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RESULTS OF THE DIVA-1 EXPEDITION OF RV “METEOR” (CRUISE M48/1)

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

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Abstract

Two of the sites sampled during the DIVA-1 cruise (Meteor 48/1) to the Angola Basin in 2000 have been studied intensively in order to highlight the diversity of meiofauna in this deep-sea region. This work contributes to the final aim to describe the species of the community of harpacticoid copepods in the Angola Basin and adds a new member to the few hitherto known deep-sea Paramesochridae. The new species belongs to the genus *Kliopsyllus*, until now only reported from beaches, the intertidal and shallow waters and thus thought to be representing a mainly interstitial group. Furthermore, *Kliopsyllus diva* sp. n. is the dominating paramesochrid copepod at the two studied sites with depths of more than 5400 m. Among other features, *K. diva* sp. n. is unique in the armature of its fourth leg, the presence of hedgehog-like arranged spinules on the exopod of the fifth leg and the relation of length and width of its furcal rami.

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Introduction

The members of the meiobenthic harpacticoid family Paramesochridae are typically small interstitial animals, cylindrical in shape, inhabiting sandy beach ground water, the intertidal and shallow waters. Recently, a few new species have been recorded from the deep sea but the genus *Kliopsyllus* Kunz, 1962 seemed to be restricted to shallow areas. The international scientific cruise DIVA-1 (“Meteor” 48/1) to the Angola Basin has now contributed new species to the genus, a discovery that is even more astonishing as they form the majority of all paramesochrid species at the sampled sites.

Of course there are deep-sea samplings for meiofauna, but they are normally studied on a higher taxonomic level or regarding copepods as working species (Thistle 1982, 1998). The lack of deep-sea *Kliopsyllus* species is probably not due to the non-existence or rareness of these animals at such sites but to the lack of taxonomists working with them.

Material and methods

The two sampling areas in the Angola Basin, station 325 (19°58.2'S, 002°59.8'E) at a depth of 5450 m and station 346 (16°16.9'S, 005°27.0'E and 16°17.0'S, 005°27.0'E) at a depth of 5389 m, are the extreme points

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of a deep-sea transect of 300 m length, sampled during the DIVA-1 campaign (“Meteor” 48/1) in July 2000.

Meiofauna was replicatedly sampled using a multicorer. Details on sampling strategy and sample treatment are described by Rose et al. (2005). The presorted adult Paramesochridae were kept in glycerine on slides and determined to species level with the aid of a Leica MZ 12.5 stereo microscope and a Leica DMR microscope.

Specimens of *Kliopsyllus diva* sp. n. selected for description were drawn from the dorsal and the lateral side before dissection. The dissected parts were mounted in glycerine on slides. Drawings were made with the aid of a camera lucida on a Leica DMR microscope equipped with differential interference contrast (DIC) at 1000× magnification. All specimens are registered in the collection of the University of Oldenburg (= UNIO collection), Department of Zoosystematics and Morphology, and kept at the German Centre for Marine Biodiversity Research (DZMB) in Wilhelmshaven, Germany. (Abbreviations 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)

Systematics

Material

The examined specimens are registered in the UNIO collection.

Female holotype: No. 2004.012/1–10 (10 slides), station 346/4–2 (16°16.9'S, 005°27.0'E), 07–27–2000, depth 5389 m. Male allotype: No. 2004.013/1–8 (8 slides), station 325/8–12 (19°58.2'S, 002°59.8'E), 07–14–2000, depth 5450 m. Female paratype 1: No. 2004.014/1–10 (10 slides), station 346/2–11 (16°17.0'S, 005°27.0'E), 07–27–2000, depth 5389 m. Female paratype 2: No. 2004.015/1–6 (6 slides), station 346/5–2 (16°16.9'S, 005°27.0'E), 07–27–2000, depth 5389 m.

Etymology

The species name *diva* refers to the DIVA-1 campaign of RV “Meteor” (cruise 48/1) to the Angola Basin in 2000. DIVA stands for: Latitudinal gradients of deep-sea biodiversity in the Atlantic Ocean.

Description

Female

Habitus (Fig. 1A and B). Total body length measured from anterior tip of rostrum to posterior margin of telson (paratype 1): 0.30 mm. Including the furcal rami: 0.36 mm.

Body cylindrical (Fig. 1A and B), slightly depressed dorsoventrally, with prosome slightly wider than urosome. Whole body covered by small round depressions resembling the surface of a golf ball. Pores are present in small numbers, distributed dorsally and laterally on cephalothorax and most of the free somites. Somitic hyaline frills only slightly developed. Posterior margin of urosomal somites ventrolaterally ornamented with minute spinules. Penultimate somite carrying a fine well developed pseudopericulum. Telson very short. Posterior margin of furcal rami ventrally fringed by spinules.

Furcal rami of adult female (Fig. 1C) cylindrical, nearly six times longer than wide, with 6 setae and a minute lateral pore: seta I absent; seta II slender, dorsally displaced; seta III slender, slightly smaller than II, situated dorsolaterally, near posterior end; setae IV and V long and slender, situated terminally; seta VI minute; seta VII slender pinnate, on dorsal surface.

Rostrum (Fig. 2A). Small, hyaline, only slightly visible underneath cephalothorax, with a pair of minute anterior sensilla. Not demarcated.

Antennule (Fig. 2A–C). Eight-segmented, whole surface covered with small depressions, segment I with long spinules along inner margin.

Armature formula: I (1): 1 small seta; II (9): 3 pinnate setae, one of which small, and 6 slender naked setae, one of which minute; III (7): 5 slender pinnate and 2 naked setae; IV (2+2): 2 pinnate setae and 2 aesthetascs fused at base; V (1): 1 long slender pinnate seta; VI (1): 1 slender pinnate seta; VII (4): 4 slender pinnate setae; VIII (5+2): 5 slender setae, one of which pinnate and two aesthetascs fused at base.

Antenna. See description of male (Fig. 3A).

Mandible (Fig. 3E–F). Coxa with slender elongated gnathobasis (Fig. 3F). Cutting edge with one large and five smaller teeth. Basis short with one plumose seta and one row of spinules. Palp biramous (Fig. 3E). Enp two-segmented: first segment bearing two slender setae, second segment with one seta, apically furnished with three naked slender basally fused setae. Exp half the length of enp, one-segmented, with one lateral pinnate slender seta and three apical pinnate slender setae.

