HABITAT PREFERENCE AND SEXUAL DIMORPHISM IN SPECIES OF SCOTTOPSYLLUS (COPEPODA, HARPACTICOIDA) WITH THE DESCRIPTION OF SCOTTOPSYLLUS (S.) PRAECIPUUS SP. N. FROM THE ANTARCTIC

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HABITAT PREFERENCE AND SEXUAL DIMORPHISM IN SPECIES OF *SCOTTOPSYLLUS* (COPEPODA, HARPACTICOIDA) WITH THE DESCRIPTION OF *SCOTTOPSYLLUS (S.) PRAECIPUUS* SP. N. FROM THE ANTARCTIC

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COPEPODA
SYSTEMATICS
ANTARCTICA
KING GEORGE ISLAND
SEXUAL DIMORPHISM
FURCAL RAMI
ECOLOGY
SEDIMENT PREFERENCE

ABSTRACT. – The habitat preferences of the 14 species of *Scottopsyllus* (Paramesochridae) are compared and related with their body-sizes. There is a group of small members capable of living interstitially and there are three very large species including the new species *Scottopsyllus (S.) praecipuus* sp. n. prefering muddy sediments. A mixed lifestyle of partly burrowing in the first millimeters of the fluid muddy sediment and of partly inhabiting the epibenthic organic fluff without emerging into the water column is assumed for the new species from shallow waters of King George Island, Antarctica. Besides this, *S. (S.) praecipuus* sp. n. reveals the most striking sexual dimorphism in furcal rami ever described for the genus. It is the only known species reducing both terminal setae IV and V to mere elevations in adult females and having these setae unmodified in the males. In female copepodids both setae are still of the male type. The new species blurs the clear distinction between the subgenera *Scottopsyllus* and *Wellsopsyllus* sensu Kunz. Since only a phylogenetic analysis will shed light on these relationships, its placement into the subgenus *Scottopsyllus* is to be regarded as tentative.

COPEPODA
SYSTÉMATIQUE
ANTARCTIQUE
ILE KING GEORGE
DIMORPHISME SEXUEL
RAMES FURCALES
ÉCOLOGIE
PRÉFÉRENCE SÉDIMENTAIRE

RÉSUMÉ. – L'habitat préférentiel des 14 espèces de *Scottopsyllus* (Paramesochridae) est comparé en relation avec la taille du corps. Il existe un groupe de petites espèces capables de vivre dans le milieu interstitiel et 3 très grandes espèces, dont *Scottopsyllus (S.) praecipuus* sp. n., préférant les sédiments vaseux. Un mode de vie mixte consistant à creuser les premiers millimètres du sédiment vaseux fluide et à vivre dans le matériel détritique épibenthique, sans pénétrer dans la colonne d'eau semble prévaloir chez *S. (S) praecipuus* des eaux peu profondes de l'île King George en Antarctique. Par ailleurs, cette espèce présente le plus remarquable dimorphisme sexuel jamais décrit dans le genre sur les rames furcales. Il s'agit de la seule espèce dont les deux soies apicales IV et V sont réduites à de simples protéburances chez la femelle adulte, alors que celles du mâle restent sans modification. Les copépodites femelles possèdent encore des soies de type mâle. La nouvelle espèce rend caduque la distinction entre les sous-genres *Scottopsyllus* et *Wellsopsyllus* sensu Kunz. Seule une analyse phylogénétique permettra d'élucider leur relation. L'espèce nouvelle est placée provisoirement dans le sous-genre *Scottopsyllus*.

INTRODUCTION

Sampling meiofauna in remote areas like the Antarctic inevitably results in the discovery of new species. New species may completely fit into existing classifications but may also question long-standing concepts.

The genus *Scottopsyllus* (Paramesochridae, Harpacticoida) has been the subject of several revisions (Kunz 1962, 1981) and assessments of its status within the family of Paramesochridae (Kunz 1981, Huys 1987). Its division into the three subgenera *Scottopsyllus*, *Intermedopsyllus* and *Wellsopsyllus* is based only on diagnostic characters and may not reflect a phylogenetic affinity. Many important characters are still not taken into account and surely a revision will have to include not only the genus *Scottopsyllus*, but the Paramesochridae as a whole. It is not the aim of this work to accomplish this but to draw attention to a few morphological as well as ecological

Table I. – Seta and spine formula of swimming legs of *Scottopsyllus (S.) praecipuus* sp. n.

	Basis	Exopod	Endopod
P1	1.0	0.121	0.010
P2	0.0	0.0.011	0
P3	0.1	0.0.011	0
P4	0.1	0.0.011	0.010

traits and environmental requirements of the different species. If one pays attention to ecological and behavioural aspects and not only to the more easily accessible morphological ones, problems with the old classification of the genus *Scottopsyllus* arise almost immediately.

LOCATION AND METHODS

The new species was collected from the sediments of Potter Cove (62°14'S, 58°40'W) at King George Island, South Shetland Islands, Antarctica. Klöser and Arntz (1994) gave a detailed description of the site. A time series in the centre of Potter Cove at a depth of about 20 m (06.11.1995 to 01.02.1996) and two transects (5 m, 10 m, 20 m, and 30 m) were sampled by scuba diving (01.02.1996 to 09.02.1996). The inner cove (transect 1) represents an unexposed area where muddy sediments predominate. The deeper sampling stations of this site are not affected by strong currents nor disturbed by icebergs as frequently as transect 2. The latter is located at the ridge between inner and outer cove with a maximum depth of 30 m, and constitutes a natural barrier for big icebergs to enter the cove. It is an exposed area with sandier sediments at least in the uppermost stations. Strong near bottom currents are always present.

Sediment corers of 80 cm^2 each were randomly pushed into the sediment and brought to the surface as undisturbed as possible. The upper 3 cm of oxidized sediment layer were preserved in 5 % formalin or frozen for grain size analysis. For sample centrifugation and specimen treatment see Veit-Köhler and Willen (1999). To obtain copepod numbers per 10 cm^2 sediment surface the supernatant of two centrifugated cores per sampling station had to be split for sorting. A meiofauna sample splitter after Jensen (1982) was used to obtain eight equal parts of which three per core were randomly selected, sorted and regarded as if 30 cm^2 of sediment surface per core had been sorted. The individual numbers of the different developmental stages of *Scottopsyllus (S.) praecipuus* sp.n. in the two parallel cores were counted and the average numbers for 10 cm^2 calculated.

Grain size analysis was conducted with freeze-dried sediment samples for the anorganic sediment components. After a treatment with H_2O_2 and HCl to destroy organic matter and calcareous particles the sediment was wet-sieved through a series of 2000 µm, 630 µm, 200 µm, 63 µm, and 20 µm meshes. The fine silt (< 20 µm) and clay (< 2 µm) fraction were determined by drying the rinsing water.

Table II. – Character differences of the three subgenera *Scottopsyllus*, *Intermedopsyllus*, and *Wellsopsyllus* as given by Kunz (1981).

	P1enp setae	P2/P3enp setae	P4exp segm.	P4enp segm.	P5exp fused with benp
Scottopsyllus	1-2	0 or tiny	3	2	No
Intermedopsyllus	2	0	2	1	Yes or No
Wellsopsyllus	1	0	3	1	No

Abbreviations used in the text : Exp : exopod; enp : endopod; benp : baseoendopod; P1-P6 : swimming legs 1-6; "enp1 P2" : first segment of endopod P2.

SYSTEMATICS

Scottopsyllus (S.) praecipuus sp. n.

Material

Males, females and numerous copepodids of all stages have been collected with sediment corers by scuba diving during a stay at JUBANY base (Dallmann Laboratory) on King George Island, South Shetland Islands, Antarctica (62°14'S, 58°40'W). The examined specimens are in the UNIOL collection of the AG Zoosystematik und Morphologie, Universität Oldenburg; the remaining specimens are in the authors' collection.

