Female

Habitus (Fig. 1). Total body length measured from anterior tip of rostrum to posterior margin of telson: 0.28 mm (holotype). Including the furcal rami: 0.32 mm.

Body cylindrical (Fig. 1A), slightly depressed dorsoventrally, with prosome only slightly wider than urosome. Whole body covered with small, round depressions resembling the surface of a golf ball. Pores and sensilla are present in small numbers, distributed dorsally and laterally on the cephalothorax and first three free somites. Somites four and five with pores only. Somitic hyaline frills only slightly developed.

The eighth free somite carries a thin but well-developed pseudoperculum. Telson very short. Furcal rami of adult female (Fig. 1B and C) long and cylindrical, six times longer than wide, with 6 visible elements: seta I not detected, seta II slender, dorsally displaced, seta III slender, stalked, clearly smaller than II, situated laterally at posterior end, seta IV and V long and slender, situated terminally, seta VI minute, situated at inner margin of caudal rami, and seta VII slender pinnate, on inner dorsal surface of furcal rami.

Telson laterally furnished with strong, chitinous, dorsally flexed appendages. The appendages carry a minute sensillum on the dorsal surface. Tips of the appendages seem to be cut through by channels, but real pores could not be detected because of cuticle at the tips of the appendages. The cuticle at the tips is not as strong as in the lateral parts of the channels.

Rostrum. Small, hyaline, only slightly visible beneath the cephalothorax, with a pair of minute, anterior sensilla.

Antennule (Fig. 2). Eight-segmented, ornamented with few cuticular depressions, segment I with spinules along inner margin.

Setal ornamentation:

- I (0)
- II (9) 3 pinnate setae and 6 slender naked setae, three of which small
- III (7) 3 long slender naked, 1 slender naked, and 3 pinnate setae, one of which small

- IV (2 + 2) 2 pinnate setae and 1 aesthetasc fused at base with long slender seta
- V (1) 1 long slender naked seta
- VI (1) 1 small naked seta
- VII (4) 1 large pinnate seta on posterior margin, 2 slender naked and 1 small pinnate seta on anterior margin
- VIII (6 + 2) 6 slender naked setae of different sizes, and 1 aesthetasc fused at base with naked seta

Antenna (Fig. 3A). Basis asetose with some small spinules. Endopod two-segmented. Enp1 with one long, pinnate abexopodal seta. Enp2 with several spinule rows, subapically with four setae, two of which slender, naked, one slender pinnate, and one small, stout pinnate seta. Apical margin with seven setae, five of which of different sizes, geniculate and pinnate, one pinnate flexible seta and one small, naked seta. Exopod one-segmented with spinule row, one inner slender seta, and four upright setae of different sizes with transversally cut, naked tips.

Mandible (Fig. 3D). Coxa with slender, elongated, terminally widening gnathobasis. Cutting edge with several strong teeth. Basis with one seta, palp biramous. Enp two-segmented: first segment bears two slender setae, second segment with one seta, apically with four naked, slender setae fused together at base. Exp half the size of enp, one-segmented, with four apical slender setae, three of which pinnate.

Maxillula (Fig. 3B). Praecoxal arthrite with two juxtaposed slender setae on anterior surface and one naked seta laterally on posterior surface. Inner margin of arthrite with seven strong, stout spines, each of characteristic shape and one strong additional seta. Coxal endite with three slender naked and one pinnate seta. Basis with endite armed with altogether eight slender setae, two of which pinnate. Enp one-segmented with six slender setae, two laterally, one of which pinnate, three apically, and one on inner margin. Exp one-segmented with two small, pinnate setae.

Maxilla (Fig. 3C). Prae-coxa and coxa fused to form syncoxa bearing three endites. No separation towards basis visible. Proximal endite slightly bilobed, one unipinnate spine on proximal lobe,