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

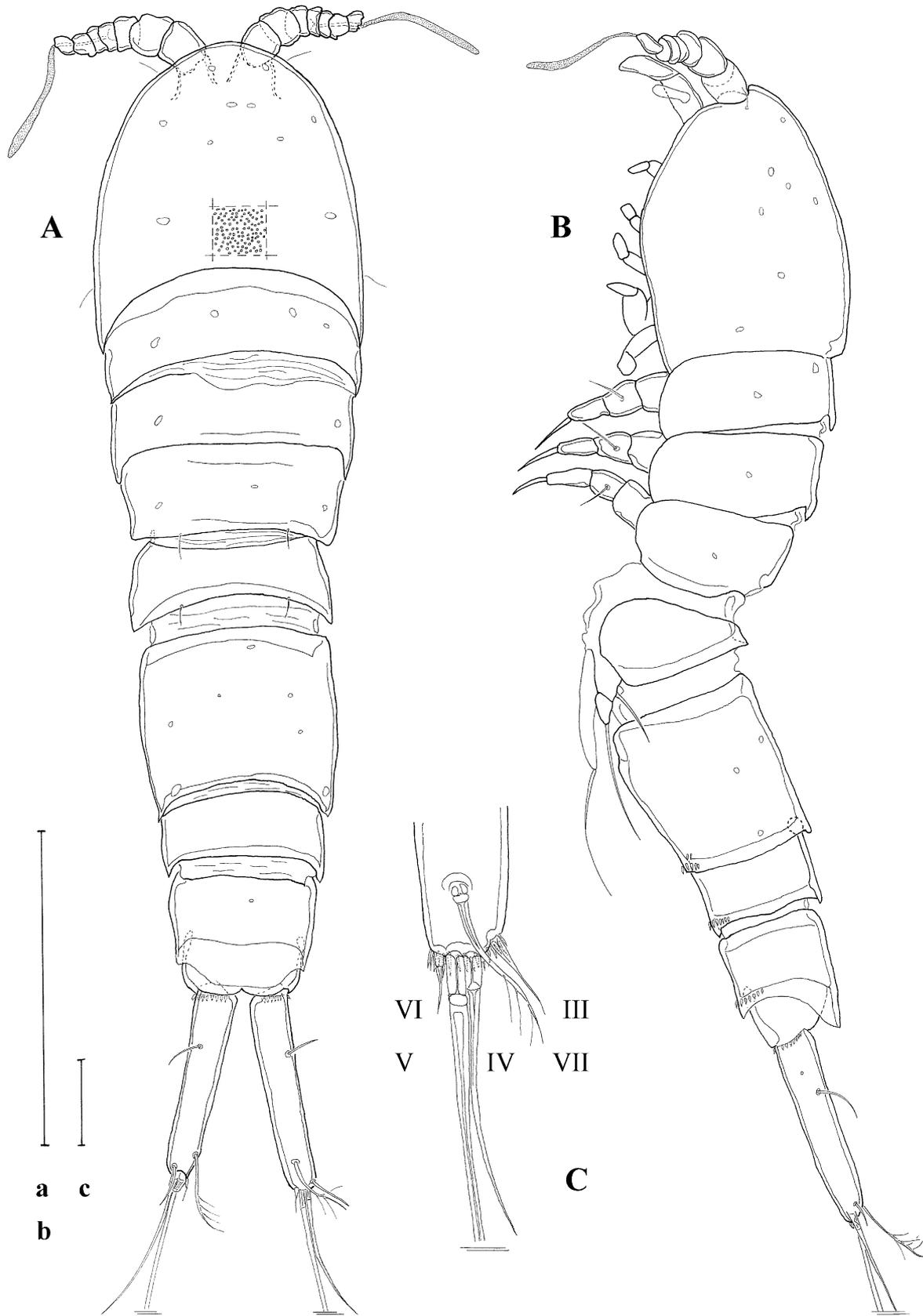


Fig. 1. *Kliopsyllus diva* sp. n.: (A) female habitus, dorsal (paratype 1); (B) female habitus, lateral (paratype 1); (C) distal part of female furcal ramus, dorsal (holotype). Scale bars = a, b, 0.1 mm; c, 0.01 mm.