Female holotype : No. 1998.048 (6 slides), 16.12.1995, 22 m depth. Male allotype : No. 1998.049 (1 slide), 01.12.1995, 22 m depth. Female paratypes : No. 1998.050 (7 slides), 06.11.1995, 19 m depth; No. 1998.051 (1 slide) 01.02.1996, 20 m depth. Male paratypes : No.1998.052 (6 slides), 16.12.1995, 22 m depth; No. 1998.053 (6 slides), 16.12.1995, 22 m depth; No. 1998.054 (1 slide), 01.02.1996, 20 m depth.

Etymology

The species name (latin *praecipuus* meaning "peculiar, distinctive, special") refers to the new characteristics of the species shown in sexual dimorphism, body-size and habitat preference in comparison to its con-geners.

Description

Female

Habitus (Fig. 1) : Total body length measured from anterior tip of rostrum to posterior margin of caudal rami : 0.9 mm (holotype). Variability in

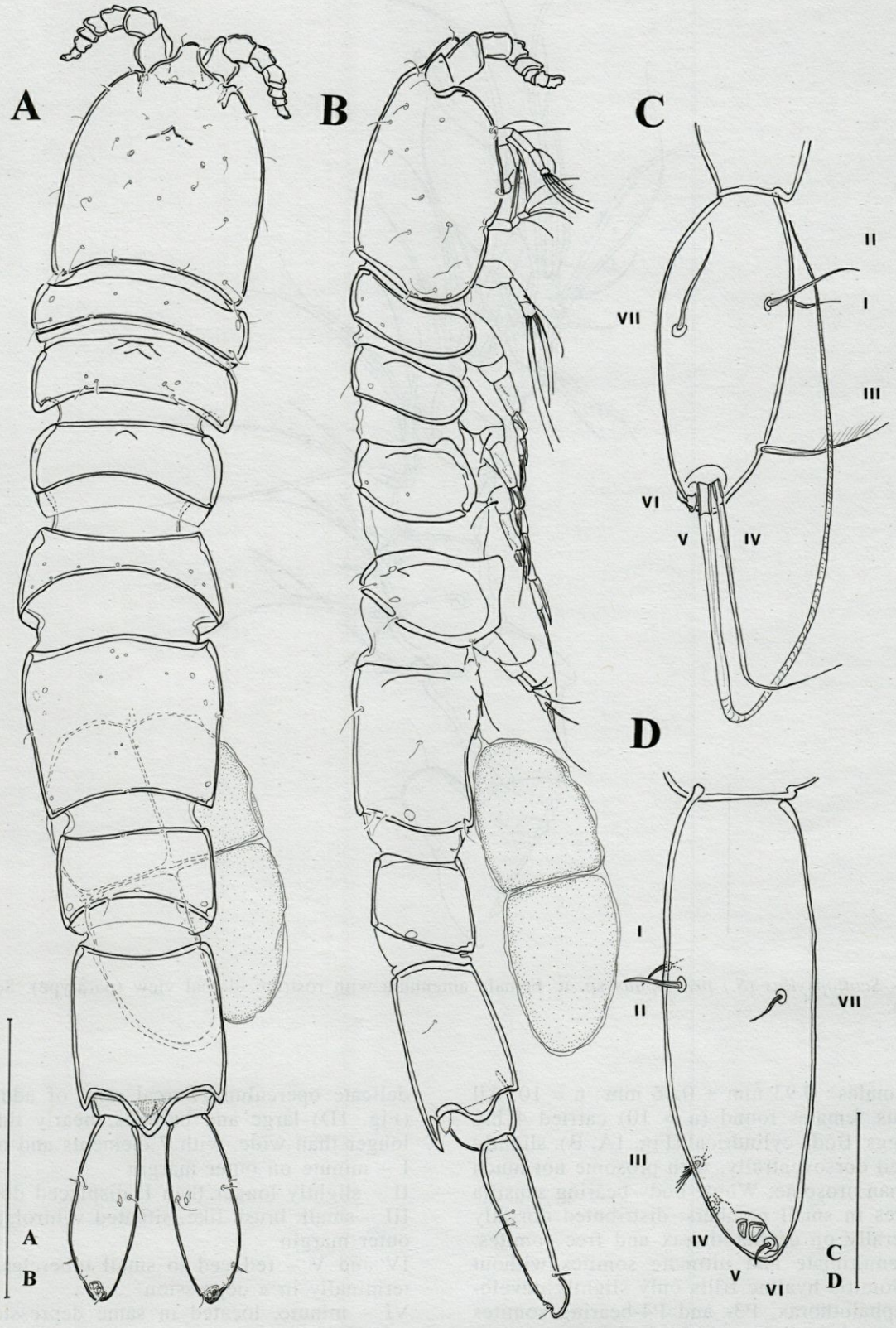

Fig. 1. – *Scottopsyllus (S.) praecipuus* sp. n. A. Female habitus, dorsal (holotype); B. Female habitus, lateral (holotype); C. Female copepodid V furcal ramus, dorsal (paratype); D. Adult female furcal ramus, dorsal (holotype). Scale bars = A, B, 0.2 mm; C, D, 0.05 mm.

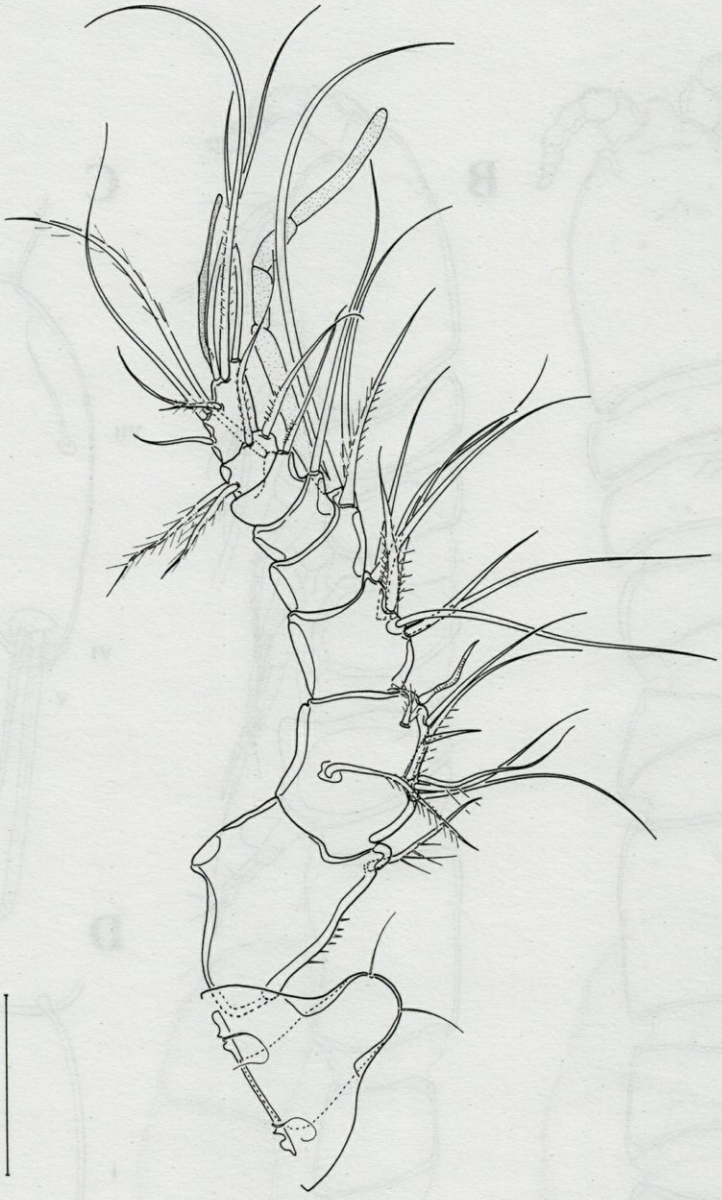

Fig. 2. – *Scottopsyllus (S.) praecipuus* sp. n. Female antennula with rostrum, dorsal view (paratype). Scale bar = 0.03 mm.