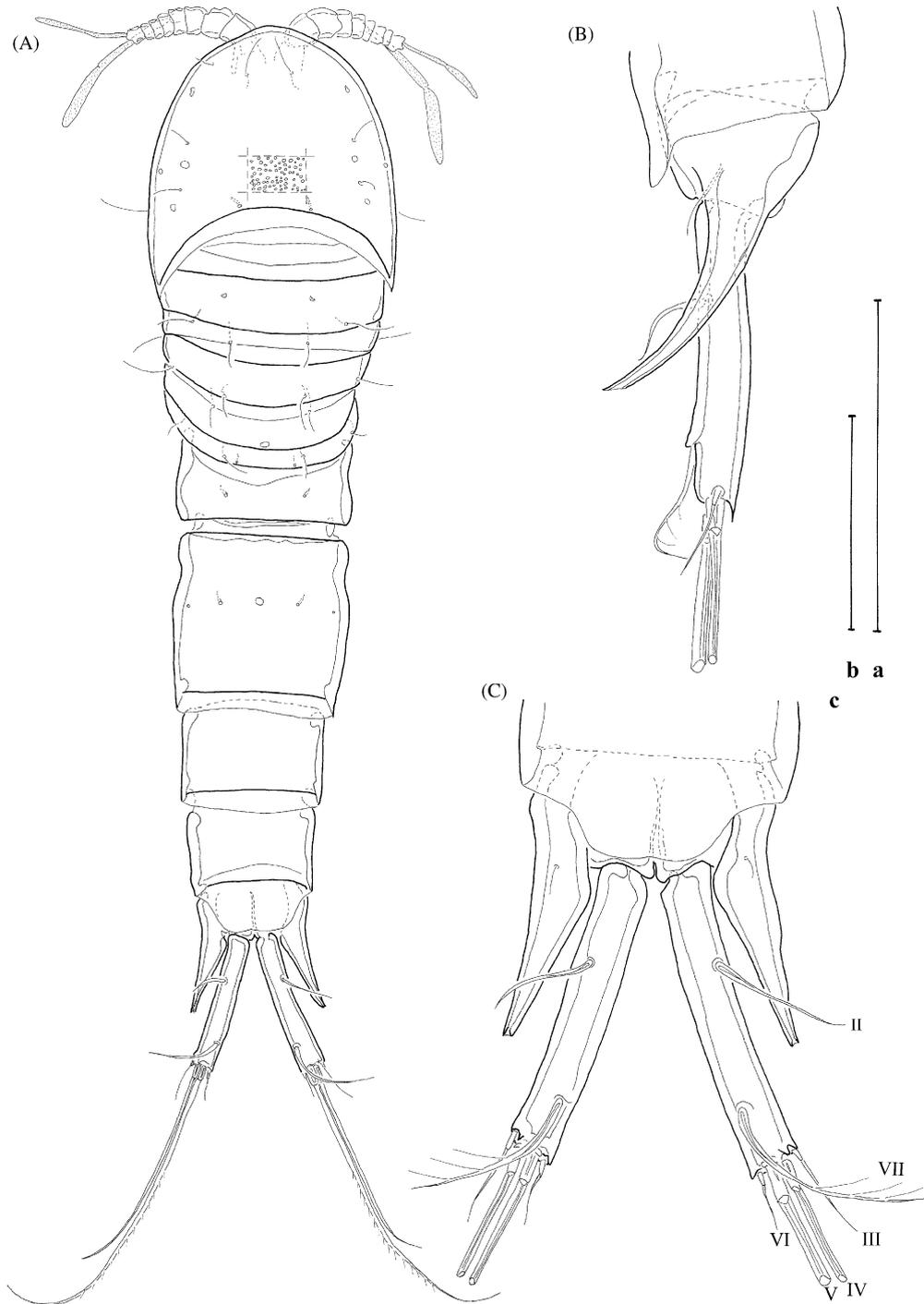


Fig. 1. *Kliopsyllus andeep* sp. n. (A) Female habitus, dorsal (Holotype). (B) Armature of telson and furcal rami, lateral view (Holotype). (C) Armature of telson and furcal rami, dorsal view (Holotype). Scale bars: *a*, 0.1 mm; *b,c*, 0.03 mm.