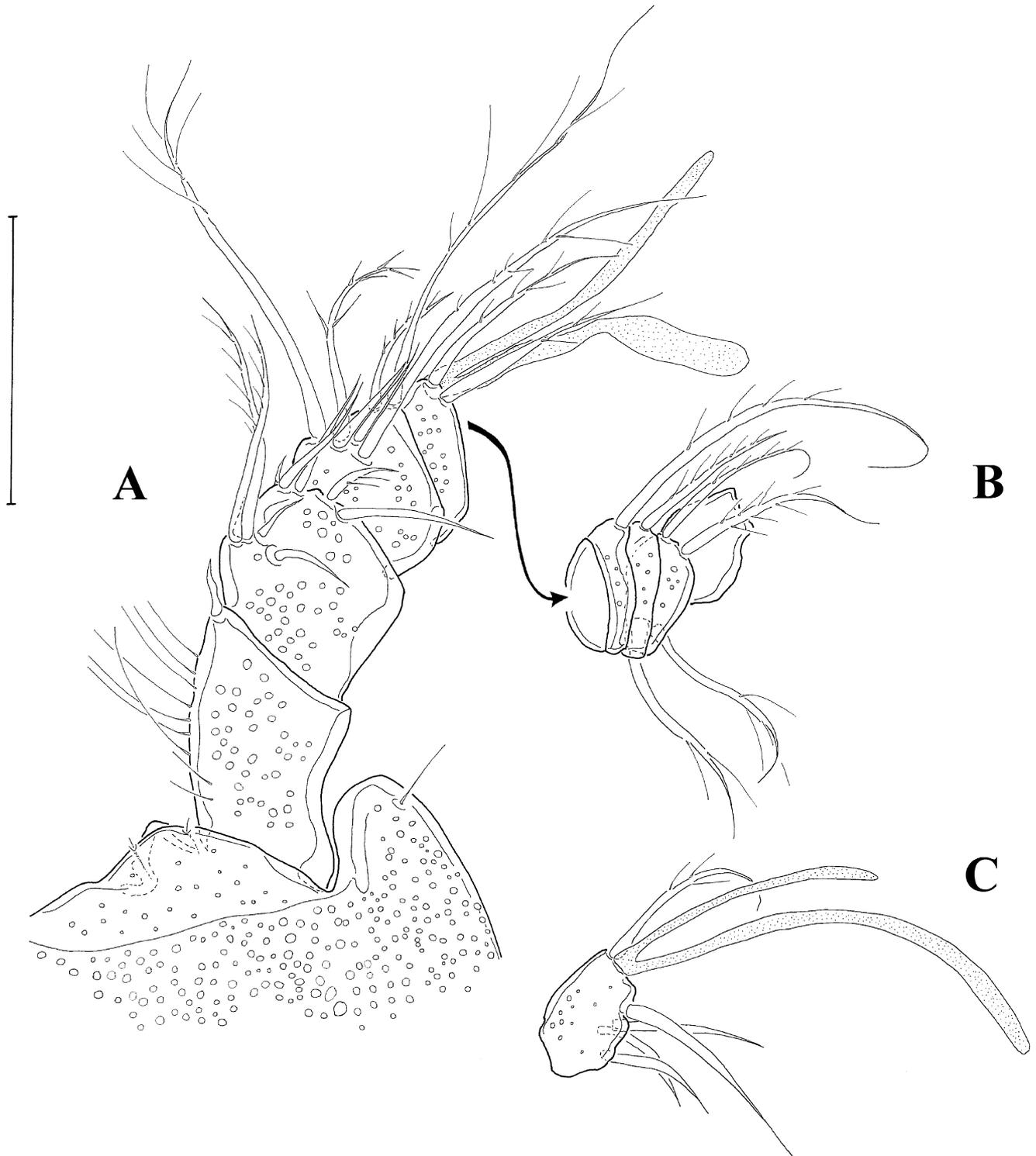


Fig. 2. *Kliopsyllus diva* sp. n. Female antennula with rostrum (holotype): (A) rostrum, segments I–IV, dorsal view; (B) setation of segments V–VII and location of segment VIII, dorsal view; (C) setation of segment VIII. Scale bar = 0.02 mm.

and one on inner margin. Exp small, one-segmented with two small naked setae.

Maxilla (Fig. 3C). Praecoxa and coxa fused to form a syncoxa bearing three endites. No separation towards

basis visible. Proximal endite slightly bilobed, two unipinnate spines on proximal lobe, one pinnate spine and one naked seta on distal lobe. Middle endite with two pinnate and one naked seta. Distal endite armed with two strong spinulose spines and one naked seta.

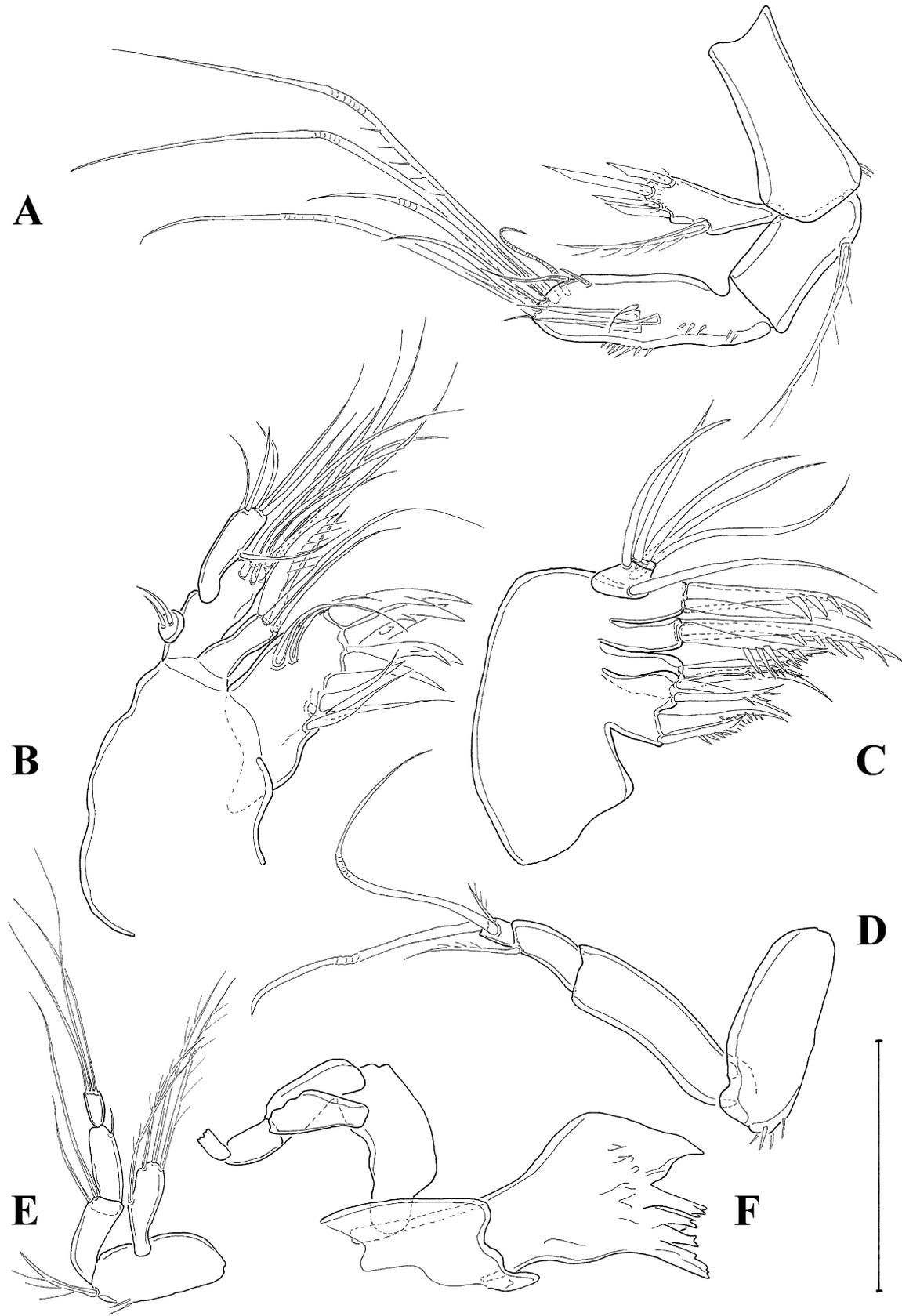


Fig. 3. *Kliopsyllus diva* sp. n.: (A) male antenna (allotype); (B) female maxillula (holotype); (C) female maxilla (holotype); (D) female maxilliped (holotype); (E) male mandibular palp (allotype); (F) female mandible (holotype). Scale bar = 0.02 mm.