other females : 0.93 mm ± 0.06 mm ; n = 10. All ovigerous females found (n > 10) carried 4 big yolky eggs. Body cylindrical (Fig. 1A, B), slightly depressed dorsoventrally, with prosome not much wider than urosome. Whole body bearing sensilla and pores in small numbers, distributed dorsally and laterally on cephalothorax and free somites. Only penultimate and ultimate somites without pores. Somitic hyaline frills only slightly developed. Cephalothorax, P3- and P4-bearing somites dorsally with delicate chitinous ornamentation. Penultimate somite carrying a strong chitinous pseudoperculum dorsally and laterally a posteriorly arched structure on either side of the body. Anal somite very short and cleft medially with delicate operculum. Furcal rami of adult female (Fig. 1D) large and bulbous, nearly three times longer than wide, with 7 elements and one pore :

I – minute on outer margin
II – slightly longer than I, displaced dorsally
III – small, brush-like, situated ventrolaterally on outer margin
IV and V – reduced to small tubercles, situated terminally in a depression
VI – minute, located in same depression as IV and V
VII – longest seta, on dorsal surface.

This reduced setation is only found in adult females. Female copepodids C V (Fig. 1C) show an ornamentation of furcal rami comparable to

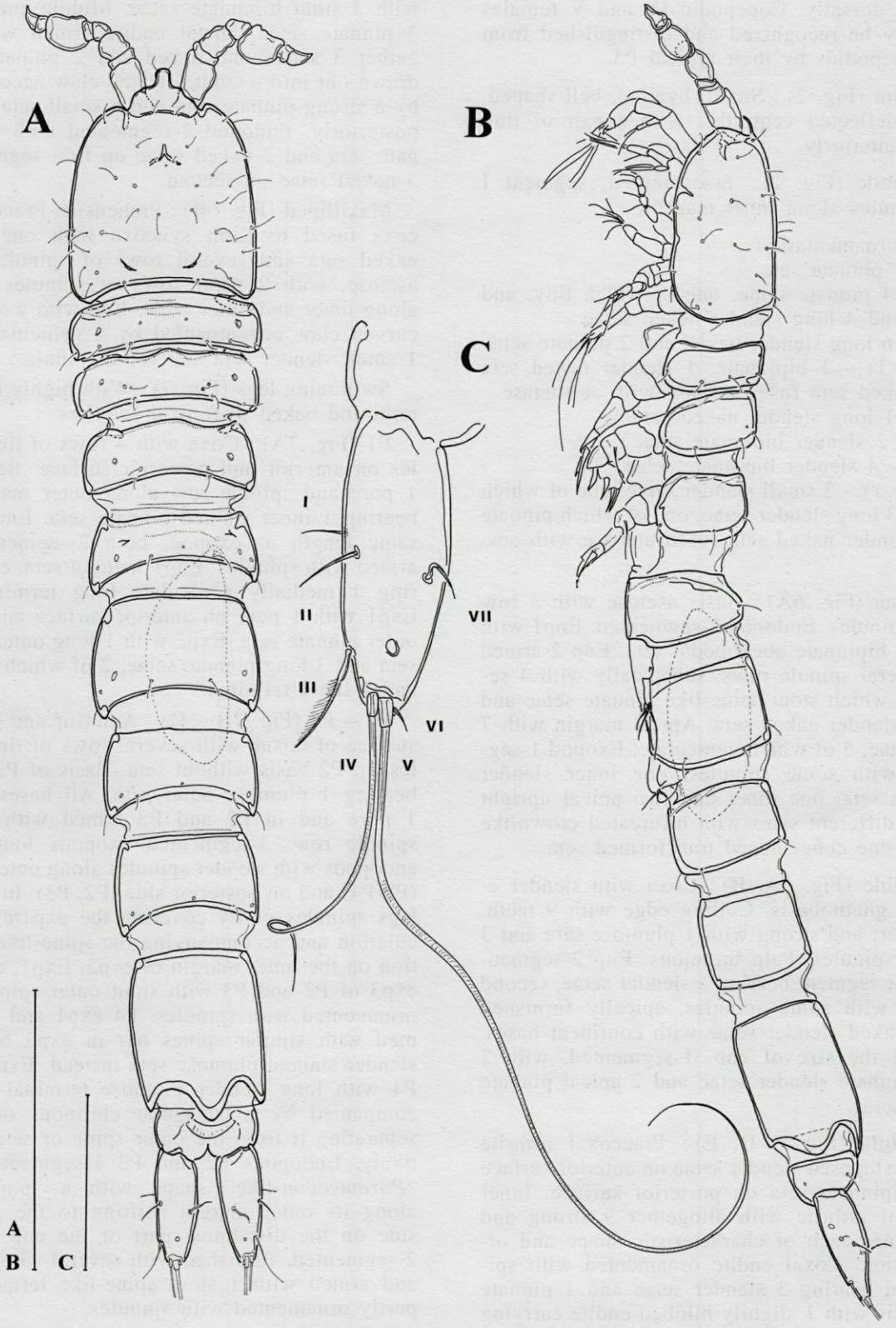

Fig. 3. – *Scottopsyllus (S.) praecipuus* sp. n. A. Male habitus, dorsal; B. Male habitus, lateral; C. Male furcal ramus, dorsal; A-C. Allotype. Scale bars = A, B. 0.2 mm; C. 0.05 mm.

adult males (Fig. 3C). The long slender setae IV and V as well as the shorter seta VII are always deflected dorsally. Copepodid IV and V females can easily be recognized and distinguished from male copepodids by their typical P5.

Rostrum (Fig. 2) : Small, hyaline, bell-shaped, slightly deflected ventrally; with a pair of tiny sensilla anteriorly.

Antennule (Fig. 2) : 8-segmented, segment I with spinules along inner margin.

Setal ornamentation :
I (1) – 1 pinnate seta
II (9) – 4 pinnate setae, one of which tiny, and 1 short and 4 long slender naked setae
III (8) – 6 long slender naked and 2 pinnate setae
IV (3 + 1) – 1 bipinnate, 1 slender naked seta and 1 naked seta fused at base with aesthetasc
V (1) – 1 long slender naked seta
VI (2) – 2 slender bipinnate setae
VII (4) – 4 slender bipinnate setae
VIII (7 + 1) – 3 small slender setae, one of which pinnate, 3 long slender setae, one of which pinnate and 1 slender naked seta fused at base with aesthetasc.

Antenna (Fig. 6A) : Basis asetose with a row of tiny spinules. Endopod 2-segmented. Enp1 with one long bipinnate abexopodal seta. Enp 2 armed with several spinule rows, subapically with 4 setae, 3 of which stout spine-like pinnate setae and 1 small slender naked seta. Apical margin with 7 naked setae, 5 of which geniculate. Exopod 1-segmented with some spinules, one inner slender bipinnate seta, one inner and two apical upright setae of different sizes with bifurcated crownlike tips and one cone-shaped transformed seta.

Mandible (Fig. 5A, B) : Coxa with slender elongated gnathobasis. Cutting edge with 9 teeth. Basis short and strong with 1 plumose seta and 3 rows of spinules. Palp biramous. Enp 2-segmented : First segment bearing 3 slender setae, second segment with some spinules, apically furnished with 7 naked slender setae with confluent bases. Exp half the size of enp, 1-segmented, with 2 lateral pinnate slender setae and 2 apical pinnate slender setae.

Maxillula (Fig. 5 D, E) : Praecoxal arthrite with 2 juxtaposed slender setae on anterior surface and 1 bipinnate seta on posterior surface. Inner margin of arthrite with altogether 9 strong and stout spines each of characteristic shape and ornamentation. Coxal endite ornamented with spinules and bearing 3 slender setae and 1 pinnate seta. Basis with 1 slightly bilobed endite carrying tiny spinules on anterior surface and armed with 5 slender naked setae and one pinnate seta. Endopod 1-segmented with 5 slender setae. Exopod one-segmented with 2 bipinnate setae and a row of spinules.