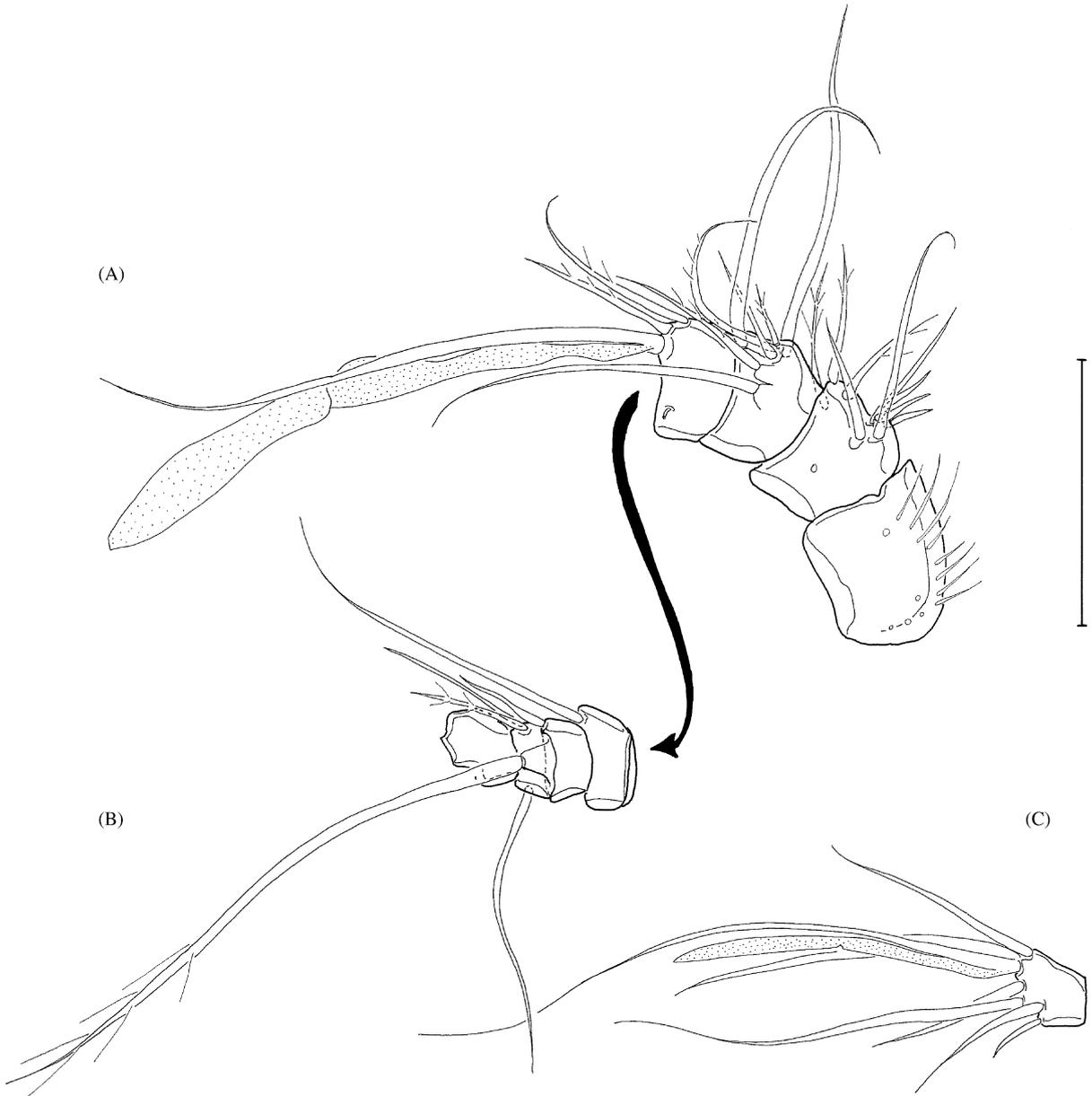


Fig. 2. *Kliopsyllus andeep* sp. n. Female antennula (Holotype). (A) Segments I–IV, dorsal view. (B) Setation of segments V–VII and location of segment VIII, dorsal view. (C) Setation of segment VIII. Scale bar = 0.02 mm.

one pinnate spine and one naked seta on distal lobe. Middle endite with one pinnate and two naked setae. Distal endite armed with two toothed spines and one naked seta. Basis with stout, toothed claw accompanied by two strong, naked setae. Enp two-segmented with one naked, one

pinnate, and one small seta on first segment, and one pinnate and three naked setae on second.

Maxilliped (Fig. 3E). Basis with a row of long spinules. Enp one-segmented with a naked seta medially, a small seta and two long, geniculate setae apically.



Fig. 3. *Kliopsyllus andeep* sp. n. (A) Female antenna (Paratype). (B) Female maxillula (Holotype). (C) Female maxilla (Holotype). (D) Female mandible (Holotype). (E) Female maxilliped (Holotype). Scale bar = 0.02 mm.

Swimming legs (Fig. 4, Table 1). With highly modified rami and naked intercoxal sclerites. Surface of P2–P4 more or less completely covered with small depressions not visible in P1.

P1 (Fig. 4A): As the P1 is comparably small and could not be separated from the cephalothorax without causing severe damage, it was kept together with the maxilliped and the mouthparts as a whole. Therefore, tiny spinules, pores, and surface structures might have been overlooked. Nevertheless, the general segmentation and setation was clearly visible.

Basis with one outer, pinnate seta. Enp slightly longer than exp, both rami two-segmented and armed with spinules, which in enp are very fine and long. Enp1 without seta, enp2 with one naked, terminal seta and one long, pinnate outer seta. Exp1 with one outer pinnate seta. Exp2 with one long, outer pinnate seta and three long, pinnate setae, two of which terminal and one inner terminal.

P2–P4 (Fig. 4B–D): Swimming legs more or less covered by round cuticular depressions. Surface of coxa in P3 (Fig. 4C) ornamented with a few spinules. Basis of P3 and P4 (Fig. 4D) bears one slightly plumose outer seta accompanied by several spinules. All bases bear row of very long and thin spinules at inner margin. Three-segmented exopods longer than endopods with spinules along outer margin, on posterior side of exp1 (P2–P4) and apically on exp3 (P2, P4). Very long, thin spinules on inner margin of exp1 (P2–P4).

Exp1, exp2, and exp3 of P2 and P3 with stout, outer spines, serrated on either side. P4 exp1 and exp2 armed with similar spines. Exp2 P2 with pore posteriorly. Exp3 in P2 and P3 with outer, subterminal spine comparable to spines of exp1 and exp2, but longer. Exp3 P2 and P3 with one strong, terminal bipinnate seta, outer spinules short, inner spinules long, and one inner, terminal pinnate seta with long spinules on inner side. Exp3 P4 with terminal outer spine furnished only on one side with feathery frill and only one additional terminal bipinnate seta with short spinules on the outer and long spinules at the inner side.

Endopods P2 and P3 one-segmented, with spinule rows along outer side and apically accompanying a long, bipinnate terminal seta.

Enp P3 anteriorly with pore (see Fig. 4C, drawn from posterior side) and with additional slightly pinnate inner seta. Enp P4 two-segmented with spinule rows on outer margin (enp1 and enp2) and apically as well as posteriorly in enp2. Enp1 P4 with inner, naked seta and enp2 terminally with outer spine with feathery frill on outer side and one inner bipinnate seta.