Basis with stout spinulose spine accompanied by two naked setae, one of which strong. Enp two-segmented with three naked setae on first segment and three naked setae on second.

Maxilliped (Fig. 3D). Syncoxa asetose, ornamented with several spinules at distal edge. Basis asetose. Enp two-segmented with a pinnate seta on enp1, a small pinnate seta and two long geniculate setae on enp2.

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

P1 (Fig. 4A). Coxa with long spinules on anterior and posterior surface. Basis with one pore and rows of long and short spinules along inner margin, one inner naked seta and one outer pinnate seta accompanied by several spinules. Enp one and a half times as long as exp, both two-segmented and armed with spinules, those in enp1 very fine and long. Enp1 without seta, enp2 bearing terminally one long seta and one short outer seta, both pinnate. Exp1 with one outer pinnate spine. Exp2 with one outer pinnate spine and terminally three long pinnate setae, the inner one of which with very long but scarce ornamentation.

P2–P4 (Fig. 4B–D). Surface of coxae naked, a few spinules in P3 only, in P2 slightly ornamented with hyaline structures. Basis of P2–P4 bearing one plumose outer seta. All bases bearing spinule row at outer margin, P2 and P3 additional spinules at inner margin. Basis of P2 only with hyaline surface structures. Three-segmented exopods slightly longer than endopods with spinules along outer margin (P2–P4) and on anterior side of exp1 (P3, P4). Very long, thin spinules on inner margin of exp1 (P2–P4).

Exp1, exp2 and exp3 of P2 and P3 with stout outer spines ornamented with short spinules on either side. P4 exp1 and exp2 armed with similar spines. Outer terminal spines in exp3 P2–P4 comparable to spines of previous segments, but longer and not as stout. Exp 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 only one terminal bipinnate seta with short spinules.

Endopods P2–P4 one-segmented, with one inner row of very long fine spinules, two separate rows of fine spinules along outer margin and additional spinule rows apically as well as on posterior surface. Enp P2 and P3 apically with long bipinnate seta. Enp P4 with two terminal setae, the inner one pinnate with long spinules, the outer one pinnate with very short spinules. In all observed specimens these two setae were crossed.

P5 (Fig. 5B). Legs fused, small exopod clearly separated from basendopodite. Benp bearing an outer basal pinnate seta and an anterior pore. Surface of benp decorated with more or less randomly distributed spinules on drawn-out endopodal parts, which are armed with two stout unipinnate setae each. Exp with three pinnate setae, outer ones smaller, innermost long. Inner margin of exp armed with hedgehog-like arranged spinules.

Genital complex and P6 (Fig. 5A). Genital field see Fig. 5A. Sixth pair of legs represented by small wavily fused outgrowths bearing two minute thorns each placed on small protrusions.

Male

Habitus (Fig. 6A and B). As in female but slightly smaller and genital somites separated (Fig. 6A).

Total body length measured from anterior tip of rostrum to posterior margin of telson (allotype): 0.29 mm. Including the furcal rami: 0.35 mm. Spermatophore can be situated on either side of body. In the described specimen two spermatophores of different states visible.

Mouthparts and swimming legs as in female, sexual dimorphisms only in antennula, P5 and P6, and in slight differences in armature of furcal rami (Fig. 6B: seta I very tiny on outer margin, seta VII naked).

Antennule (Fig. 7A and B). Seven-segmented. Segment I with spinule row along inner margin, segment V laterally displaced, segment VI rounded and bulbous (Fig. 7A). Following segments not completely separated forming segment VII (Fig. 7B).

Armature formula: I (1): 1 seta; II (1): 1 slender naked seta; III (8): 1 slender pinnate seta, 7 slender naked setae of different sizes; IV (3): 3 slender naked setae; V (2): 1 short and 1 long slender naked seta; VI (4+1): 1 larger pinnate seta, 3 slender naked setae, 1 aesthetasc; VII (9+1): 9 slender naked setae one of which fused at base with terminal aesthetasc.

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

P5 (Fig. 5C) and P6 (Fig. 5D). Legs of P5 fused in the middle. Exopod clearly separated from basendopodite.