Maxilla (Fig. 5C) : Praecoxa and coxa fused to form syncoxa bearing 3 endites. Proximal endite with 3 stout bipinnate setae. Middle endite with 3 pinnate setae. Distal endite armed with altogether 3 setae, one naked and 2 pinnate. Basis drawn out into a stout serrated claw accompanied by a strong pinnate seta and a small seta situated posteriorly. Endopod 2-segmented with one pinnate seta and 2 naked setae on first segment and 3 naked setae on second.

Maxilliped (Fig. 6B) : Prehensile. Praecoxa and coxa fused to form syncoxa with one slender naked seta and several rows of spinules. Basis asetose, with 2 short rows of spinules running along inner and outer edge. Enp with a subapical curved claw accompanied by 2 geniculate setae, 1 small slender seta and some spinules.

Swimming legs (Fig. 7) : With highly modified rami and naked intercoxal sclerites.

P1 (Fig. 7A) : Coxa with 4 rows of tiny spinules on anterior and posterior surface. Basis with 1 pore and spinule row along outer margin and bearing 1 inner stalked pinnate seta. Endopod of same length as exopod, both 2-segmented and armed with spinules. Enp1 without seta, enp2 bearing 1 medially geniculate long terminal seta. Exp1 with 1 pore on anterior surface and 1 long outer pinnate seta. Exp2 with 1 long outer pinnate seta and 3 long pinnate setae, 2 of which terminal and 1 inner terminal.

P2 – P4 (Fig. 7B – D) : Anterior and posterior surface of coxae with several rows of tiny spinules. In P2 basis without seta. Basis of P3 and P4 bearing 1 plumose outer seta. All bases bearing 1 pore and in P2 and P3 armed with anterior spinule row. 3-segmented exopods longer than endopods with slender spinules along outer margin (P2-P4) and on posterior side (P2, P3). In all three legs spinules partly covering the exp1/exp2 articulation and accompanying the spine-like elongation on the inner margin of exp2. Exp1, exp2 and exp3 of P2 and P3 with stout outer spines being ornamented with spinules. P4 exp1 and exp2 armed with similar spines but in exp3 bearing a slender stalked plumose seta instead. Exp3 in P2-P4 with long slender plumose terminal seta accompanied by a triangular chitinous outgrowth separating it from the outer spine or seta respectively. Endopods P2 and P3 1-segmented, of a "*Paramecium*-like" shape with a spinule row along its outer margin shifting to the posterior side on the distalmost part of the enp. Enp P4 2-segmented, furnished with several spinule rows and armed with 1 stout spine-like terminal seta partly ornamented with spinules.

P5 (Fig. 8A) : Legs fused medially forming a large leaf-like structure. Small exopod clearly separated from basendopodite. Benp bearing an outer basal plumose seta and 3 anterior pores on both sides and 1 medially located pore. The sur-

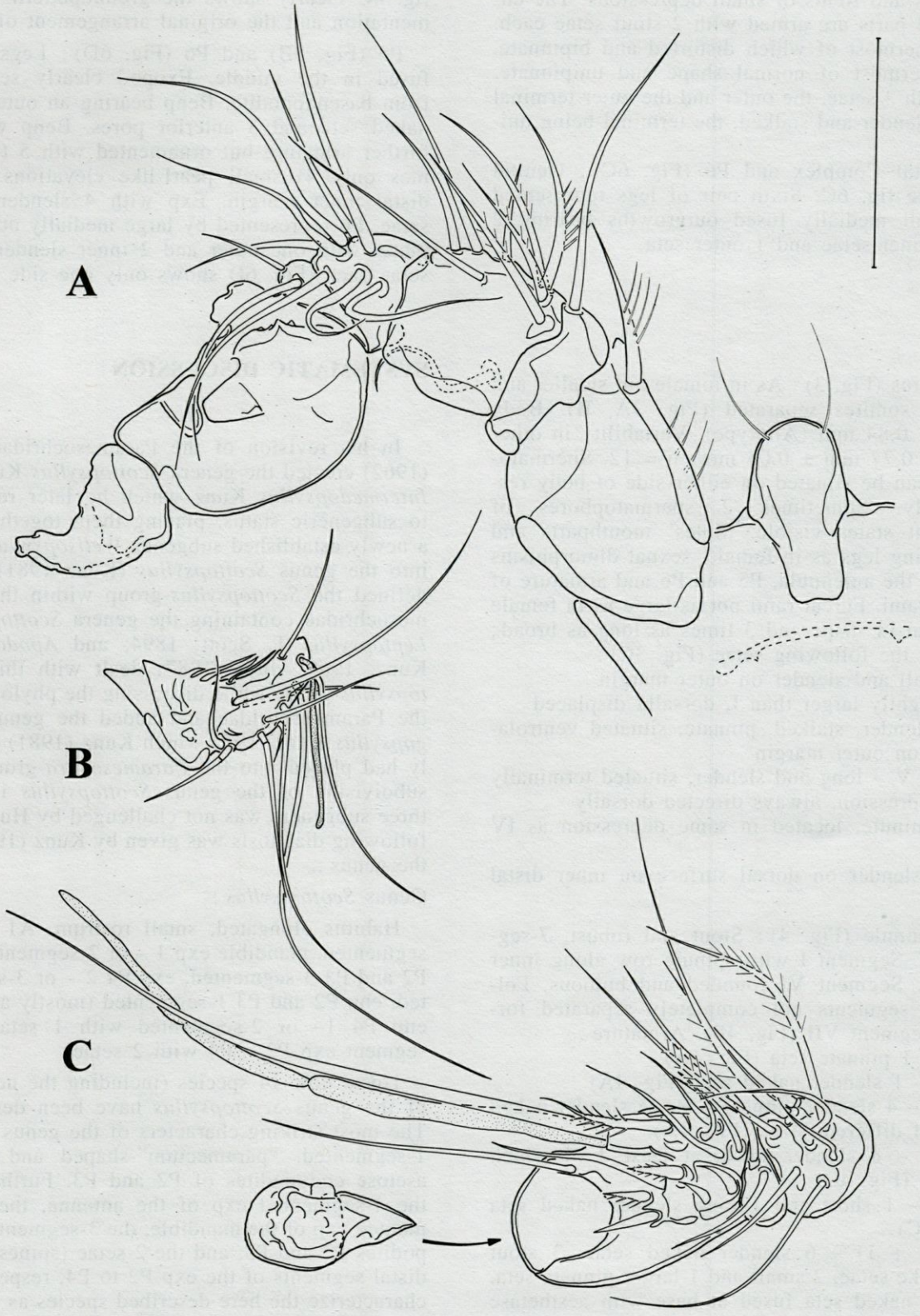

Fig. 4. – *Scottopsyllus (S.) praecipuus* sp. n. Male antennula with rostrum; A. Rostrum, segmentation of antennula and setation of segments I – V, ventral view (allotype); B. Setation of segment VII, ventral view (paratype); C. Setation of segments IV – VI and location of segment VII, inner view (paratype). Scale bar = 0.03 mm.

face of the benp is decorated with rows of tiny spinules and fields of small depressions. The endopodal parts are armed with 2 stout setae each. The innermost of which distorted and bipinnate, the outermost of normal shape and unipinnate. Exp with 3 setae, the outer and the outer terminal being slender and stalked, the terminal being unipinnate.

Genital Complex and P6 (Fig. 6C) : Genital field see fig. 6C. Sixth pair of legs represented by small medially fused outgrowths bearing 2 small inner setae and 1 outer seta.