P5 (Fig. 5A): Legs fused, small exopod clearly separated from basendopodite. Benp bears an outer, basal plumose seta and an anterior pore. The surface of the benp is decorated with three spinule rows on each of the drawn-out, endopodal parts. Benp each with two stout terminal setae, the outer pinnate, the inner bipinnate. Exp with three stalked setae, the outermost pinnate and longer than the other ones. Inner margin of enp armed with two separate spinule rows.

Genital complex and P6 (Fig. 5B): Genital field (see Fig. 5B). Sixth leg represented by small, fused outgrowth, with a plumose seta and a small thorn placed on a slight protrusion.

4. Discussion

4.1. Systematics

4.1.1. History of the genus *Kliopsyllus*

Kliopsyllus was erected by Kunz (1962) who grouped species that formerly belonged to the genera *Paramesochra* T. Scott, 1892, *Emertonia* Wilson, 1932, and *Leptopsyllus* T. Scott, 1894. He did not incorporate *Paramesochra acutata* Klie, 1935, that had been placed in the new genus *Emertonia* by Nicholls (1945). Because *Paramesochra acutata* (= *Emertonia acutata* (Klie, 1935), after Nicholls (1945)), showed some clear typical characters of the genus *Paramesochra*, such as two-segmented endopods in P2–P4 with one terminal seta on the enp2, it was not accepted in the new genus *Kliopsyllus* by Kunz.

At present, *Kliopsyllus* contains 29 species (including that described in this paper) and seven subspecies (compare Bodin, 1997). According to Wells and Rao (1987), the taxonomic position of *Kliopsyllus arenicolus* (Krishnaswamy, 1957), *Kliopsyllus wilsoni* (Krishnaswamy, 1957), *Kliopsyllus longifurcatus*

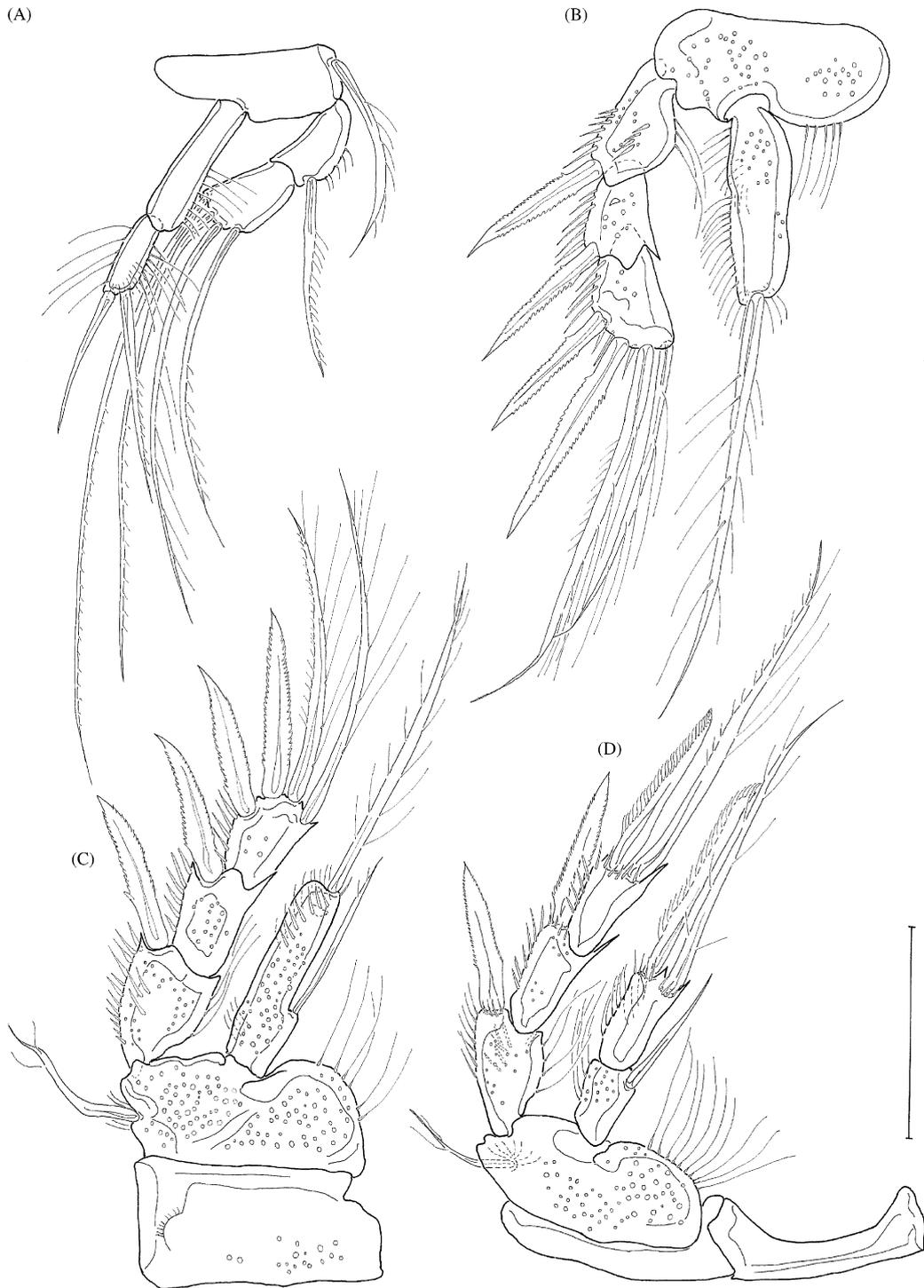


Fig. 4. *Kliopsyllus andeep* sp. n. (A) Female P1 (Holotype). (B) Female P2 (Paratype). (C) Female P3 (Paratype). (D) Female P4 with intercoxal sclerite (Paratype). Scale bar = 0.02 mm.