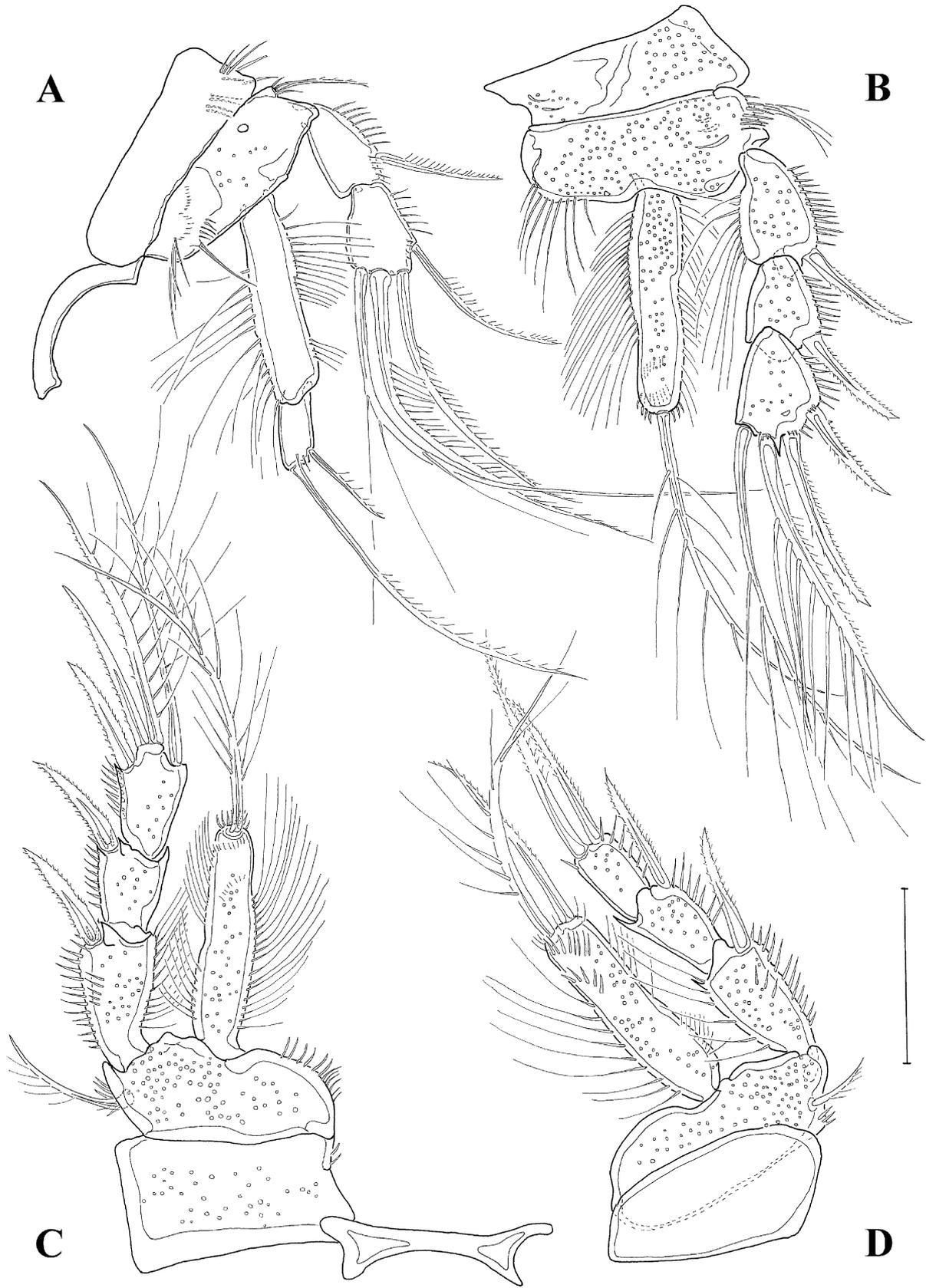


Fig. 4. *Kliopsyllus diva* sp. n.: (A) female P1 with intercoxal sclerite (holotype); (B) female P2 (paratype 2); (C) female P3 with intercoxal sclerite (paratype 2); (D) female P4 (holotype). Scale bar = 0.02 mm.

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

	Basis	Exopod	Endopod
P1	1.1	0.121	0.011
P2	0.1	0.0.121	010
P3	0.1	0.0.121	010
P4	0.1	0.0.020	020

Benp bearing an outer basal pinnate seta and one anterior pore, some randomly distributed spinules and one unipinnate seta on the slightly drawn out endopodal part. Exp with three pinnate setae, innermost longest, and hedgehog-like arranged spinules on inner margin.

P6 represented by very delicate medially touching plates decorated with spinules, one outer pinnate and two naked inner setae and one pore each.