Male

Habitus (Fig. 3) : As in female but smaller and genital somites separated (Fig. 3A, B). Body length : 0.84 mm (Allotype). Variability in other males : 0.77 mm ± 0.05 mm; n = 12. Spermatophore can be situated on either side of body respectively. Sometimes 2 spermatophores of different states visible. Males' mouthparts and swimming legs as in female, sexual dimorphisms only in the antennula, P5 and P6 and armature of furcal rami. Furcal rami not as large as in female elliptical in shape and 3 times as long as broad; bearing the following setae (Fig. 3C) :

I – small and slender on outer margin
II – slightly larger than I, dorsally displaced
III – slender, stalked, pinnate, situated ventrolaterally on outer margin
IV and V – long and slender, situated terminally in a depression, always directed dorsally
VI – minute, located in same depression as IV and V
VII – slender on dorsal surface on inner distal edge.

Antennule (Fig. 4) : Stout and robust, 7-segmented. Segment I with spinule row along inner margin. Segment VI rounded and bulbous. Following segments not completely separated forming segment VII (Fig. 4B). Armature :

I (1) – 1 pinnate seta (Fig. 4A)
II (1) – 1 slender naked seta (Fig. 4A)
III (9) – 4 slender pinnate setae, 5 slender naked setae of different sizes (Fig. 4A)
IV (8) – 8 slender setae, at least 3 of which pinnate (Fig. 4C)
V (2) – 1 short and 1 long slender naked seta (Fig. 4C)
VI (13 + 1) – 6 slender naked setae, 3 stout scale-like setae, 2 small and 1 larger pinnate seta, 1 long naked seta fused at base with aesthetasc (Fig. 4C)
VII (12 + 1) – 1 tiny slender seta accompanied by 1 small and 2 small elongated scales, 8 slender setae of different sizes, 2 stalked setae and 1 slender setae fused at base with aesthetasc (Fig. 4B).

The inner view of segments IV, V and VI in fig. 4C clearly shows the groundpattern of segmentation and the original arrangement of setae.

P5 (Fig. 8B) and P6 (Fig. 6D) : Legs of P5 fused in the middle. Exopod clearly separated from basendopodite. Benp bearing an outer basal naked seta and 3 anterior pores. Benp with no further armature but ornamented with 5 (sometimes only 4) small pearl-like elevations on its distal inner margin. Exp with 4 slender naked setae. P6 represented by large medially not fused plates with one outer and 2 inner slender naked setae each (Fig. 6D shows only one side of P6).

SYSTEMATIC DISCUSSION

In his revision of the Paramesochridae Kunz (1962) erected the genera *Scottopsyllus* Kunz and *Intermedopsyllus* Kunz which he later relegated to subgeneric status, placing them together with a newly established subgenus *Wellsopsyllus* Kunz into the genus *Scottopsyllus* (Kunz 1981). Kunz defined the *Scottopsyllus*-group within the Paramesochridae containing the genera *Scottopsyllus*, *Leptopsyllus* T. Scott, 1894, and *Apodopsyllus* Kunz, 1962. Huys (1987) dealt with this *Scottopsyllus*-group while discussing the phylogeny of the Paramesochridae and added the genus *Caligopsyllus* Kunz, 1975 which Kunz (1981) formerly had placed into the *Paramesochra*-group. The subdivision of the genus *Scottopsyllus* into the three subgenera was not challenged by Huys. The following diagnosis was given by Kunz (1981) for the genus :

Genus *Scottopsyllus* :

Habitus elongated, small rostrum, A1 exp 1-segmented, mandible exp 1 – or 2-segmented, exp P2 and P3 3-segmented, exp P4 2 – or 3-segmented, enp P2 and P3 1-segmented (mostly asetose), enp P4 1– or 2-segmented with 1 seta, distal segment exp P2 – P4 with 2 setae.

Up to now 14 species (including the new one) of the genus *Scottopsyllus* have been described. The most striking characters of the genus are the 1-segmented, "paramecium"-shaped and mostly asetose endopodites of P2 and P3. Furthermore, the 1-segmented exp of the antenna, the 1-segmented exp of the mandible, the 3-segmented exopodites P2 and P3, and the 2 setae (spines) at the distal segments of the exp P2 to P4, respectively, characterize the here described species as a member of the genus *Scottopsyllus* sensu Kunz. Whereas the subgenus *Intermedopsyllus* has a 2-segmented exp P4 with a fusion of the 2 proximal segments and the subgenus *Wellsopsyllus*, among other characters (see Table II), a 1-segmented enp P4, the new species *Scottopsyllus (S.)*

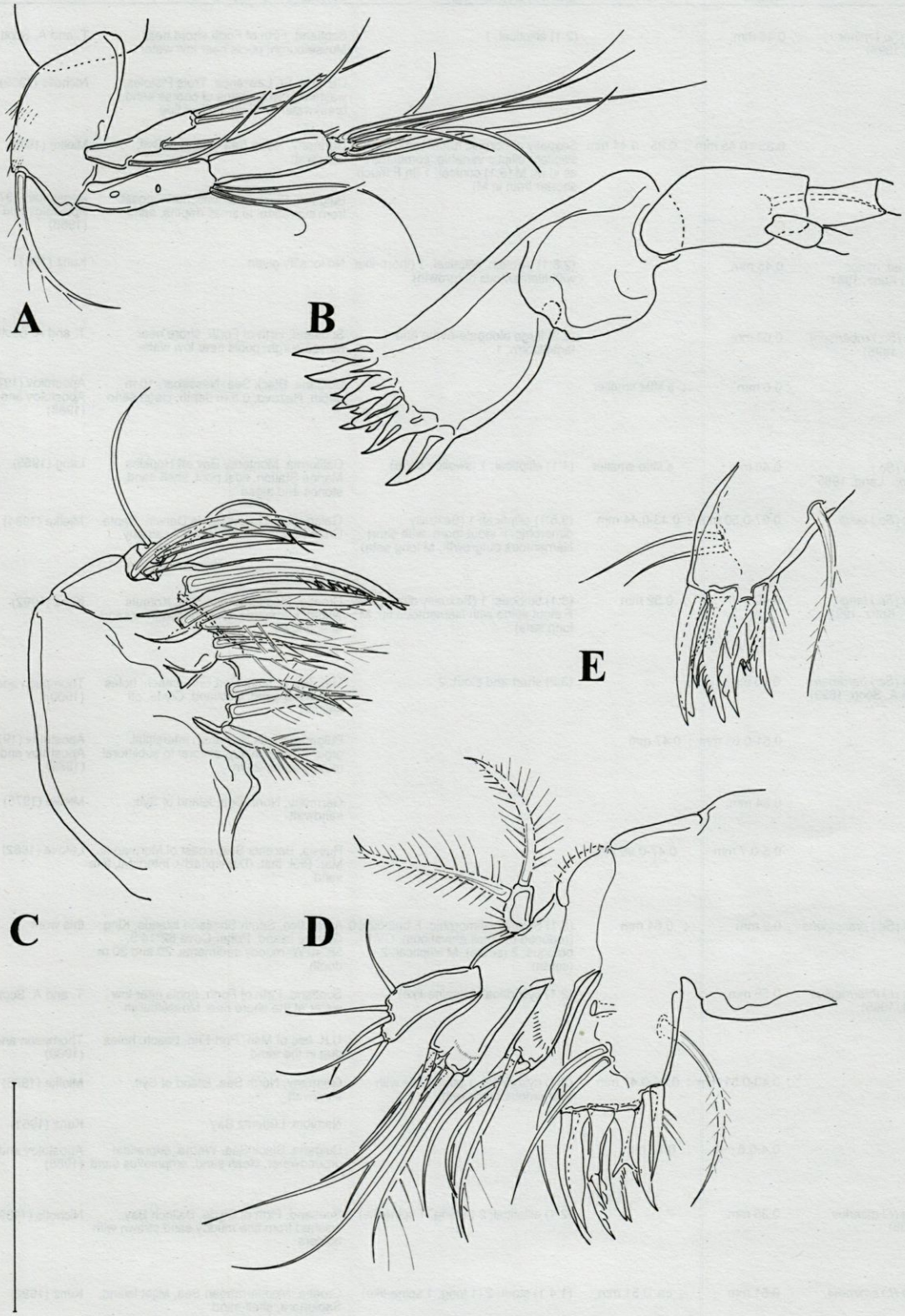

Fig. 5. – *Scottopsyllus (S.) praecipuus* sp. n. A. Female mandibular palp (holotype); B. Female mandible, setation of enp and exp omitted (paratype); C. Female maxilla (holotype); D. Female maxillula (paratype); E. Female maxillula praecoxal arthrite, rear view (paratype). Scale bar = 0.03 mm.