Table 1
Seta and spine formula of swimming legs of female *Kliopsyllus andeep* sp. n

	Basis	Exopod	Endopod
P1	0.1	0.121	0.011
P2	0.0	0.0.112	010
P3	0.1	0.0.121	110
P4	0.1	0.0.020	1.020

Scheibel, 1975 and *Kliopsyllus paraholsaticus* Mielke, 1975 remains uncertain because Wells and Rao were not convinced that the four species were distinct from *Kliopsyllus holsaticus* (Klie, 1929). *Kliopsyllus gracilis* (Wilson, 1932) and *Kliopsyllus laurenticus* (Nicholls, 1939) are of uncertain systematic position (Kunz, 1962, 1981) because of a one-segmented exopod in the P1 in the first species and two-segmented exopods P2–P4 in the latter species.

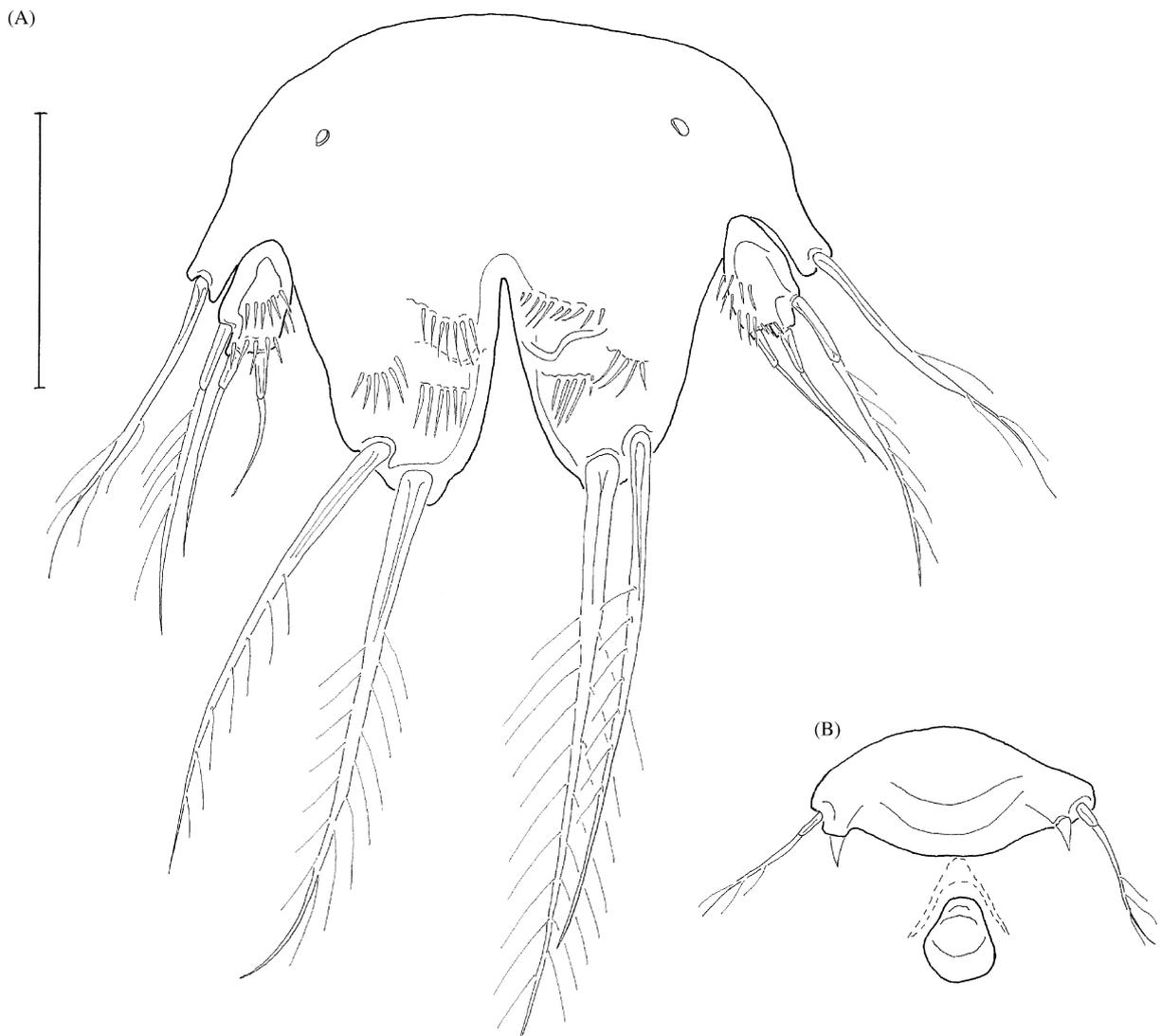


Fig. 5. *Kliopsyllus andeep* sp. n. (A) Female P5 (Paratype). (B) Female P6 and genital field (Paratype). Scale bar = 0.02 mm.