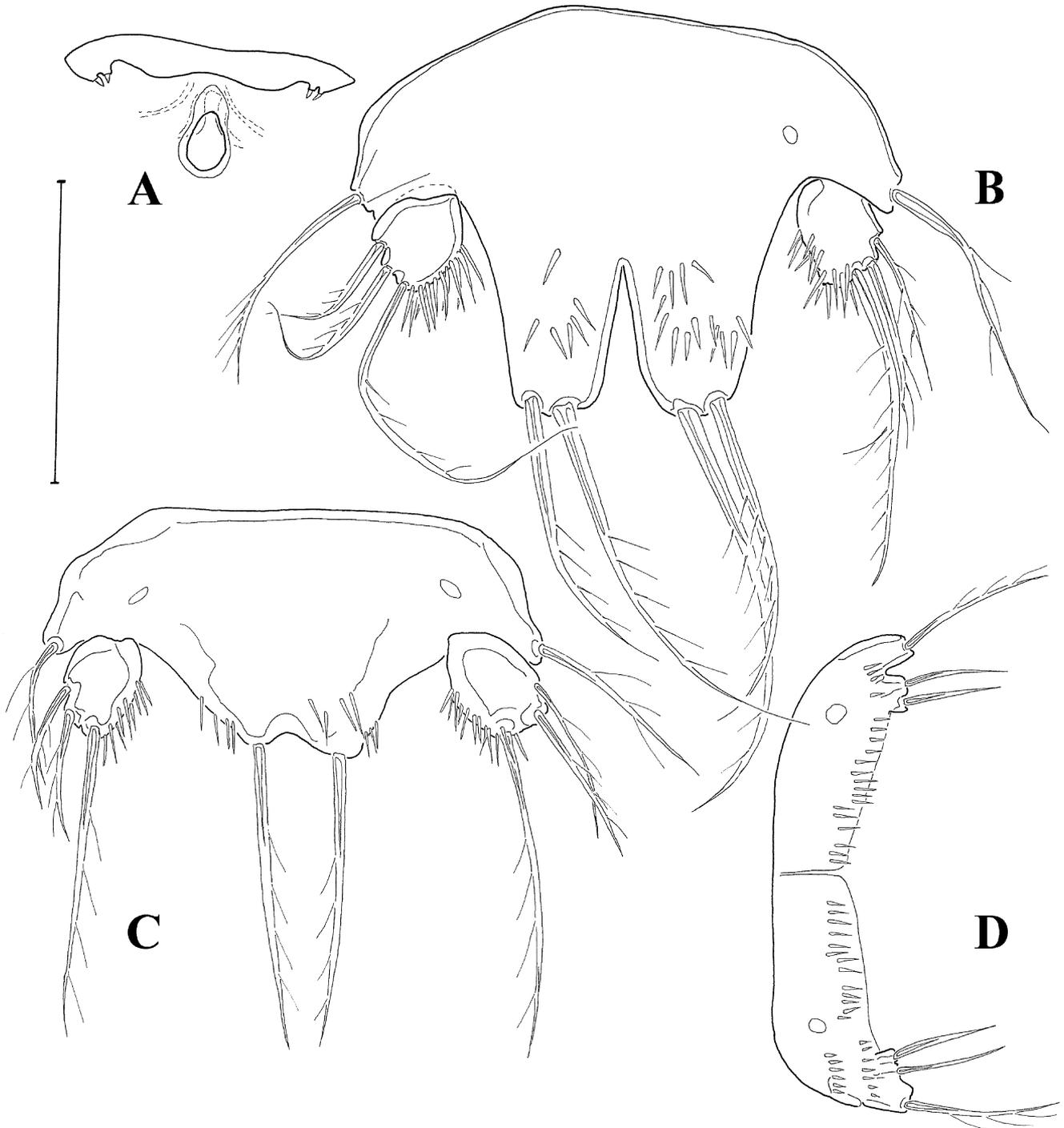


Fig. 5. *Kliopsyllus diva* sp. n.: (A) female P6 and genital field (holotype); (B) female P5 (holotype); (C) male P5 (allotype); (D) male P6 (allotype). Scale bar = 0.03 mm.

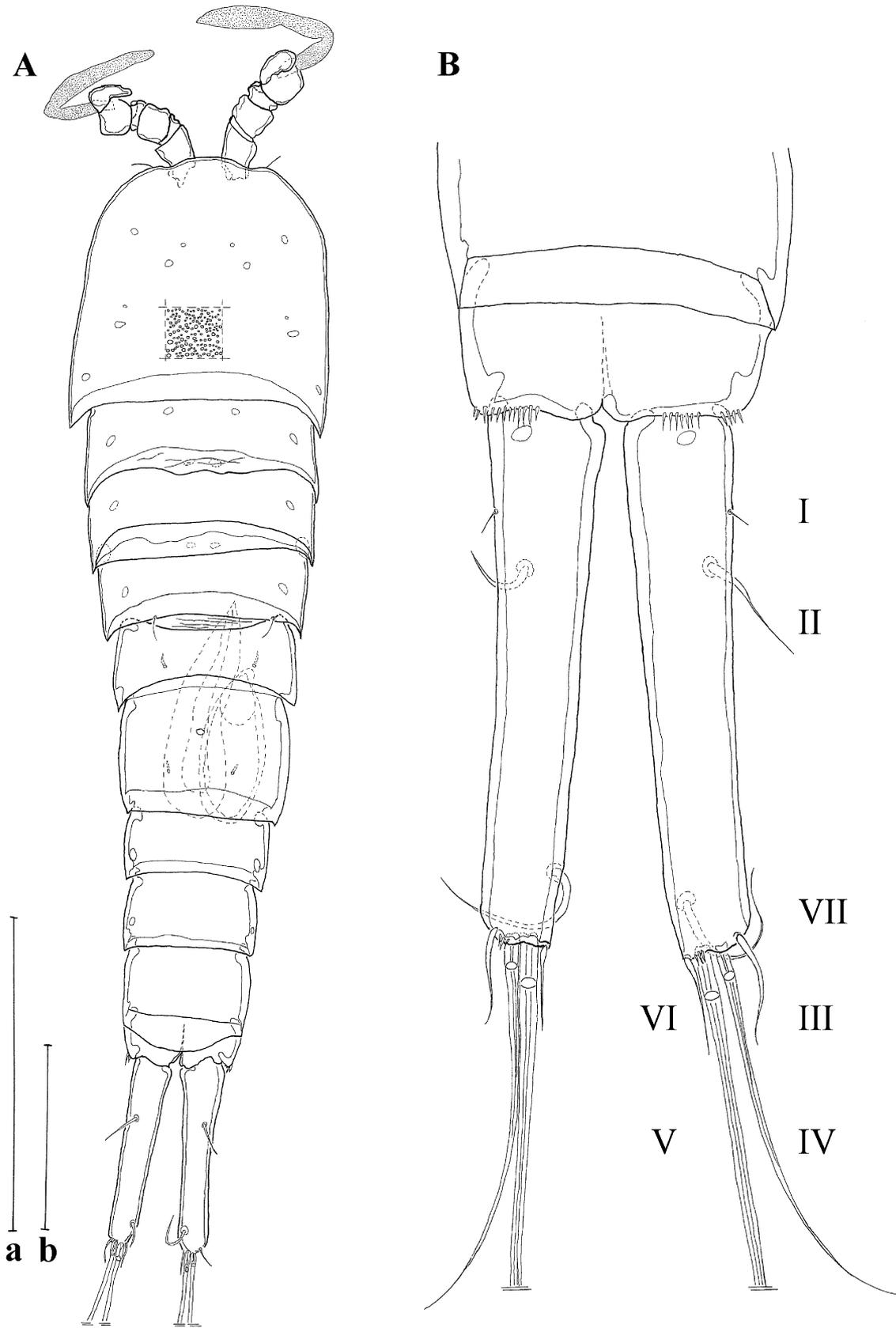


Fig. 6. *Kliopsyllus diva* sp. n.: (A) male habitus, dorsal (allotype); (B) male anal somite and furcal rami ventral (allotype); Scale bars = a, 0.1 mm; b, 0.02 mm.