Table III. – Species of the genus *Scottopsyllus* with the subgenera *Scottopsyllus*, *Intermedopsyllus* and *Wellsopsyllus* according to Bodin (1998); (F = Female; M = Male).

Species	Body-size female	male	Furcal rami (length:breadth) form; number of well developed setae	Location, Depth, Sediment	Record
Scottopsyllus (Sc.) minor (T. & A. Scott, 1895)	0.46 mm;		(2:1) elliptical; 1	Scotland, Firth of Forth,shore near Musselburgh, pools near low water	T. and A. Scott (1895a)
				Canada, St. Lawrence, Trois Pistoles, washed from samples of coarse sand, breakwater level during low tide	Nicholls (1939)
	0.35 - 0.45 mm	; 0.35 - 0.44 mm	Sexually dimorphic furcal rami: F (2:1) swollen, elliptic variable, sometimes as in M; M (3:1) conical; 1 (in F much shorter than in M)	Germany, North Sea, Island of Sylt, Sandwatt	Mielke (1975)
				Bulgaria, Black Sea: Mitschurin, coast, from supratidal to small depths, sand	Apostolov (1972) Apostolov and Marinov (1988)
Scottopsyllus aff. minor (T. & A. Scott) Kunz, 1981	0.45 mm;		(2.8:1) swollen, elliptical; 1 (thorn-like with filamentous outgrowth)	No locality given	Kunz (1981)
Scottopsyllus (Sc.) robertsoni (T. & A. Scott, 1895)	0.63 mm;		(3.2) large elongate-ovate and lamelliform; 1.	Scotland, Firth of Forth, shore near Musselburgh, pools near low water	T. and A. Scott (1895a)
	0.6 mm	; a little smaller		Bulgaria, Black Sea: Nessebar, 10 m depth, Rezovo, 0.5 m depth, clean sand	Apostolov (1972) Apostolov and Marinov (1988)
Scottopsyllus (Sc.) pararobertsoni Lang, 1965	0.46 mm	; a little smaller	(4:1) elliptical; 1 (swollen base)	California, Monterey Bay off Hopkins Marine Station, tidal pool, shell-sand, stones and algae	Lang (1965)
Scottopsyllus (Sc.) langi Mielke, 1984	0.37-0.50 mm	; 0.43-0.44 mm	(3.5:1) elliptical; 1 (Sexually dimorphic: F stout thorn, with short filamentous outgrowth, M long seta)	Galapagos: Tower: Bahía Darwin; Santa Cruz: Puerto Nuñez, Bahía Academy	Mielke (1984)
Scottopsyllus (Sc.) langi continentalis Kunz, 1992	0.40 mm	; 0.32 mm	(3:1) bulbous; 1 (Sexually dimorphic: F stout spine with filamentous tip; M long seta)	Croatia, Mediterranean Sea, Korcula Island, Lumbarda south beach, fine sand at sea level	Kunz (1992)
Scottopsyllus (Sc.) herdmani (Thompson & A. Scott, 1899)	0.65 mm;		(3:2) short and stout; 2	U.K. Isle of Man, Port Erin, beach: holes dug in the sand; Scotland, Clyde, off Millport	Thompson and A.Scott (1900)
	0.51-0.65 mm	; 0.47 mm		Bulgaria, Black Sea, from interstitial ground water in supralittoral to sublittoral muddy sand, 20 m	Apostolov (1972) Apostolov and Marinov (1988)
	0.54 mm;			Germany, North Sea, Island of Sylt, sandwatt	Mielke (1975)
	0.5-0.7 mm	; 0.47-0.65 mm		Russia, Barents Sea, coast of Murmansk, Mar. Biol. Inst. (Dalniipliazh), intertidal, fine sand	Letova (1982)
Scottopsyllus (Sc.) praecipuus sp. n.	0.9 mm	; 0.84 mm	(3:1) Sexually dimorphic: F bulbous; 0 (reduced to small elevations). CV F bulbous; 2 (setae). M elliptical; 2 (setae)	Antarctica, South Shetland Islands, King George Island, Potter Cove 62°14'S, 58°40'W, muddy sediments, 20 and 30 m depth	this work
Scottopsyllus (I.) intermedius (T. & A. Scott, 1895)	0.58 mm;		(2:1) cylindrical; 1 (spine-like)	Scotland, Firth of Forth, pools near low water at the shore near Musselburgh	T. and A. Scott (1895b)
				U.K. Isle of Man, Port Erin, beach: holes dug in the sand	Thompson and A.Scott (1900)
	0.43-0.51 mm	; 0.36-0.47 mm	(2:1) cylindrical; 1 (spine-like with filamentous outgrowth)	Germany, North Sea, Island of Sylt, sandwatt	Mielke (1975)
				Namibia, Lüderitz Bay	Kunz (1951)
	0.4-0.6 mm	; 0.42 mm		Bulgaria, Black Sea, Warna, supratidal groundwater, clean sand, amphioxus sand	Apostolov and Marinov (1988)
Scottopsyllus (I.) minutus (Nicholls, 1939)	0.38 mm;		(2.1) elliptical; 2 (1 long, 1 spinelike)	Scotland, Firth of Clyde, Balloch Bay, washed from fine muddy sand strewn with bolders	Nicholls (1939)
Scottopsyllus (I.) smirnovi Kunz, 1992	0.51 mm	; ca. 0.51 mm	(1.4:1) stout; 2 (1 long, 1 spine-like)	Croatia, Mediterranean Sea, Mljet Island, Saplunara, shell-sand	Kunz (1992)
Scottopsyllus (W.) gigas (Wells, 1965)		; 0.8 mm	(ca. 2:1) stout, conical; 2	Scotland, Fladen 58°20'N 00°30'E 146 m, mud	Wells (1965)
Scottopsyllus (W.) runtzi (Soyer, 1975)	0.44-0.72 mm	; 0.38-0.47 mm	(ca. 1:1) stout, conical; 2	Kerguelen: Port Kirk, Anse du Tranchant, Baie Charrier; littoral sands, in neighbourhood of estuaries	Soyer (1975)
Scottopsyllus (W.) abyssalis (Becker,Noodt&Schriever, 1979)	0.95 mm (both)		(2.5:1) elliptical; 2	Peru Trench "Anton Bruun" 12°04'S 78°05'W, 2000 m	Becker, Noodt and Schriever (1979)