Wells et al. (1975) incorporated the whole genus of *Krishnapsyllus* Kunz, 1974 into *Kliopsyllus*. When Kunz (1974) erected the genus *Krishnapsyllus*, he grouped the two species *Kliopsyllus furcavaricatus* (Kunz, 1974) (described as *Krishnapsyllus furcavaricatus*) and *Kliopsyllus longisetosus* (Krishnaswamy, 1951) (described as *Paramesochra longisetosa*) because they had large, lateral, chitinous appendages on the telson. He stated that this character cannot be found in other Paramesochridae, but he did not realize that it was he himself who described the first Paramesochridae, *Paramesochra pterocaudata* Kunz, 1936, with arched appendages at the telson (Kunz, 1936).

4.1.2. Characterization of *Kliopsyllus* within the Paramesochridae

Because a complete revision of the genus is beyond the scope of this paper, autapomorphies that indicate a possible monophyletic origin of *Kliopsyllus* cannot be given. *Kliopsyllus* might be a collection of species that share certain plesiomorphic characteristics, which can be found in other taxa of Paramesochridae. Because in most of the species the mouthparts are not adequately described, the diagnosis given for the known *Kliopsyllus* species can only be a working diagnosis. It is based on the segmentation and armature of the swimming legs (derived from drawings): P1 exp two-segmented, enp one (doubtful because of insufficient description quality) or two segments; P2–P3 exp three-segmented, enp one-segmented with one seta; P4 exp three-segmented, exp3 with two or three setae, enp one-segmented with one or two setae.

Huys (1987) erected a cladogram of the Paramesochridae. He remarked that within a *Paramesochra*-group that included *Paramesochra*, *Kliopsyllus* and *Kunzia*, a lineage *Kliopsyllus*-*Kunzia* could be defined by three “apomorphies: (1) endopodite P2–P4 uniaarticulated; (2) exopodite P1 with 4 setae on distal segment (parallel evolution in *Scottopsyllus*-group); (3) distal segment exopodite P4 with 3 setae”. But having a closer look at other Paramesochridae, it becomes obvious that the characteristics given by Huys are no apomorphies according to Hennig (1966): Uniaarticulated endopodites in P2–P4 (1) can also

be found in species of *Scottopsyllus* (*Intermedopsyllus*) Kunz, 1981 and *Scottopsyllus* (*Wellsopsyllus*) Kunz, 1981 (according to Huys a parallel evolution). The exp P1 has four setae on the distal segment (2) not only in Huys’ *Scottopsyllus*-group including *Scottopsyllus* Kunz, 1962, *Leptopsyllus*, *Apodopsyllus* Kunz, 1962 and *Caligopsyllus* Kunz, 1975 but also in *Paramesochra* (both cases parallel evolutions according to Huys). And the distal segment of exp P4 (3) does not carry three but two or three setae in *Kliopsyllus* and two in *Kunzia*, which can also be observed in *Paramesochra* (two to four setae), *Scottopsyllus* (two setae), *Apodopsyllus* (two setae), and some *Leptopsyllus*-species (two setae).

A comparison of segmentation and armature of the swimming legs of different Paramesochridae, in general, can be used to further illustrate this unsatisfactory situation. Within the Paramesochrinae Huys, 1987, similar segmentation of P1 as in *Kliopsyllus* can be found in *Paramesochra*, *Scottopsyllus*, *Apodopsyllus*, *Biuncus* Huys, 1996, and *Leptopsyllus*. Numbers of segments and endopodal setae of P2 and P3 of *Kliopsyllus* are comparable to *Kunzia* and some *Scottopsyllus* (*Scottopsyllus*) Kunz, 1962 species. Numbers of segments and exopodal and endopodal setae of P4 are comparable to *Kunzia*, *Scottopsyllus* (*Wellsopsyllus*) and *Leptopsyllus* Lang, 1944 but in no case to *Paramesochra*, the nearest relatives of the *Kliopsyllus*-*Kunzia* lineage according to Huys. These observations clearly show that apomorphies based on single characters have to be found for the different genera, as the existing system in many parts is based only on different combinations of the same characters. A thorough revision of the Paramesochridae is needed.

4.1.3. Placement of *K. andeep* sp. n. and differentiation from congeners

Given the current taxonomic situation, I have placed the new species provisionally in *Kliopsyllus* because the species’ characters agree with the short diagnosis given above in the combination of many characters, such as the two-segmented exp and enp of P1, the three-segmented exp P2–P4, two setae in exp3 P4, and a one-segmented enp with one seta in P2.

A one-segmented enp with a terminal seta is also present in P3, but in contrast to the other *Kliopsyllus* species, an additional inner seta can be observed in *K. andeep*. Another difference is a two-segmented enp in P4, which carries, additionally to the two apical setae observed in other *Kliopsyllus* species, another inner seta at the enp1. This inner seta at enp1 P4 can also be observed in *Paramesochra*, but never in combination with two but always only one well-developed apical seta at the enp2 P4 and always together with two-segmented endopods in P2 and P3. Only *Scottopsyllus* has the same combination of one-segmented enp P2 and P3 and a two-segmented enp P4, but with the difference that *Scottopsyllus* bears no setae on the enp P2 and P3 and only one seta at the enp P4.