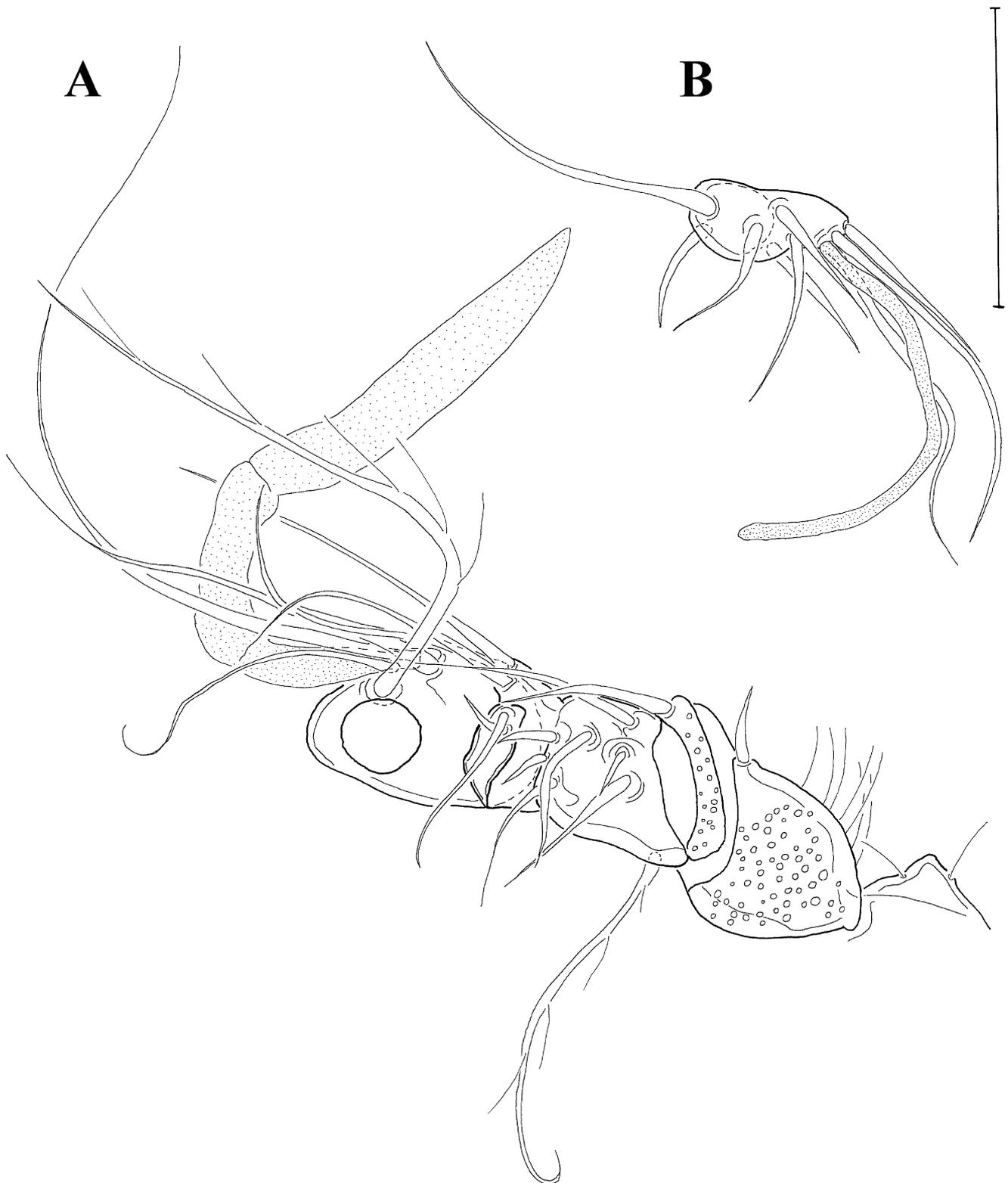


Fig. 7. *Kliopsyllus diva* sp. n. male antennula with rostrum (allotype): (A) rostrum, setation of segments I–VI, anterior view; (B) setation of segment VII, anterior view. Scale bar = 0.02 mm.

Systematic discussion

Kliopsyllus was erected by Kunz (1962) by grouping species that formerly belonged to the genera *Parameso-*

chra T. Scott, 1892, *Emertonia* Wilson, 1932, and *Leptopsyllus* T. Scott, 1894. The former *Paramesochra acutata* Klie, 1935, later *Emertonia acutata* after Nicholls (1945), was not incorporated into the new

genus because it shows some clear typical characters of the genus *Paramesochra*, such as two-segmented endopods in P2–P4 with 1 terminal seta on the enp2.

At present, *Kliopsyllus* contains 28 species (including that described in this paper) and seven subspecies. Wells and Rao (1987) questioned the taxonomic position of *Kliopsyllus arenicolus* (Krishnaswamy, 1957), *Kliopsyllus wilsoni* (Krishnaswamy, 1957), *Kliopsyllus longifurcatus* Scheibel, 1975 and *Kliopsyllus paraholstaticus* Mielke, 1975 as they 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.

For the time being, autapomorphies that indicate a possible monophyletic origin of *Kliopsyllus* cannot be given. *Kliopsyllus* seems to be a collection of species that share certain plesiomorphic characteristics which can be found in other taxa of Paramesochridae as well. As 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.

Comparing segmentation and armature of the swimming legs of different Paramesochridae it becomes obvious why the genus *Kliopsyllus* has to be redefined: Within the Paramesochrinae Huys, 1987, similar segmentation of P1 as in *Kliopsyllus* can be found in *Paramesochra*, *Scottopsyllus* Kunz, 1962, *Apodopsyllus* Kunz, 1962, *Biuncus* Huys, 1996, and *Leptopsyllus*. Numbers of segments and endopodal setae of P2 and P3 of *Kliopsyllus* are comparable to *Kunzia* Wells, 1967 and some *Scottopsyllus* (*Scottopsyllus*) species. Numbers of segments and exopodal and endopodal setae of P4 in *Kliopsyllus* are comparable to *Kunzia*, *Scottopsyllus* (*Wellsopsyllus*) Kunz, 1981 and *Leptopsyllus* but in no case to *Paramesochra*, the nearest relatives of a *Kliopsyllus*–*Kunzia* lineage defined by Huys (1987). There is the need of finding apomorphies based on single characters for the different genera of Paramesochridae. The existing system in many parts is obviously based only on different combinations of the same characters.

Given the current taxonomic situation, the new species is placed provisionally in *Kliopsyllus*. This decision is based on the species' combination of characters such as the two-segmented exp and enp of P1, the 3-segmented exp P2–P4, two setae in exp3 P4,

one-segmented enp with one seta in P2 and P3, and one-segmented enp with two setae in P4.

K. diva sp. n. is unique within the genus and can be distinguished from the other species by the following features (the comparisons were made by using original descriptions and additional literature (Bodin 1997)):

As these comparisons are based on literature, antennule, antenna and mouthparts cannot be checked in detail for all species. However, it can be stated that setae with transversal tips on the antenna exp somewhat resembling the four setae of *Kliopsyllus diva* sp. n., are visible in the drawings of many of the more recently described species, though normally less in number. *Kliopsyllus unguiseta* Mielke, 1984, *Kliopsyllus similis* Mielke, 1984 and *Kliopsyllus regulextans* Mielke, 1984 from the Galapagos Islands show two transformed setae on the antenna exp, *Kliopsyllus panamensis* (Mielke, 1984) and *Kliopsyllus constrictus pacificus* Mielke, 1984 and *Kliopsyllus chilensis* Mielke, 1985 have one transformed seta on the antenna exp (Mielke 1984a, b, 1985). However, in contrast to all these species who show transversal brushlike tips, *K. diva* sp. n. has setae with tips that are transversally cut but bare.