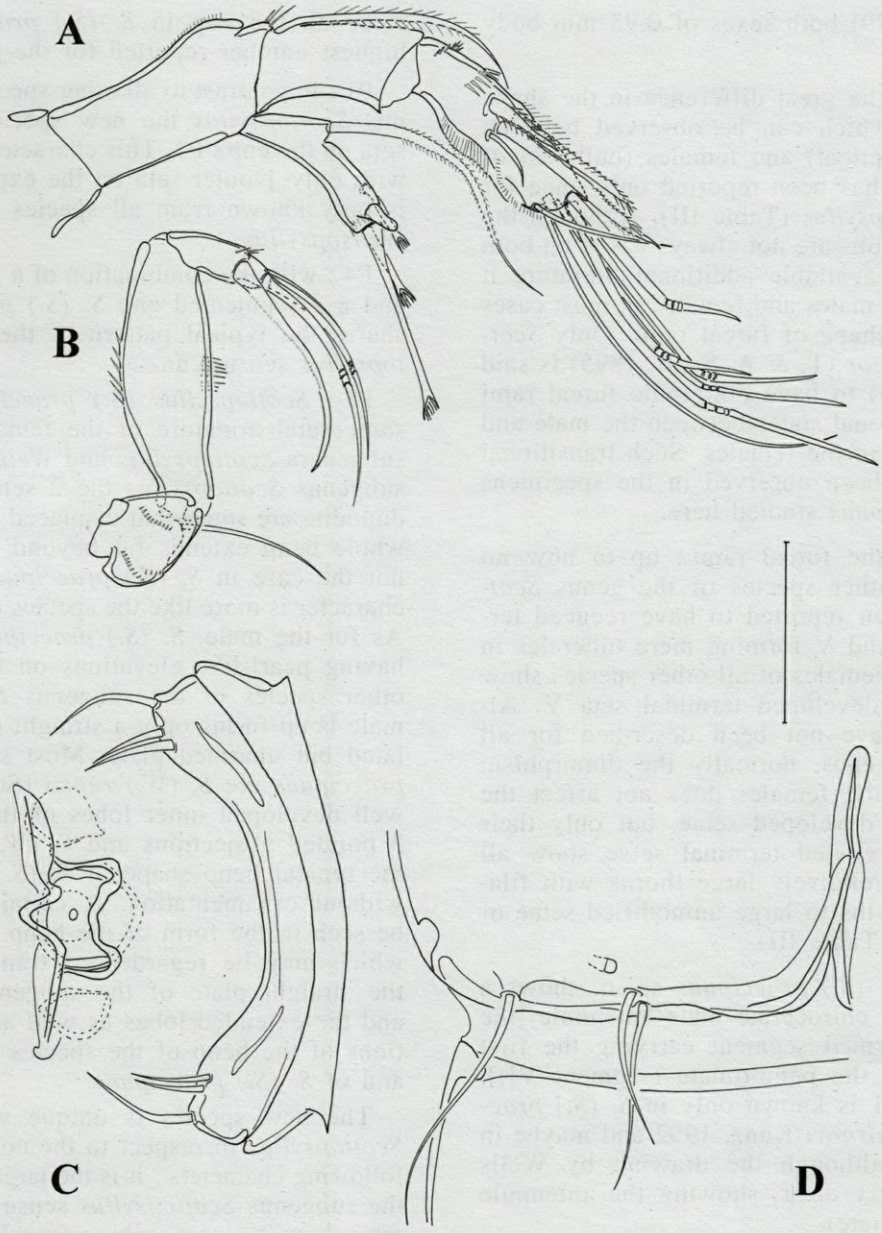

Fig. 6. – *Scottopsyllus (S.) praecipuus* sp. n. A. Female antenna (paratype); B. Female maxilliped (holotype); C. Female P6 and genital field (paratype); D. Male P6 (allotype), only one side shown. Scale bar = 0.03 mm.

praecipuus retains 3 well separated segments in the exp P4 and a 2-segmented enp. This is used here to provisionally place it into the subgenus *Scottopsyllus* sensu Kunz. The only other species known so far which does not properly fit into Kunz' classification (1981) is the subsequently described *Scottopsyllus langi* Mielke, 1984 showing an incomplete fusion of the 2 proximal segments of exp P4 and being transitional between the subgenera *Scottopsyllus* and *Intermedopsyllus* (Mielke 1984). However, because of 5 long inner basal "setoid elements" (no real setae but very long spinules) at P1, Mielke placed it into the subgenus *Scottopsyllus* where this character is common in some species.

Within the genus *Scottopsyllus (S.) praecipuus* can be separated from the other species by the following characters (the comparisons were made using original descriptions and additional literature) :

Body-size : with 0.9 mm length in the female and 0.84 mm in the male it is the largest species of the subgenus *Scottopsyllus*, the members of which on average are 0.4 mm long (see table III). Only females of *Scottopsyllus (S.) herdmani* (Thompson & A.Scott, 1899) can reach sizes of 0.7 mm (Letova 1982). Two species of the subgenus *Wellsopsyllus* reach similar sizes : *Scottopsyllus (Wellsopsyllus) gigas* (Wells, 1965) has males of 0.8 mm and *S. (W.) abyssalis* (Becker, Noodt

& Schriever, 1979) both sexes of 0.95 mm body length.

Furcal rami : the great difference in the shape of furcal rami which can be observed between adult males (elliptical) and females (bulbous) of the new species has been reported only once for the genus *Scottopsyllus* (Table III). Although the original descriptions are not always based on both sexes, from the available additional literature it can be seen, that males and females in most cases share the same shape of furcal rami. Only *Scottopsyllus (S.) minor* (T. & A. Scott, 1895) is said by Mielke (1975) to have dimorphic furcal rami and even transitional states between the male and the female form in the females. Such transitional forms have not been observed in the specimens of *S. (S.) praecipuus* studied here.

Armature of the furcal rami : up to now no female of any other species of the genus *Scottopsyllus* has been reported to have reduced terminal setae IV and V forming mere tubercles in the adult stage. Females of all other species show at least a well developed terminal seta V. Although males have not been described for all species of the genus, normally the dimorphism between males and females does not affect the number of well developed setae, but only their shape. Well developed terminal setae show all variations from relatively large thorns with filamentous outgrowths to large unmodified setae of various lengths (Table III).

Antennule : *S. (S.) praecipuus* sp. n. shows a seven-segmented chirocerate male antennule [the bulbous, transformed segment carrying the first aesthetasc being the penultimate (segment VI)]. A chirocerate A1 is known only in *S. (S.) praecipuus*, *S. (I.) smirnovi* Kunz, 1992 and maybe in *S. (W.) gigas* (although the drawing by Wells (1965) is not very clear, showing the antennule in the reflexed state).

Antenna : the peculiar setae with crownlike tips can be found at the exp of at least the following species : *S. (S.) aff minor* (T. & A. Scott) Kunz, 1981, *S. (S.) langi* Mielke, 1984, *S. (S.) langi continentalis* Kunz, 1992, *S. (S.) herdmani* (drawing by Letova 1982) and *S. (S.) praecipuus*. But in none of these species except *S. (S.) praecipuus* does the exp carry 3 setae with crownlike tips together with a blunt, transformed seta.

Mandible : a first enp segment carrying 3 setae as in *S. (S.) praecipuus* is present also in *S. (S.) robertsoni* (T. & A. Scott, 1895a), *S. (S.) minor* (T. & A. Scott, 1895a), and *S. (I.) intermedius* (T. & A. Scott, 1895b).

Maxilla : a basis with a claw, accompanied by a long seta and a small tiny seta on the opposite side is unique within the genus *Scottopsyllus* and in the family Paramesochridae as a whole. Six setae on the enp in *S. (S.) praecipuus* are the highest number reported for the genus.

P1 : in contrast to all other species of the subgenus *Scottopsyllus* the new species bears only 1 seta on the enp2 P1. This character in combination with only 1 outer seta on the exp1 P1 up to now is only known from all species of the subgenus *Wellsopsyllus*.

P4 : with the combination of a 3-segmented exp and a 2-segmented enp *S. (S.) praecipuus* sp. n. shares the typical pattern of the subgenus *Scottopsyllus* sensu Kunz.