Still the most striking features are its thorn-like appendages at the telson, which have only been observed in three other Paramesochridae, two of which are species of *Kliopsyllus* (see below). The existence of this outstanding character in species of different genera additionally emphasizes the necessity for checking the systematics of the family because it is doubtful that such a complicated feature could have evolved twice.

The unique armature and segmentation of P3 and P4, the thorn-like appendages on the telson, and the ecological circumstances making it the first deep-sea Paramesochridae with this very rare feature are the decisive factors for presenting *K. andeep* sp. n. as a species new to science.

5. Ecology

K. andeep sp. n. is most similar to *Kliopsyllus furcavaricatus* and *Kliopsyllus longisetosus*. Only one additional species of Paramesochridae with the same appendages at the telson exists: *Paramesochra pterocaudata*.

Kliopsyllus furcavaricatus (Kunz, 1974) was described from 3 m depth on coral sand in a coral reef north of the port in Tanga (Tanzania, East Africa). It has strongly developed, dorsally flexed thorns on the telson. Its furcal rami can be spread laterally by a pair of strong muscles in the fourth abdominal segment (Kunz, 1974). The flexed

thorns, an elastic component of the exoskeleton, serve as antagonistic structures, pushing the furcal rami back to their former position when the muscles relax.

Kunz (1974) presented two possible explanations for the furcal-rami spreading system. First, the animal might use the mechanism for its movements through the interstitial habitat, using the structure to support itself on the grains behind it. He indicates that a sensory structure at the tip of each thorn could be used for rearward orientation. Secondly, the animal could anchor itself between the sand grains when interstitial water moves due to wave action. Unluckily, Kunz could not provide live observations, nor can I for the new species. Only two other known Paramesochridae, *Kliopsyllus longisetosus* (Krishnaswamy, 1951) from Madras (India) and *Paramesochra pterocaudata* from Amphioxus-sands at Helgoland, have the same thorns on the anal somite, but the simple descriptions give no hint as to the existence of the muscles.

K. andeep sp. n. from the Antarctic presumably lives in the organic fluff layer (Vanreusel and De Mesel, 2003) or at most in the first millimeters of the gray, clayey silt (Howe, 2003) of the deep-sea site sampled. There is no need for holding on in between the sand grains, firstly as there is no interstitial habitat in such a sediment, secondly as there is no wave action. Another new *Kliopsyllus* species (from the Angola Basin, DIVA cruise, Meteor 48/1) with thorns has been collected at a depth of about 5400 m and will be described in a forthcoming paper, but so far no specimens with spread furcal rami have been found either in the ANDEEP or in the DIVA material. This circumstance is not surprising because these animals do not seem to have the strong muscle observed by Kunz in the interstitial, shallow-water species.

Acknowledgments

The author thanks Dr. Ann Vanreusel and Ilse De Mesel as well as Prof. Dr. Andrew Gooday for sampling the material on board FS Polarstern. The service team of the DZMB, Jutta Heitfeld, Annika Henche, and Marco Bruhn centrifugated the

samples and sorted the meiofauna. The members of the Department of Zoosystematics and Morphology of the University of Oldenburg compiled the picture catalog of the Paramesochridae, an invaluable help for taxonomic work. Dr. Elke Willen and Prof. Dr. David Thistle are especially thanked for their helpful and valuable criticisms of the manuscript. This is ANDEEP publication No. 33.