P4

With two setae at the exp3 P4 and two well developed non-transformed pinnate setae – one with long and one with very short spinules – on the enp P4 *K. diva* sp. n. so far is the only known species showing this combination of characters. Most commonly two setae at exp3 P4 are combined with only one seta at enp P4. Even species with two setae at the enp such as *Kliopsyllus atlanticus* Kunz, 1983, *Kliopsyllus californicus* Kunz, 1981, *Kliopsyllus holsaticus* (Kunz, 1981; Wells and Rao 1987), *Kliopsyllus holsaticus varians* (Kunz, 1951), *Kliopsyllus perharidiensis* (Wells, 1963), (Kunz 1971), *Kliopsyllus similis* and *Kliopsyllus unguiseta* normally present one well-developed transformed seta with brushlike tip accompanied by a small or very small inner seta. What is more, even the very peculiar species of *Kliopsyllus furcavaricatus* (Kunz, 1974) has a brushlike seta with an accompanying small seta. Only in *Kliopsyllus spiniger spiniger* Wells, Kunz & Rao, 1975 (Mielke 1984a) and *Kliopsyllus spiniger ornatus* Kunz, 1981 the authors describe a long, well-developed, sometimes bipinnate seta together with the transformed brushlike one.

P5

Up to this day no *Kliopsyllus* species with this form of randomly distributed spinules at the benp and hedgehog-like arranged spinules at the inner margin of exp has been described. Spinules, if drawn, are typically placed in rows. However, due to the minute size of the animals and optical devices with comparably low resolution in case of the older descriptions, these

characters might well have been overlooked by former authors.

Furcal Rami

Of the hitherto described species only *K. spiniger* and *K. spiniger ornatus* (Wells et al. 1975; Kunz 1981) with their highly transformed furcal rami exceed *K. diva* sp. n. in the relation between length and width of furcal rami. *K. diva* sp. n. has furcal rami that are about six times longer than broad.

The typical combination of its characteristics with the unique armature of P4, the hedgehog-like arranged spinules on exp P5, the length:width relation of furcal rami, are the decisive factors for presenting *K. diva* sp. n. from the Angola Basin as a species new to science. In addition, the ecological circumstances making it the first deep-sea *Kliopsyllus* are especially emphasized.

Ecology

Occurrence and abundance

At the two sites studied, strongly differing numbers of Paramesochridae were found. While at site 346 altogether 65 Paramesochridae were reported, site 325 revealed only 16 individuals. At site 325 altogether 0.275 m² were investigated while site 346 contributed with 0.314 m² to the study because of an additional haul. However, higher individual numbers at site 346 are not due to the larger area sampled, as individual density at site 325 (0.06 ind. 10 cm⁻²) is very low compared to site 346 with 0.21 ind. 10 cm⁻².

So far nine different species of Paramesochridae can be distinguished. At least five of them belong to the genus *Kliopsyllus*. *K. diva* sp. n. is represented by 16 females at site 346 and 6 females at site 325. Only two males were found, one at each site. This makes it the most abundant species of Paramesochridae at the two sampled sites of the Angola Basin.

Ecological discussion

The differences in individual densities of Paramesochridae at site 346 and site 325 are supported by the findings of all colleagues working with benthic copepods from the DIVA-1 samples. Rose et al. (2005) show that the density of harpacticoid copepods is four times higher at site 346 than at site 325. Paramesochridae clearly follow these findings. The limiting factor for Paramesochridae, as well as for other harpacticoid copepods, to establish higher individual densities seems to be the gradient of the total organic carbon content between the low productivity area of site 325 and the considerably

higher values at site 346 (Kröncke and Türkay 2003). *K. diva* sp. n. dominates the Paramesochridae at site 346 and is the second most abundant species at site 325. However, due to the generally low individual densities it can be postulated that even more replicate samples would have been necessary to make a final statement about the factual distribution of Paramesochridae in the Angola Basin.

K. diva sp. n. is the first species of its genus to be reported from the deep sea. As far as the records of the 27 species and seven subspecies known (for records see Bodin (1997)) have been revised, none of the species has been described for comparable depths. Becker et al. (1979) placed a deep-sea species in *Kliopsyllus*, but it was removed by Kunz (1981) and renamed *Scottopsyllus* (*Wellsopsyllus*) *abyssalis* (Becker, Noodt & Schriever 1979).

Most of the Paramesochridae are described from sandy sediments on beaches, the intertidal and shallow waters. They are supposed to lead an interstitial lifestyle, as they have an average body length of about 0.4 mm, normally not exceeding 0.5–0.6 mm. Even the largest *Kliopsyllus*-species, *Kliopsyllus major* (Nicholls, 1939), from a depth of about 8 m in the St. Lawrence River (Baie de Mille Vaches, Canada), despite its size (female: 0.8 mm; male: 0.7 mm) seems to live interstitially in very coarse sand (Nicholls 1939).

On the other hand, species such as *S. (W.) abyssalis* (0.95 mm) from 2000 m depth in the Peru Trench (Becker et al. 1979) or *Scottopsyllus* (*Scottopsyllus*) *praecipuus* Veit-Köhler, 2000 (male: 0.84 mm; female: 0.9 mm) from 20 and 30 m depth from King George Island, Antarctica are the exceptions (Veit-Köhler 2000). As both of them are living in undisturbed habitats dominated by silt and clay, they might have undergone an enlargement which enables them to burrow in fluid muds. Although *K. diva* sp. n. lives in a silt and clay deep-sea sediment (Kröncke and Türkay 2003), which is not suitable for an interstitial lifestyle, it stayed as small as the overwhelming majority of the hitherto known *Kliopsyllus* species. Obviously *K. diva* sp. n. seems to be restricted to the epibenthic nutrient containing fluff.

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