References

- Alongi, D.M., 1992. Bathymetric patterns of deep-sea benthic communities from bathyal to abyssal depths in the western South Pacific (Solomon and Coral Seas). *Deep-Sea Research* 39 (3/4), 549–565.
- Becker, K.-H., Noodt, W., Schriever, G., 1979. Eidonomie und Taxonomie abyssaler Harpacticoida (Crustacea, Copepoda) Teil II. Paramesochridae, Cylindropsyllidae und Cleto-didae. *Meteor Forschungs Ergebnisse D* 31, 1–37.
- Bodin, Ph., 1997. Catalogue of the new marine Harpacticoid Copepods. Documents de travail de l'Institut royale des Sciences naturelles de Belgique, vol. 89, 304pp.
- Hennig, W., 1966. Phylogenetic Systematics. University of Illinois Press, Urbana, Chicago, London, 264pp.
- Herman, R.L., Dahms, H.U., 1992. Meiofauna communities along a depth transect off Halley Bay (Weddell Sea-Antarctica). *Polar Biology* 12, 313–320.
- Howe, J.A., 2003. Recent depositional environments of the north western Weddell Sea and South Sandwich Trench. In: Fütterer, D.K., Brandt, A., Poore, G.C.B. (Eds.), *The Expeditions ANTARKTIS-XIX/3-4 of the Research Vessel POLARSTERN in 2002*. *Berichte zur Polarforschung* 470, 124–127.
- Huys, R., 1987. *Paramesochra* T. Scott, 1892 (Copepoda, Harpacticoida): a revised key, including a new species from the SW Dutch coast and some remarks on the phylogeny of the Paramesochridae. *Hydrobiologia* 144, 193–210.
- Itô, T., 1982. Harpacticoid copepods from the Pacific abyssal off Mindanao. I. Cerviniidae. *Journal of the Faculty of Science Hokkaido University* 23 (1), 63–127.
- Itô, T., 1983. Harpacticoid copepods from the Pacific abyssal off Mindanao. II. Cerviniidae (cont.), Thalestridae, and Ameiridae. *Publications of the Seto Marine Biological Laboratory* 28 (1/4), 151–254.
- Krishnaswamy, S., 1951. Three new species of sand-dwelling copepods from the Madras coast. *Annals and Magazine of Natural History* 12 (4), 273–280.
- Krishnaswamy, S., 1957. Two new psammophilous copepods from Madras. *Zoologischer Anzeiger* 159, 230–235.
- Kunz, H., 1936. Neue Harpacticoiden (Crustacea Copepoda) von Helgoland. *Kieler Meeresforschungen* 1, 352–358.
- Kunz, H., 1962. Revision der Paramesochridae (Crust. Copepoda). *Kieler Meeresforschungen* 18 (2), 245–257.
- Kunz, H., 1974. Zwei neue afrikanische Paramesochridae (Copepoda Harpacticoida) mit Darstellung eines Bewegungsmechanismus für die Furkaläste. *Mikrofauna des Meeresbodens* 36, 1–20.
- Kunz, H., 1981. Beitrag zur Systematik der Paramesochridae (Copepoda, Harpacticoida) mit Beschreibung einiger neuer Arten. *Mitteilungen des Zoologischen Museums der Universität Kiel* I 8, 2–33.
- McIntyre, A.D., Warwick, R.M., 1984. Meiofauna techniques. In: Holme, N.A., McIntyre, A.D. (Eds.), *Methods for the Study of Marine Benthos*. Blackwell, Oxford, pp. 217–244.
- Moura, G., Pottek, M., 1998. *Selenopsyllus*, a new genus of Cylindropsyllinae (Copepoda, Harpacticoida) from Atlantic and Antarctic Deep waters. *Senckenbergiana Maritima* 28 (4/6), 185–209.
- Nicholls, A.G., 1945. Marine Copepoda from western Australia. V. A new species of *Paramesochra*, with an account of a new harpacticoid family, the Remaneidae, and its affinities. *Journal of the Royal Society of Western Australia* 29, 91–105.
- Por, F.D., 1969. Deep-sea Cerviniidae (Copepoda: Harpacticoida) from the western Indian Ocean, collected with R/V Anton Bruun in 1964. *Smithsonian Contributions to Zoology* 29, 1–60.
- Thistle, D., 1978. Harpacticoid dispersion patterns: implications for deep-sea diversity maintenance. *Journal of Marine Research* 36, 377–397.
- Thistle, D., 1979. Deep-sea harpacticoid copepod diversity maintenance: the role of Polychaetes. *Marine Biology* 52, 371–376.
- Thistle, D., 1982. Aspects of the natural history of the harpacticoid copepods of San Diego Trough. *Biological Oceanography* 1 (3), 225–238.
- Thistle, D., 1998. Harpacticoid copepod diversity at two physically reworked sites in the deep sea. *Deep-Sea Research II* 45, 13–24.
- Thistle, D., Eckman, J.E., 1990. The effect of a biologically produced structure on the benthic copepods of a deep-sea site. *Deep-Sea Research* 37 (4), 541–554.
- Thistle, D., Hilbig, B., Eckman, J.E., 1993. Are polychaetes sources of habitat heterogeneity for harpacticoid copepods in the deep-sea? *Deep-Sea Research I* 40 (1), 151–157.
- Vanhove, S., Wittoeck, J., Desmet, G., Van den Berghe, B., Herman, R.L., Bak, R.P.M., Nieuwland, G., Vosjan, J.H., Boldrin, A., Rabitti, S., Vincx, M., 1995. Deep-sea meiofauna communities in Antarctica: structural analysis and relation with the environment. *Marine Ecology Progress Series* 127, 65–76.
- Vanreusel, A., De Mesel, I., 2003. Biogeography and biodiversity patterns of the metazoan meiobenthos in deep Antarctic waters with special emphasis on free-living marine nematodes. In: Fütterer, D.K., Brandt, A., Poore, G.C.B. (Eds.), *The Expeditions ANTARKTIS-XIX/3-4 of the Research Vessel POLARSTERN in 2002*. *Berichte zur Polarforschung*, vol. 470, pp. 57–60.

- Veit-Köhler, G., in press. First deep-sea record of the genus *Kliopsyllus* Kunz, 1962 (Copepoda: Harpacticoida) with the description of *Kliopsyllus diva* sp. n.—the most abundant member of Paramesochridae at two different sites of the Angola Basin. *Organisms, Diversity and Evolution*.
- Wells, J.B.J., Rao, G.C., 1987. Littoral Harpacticoida (Crustacea: Copepoda) from Andaman and Nicobar Islands. *Memoirs of the Zoological Survey of India* 16 (4), 1–385.
- Wells, J.B.J., Kunz, H., Rao, G.C., 1975. A review of the mechanisms for movement of the caudal furca in the family Paramesochridae (Copepoda Harpacticoida), with a description of a new species of *Kliopsyllus* Kunz. *Mikrofauna des Meeresbodens* 53, 1–16.