P5 : *Scottopsyllus (S.) praecipuus* shows the same setal armature of the female P5 as in the subgenera *Scottopsyllus* and *Wellsopsyllus*. In the subgenus *Scottopsyllus* the 2 setae of the basendopodite are somewhat displaced medially and the whole benp extends far beyond the exp. This is not the case in *S. (S.) praecipuus* which in this character is more like the species of *Wellsopsyllus*. As for the male, *S. (S.) praecipuus* is unique in having pearl-like elevations on the benp. In the other species of the subgenus *Scottopsyllus* the male benp forms only a straight or slightly undulated but unarmed plate. Most similar to *S. (S.) praecipuus* are *S. (W.) runtzi* (Soyer, 1975) with well developed inner lobes of the benp carrying 3 pointed projections and *S. (W.) abyssalis* with the typical benp shape of *S. (S.) praecipuus* but without ornamentation. A certain similarity can be seen in the form of the benp of *S. (W.) gigas* which may be regarded as transitional between the straight plate of the subgenus *Scottopsyllus* and the extended lobes as well as the ornamentations of the benp of the species of *Wellsopsyllus* and of *S. (S.) praecipuus*.

The new species is unique within the genus *Scottopsyllus* in respect to the combination of the following characters : it is the largest species within the subgenus *Scottopsyllus* sensu Kunz, its furcal rami show the most striking sexual dimorphism ever described for the genus *Scottopsyllus*, the 2 terminal setae IV and V of the furcal rami of the female are reduced to mere tubercles in the adult stage, the exp of the antenna has 3 setae with crownlike tips and a blunt transformed seta, the basis of the maxilla has a seta accompanying the claw on one side and another small tiny seta on the other side of the claw, the male P5 shows pearl-like elevations on an otherwise typically shaped benp. The armature of P1 with only 1 seta on the enp2 and only 1 outer seta on the exp1 P1 is unique for the subgenus *Scottopsyllus* sensu Kunz.

From the discussion it becomes clear, that *S. (S.) praecipuus* shares many characters such as body-size, the chirocerate A1 of the males, the P1, the shape of the benp P5 in both sexes and the armature of the males' furcal rami (Table III) not with the members of the subgenus *Scottopsyllus* sensu Kunz, but with the species of the subge-

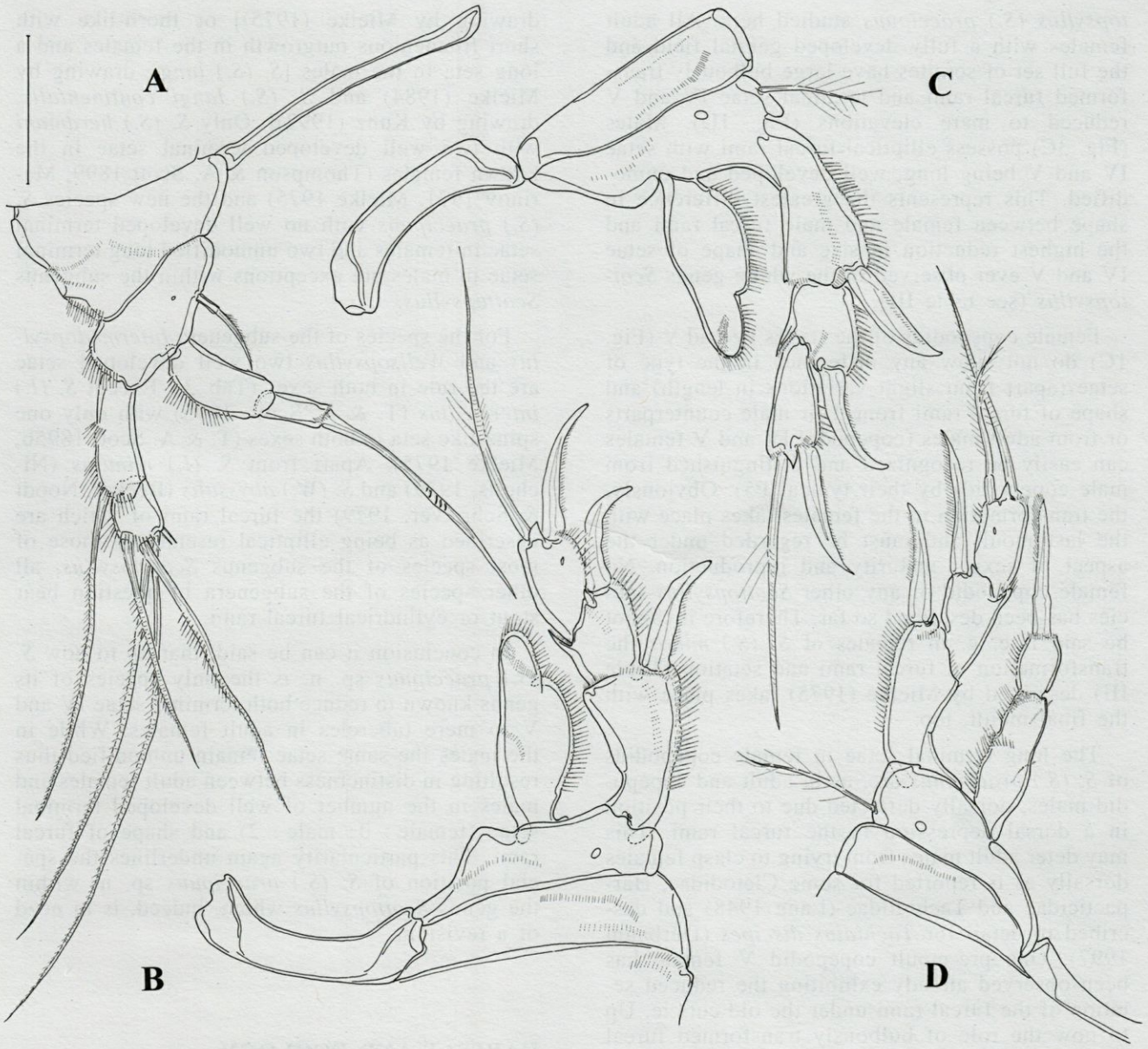

Fig. 7. – *Scottopsyllus (S.) praecipuus* sp. n. A. Female P1 with intercoxal sclerite (paratype); B. Female P2 with intercoxal sclerite (paratype); C. Female P3 with intercoxal sclerite (paratype); D. Female P4 with intercoxal sclerite (paratype). Scale bar = 0.03 mm.

nus *Wellsopsyllus*. On the other hand such facts as the enp P4 being 2-segmented, the hint that there is a population of *S. (S.) herdmani* of the German Bight with only 1 seta on the enp P1 (Kunz 1937, Mielke 1975) and additional characters like setae with crownlike tips on the exp of the antenna and 3 setae on the first segment of the mandible enp plead for placement of *S. (S.) praecipuus* sp. n. into the subgenus *Scottopsyllus* sensu Kunz. The new species shows that there is no clear distinction between the subgenera *Scottopsyllus* and *Wellsopsyllus*. Only a phylogenetic analysis will shed light on these relationships. For the time being the new species is placed tentatively into the subgenus *Scottopsyllus*.

SEXUAL DIMORPHISM IN THE GENUS *SCOTTOPSYLLUS*

As Schminke (1991) points out, sexual dimorphism in furcal rami is of common occurrence in Parastenocarididae. It is a widespread phenomenon also in other families of Harpacticoida such as in Tetragonicipitidae (Mielke 1989), Cletodidae (Lorenzen 1969), and Canthocamptidae (Boxshall & Evstigneeva 1994). In some of these cases the furcal rami are not only dimorphic, but even polymorphic with transitional forms within females of the same species. So far such a polymorphism has not been found in the population of *Scot-*

topsyllus (S.) praecipuus studied here. All adult females with a fully developed genital field and the full set of somites have large bulbously transformed furcal rami and terminal setae IV and V reduced to mere elevations (Fig. 1D). Males (Fig. 3C) possess elliptical furcal rami with setae IV and V being long, well developed and unmodified. This represents the greatest difference in shape between female and male furcal rami and the highest reduction in size and shape of setae IV and V ever observed in the whole genus *Scottopsyllus* (see table III).

Female copepodids of the stages IV and V (Fig. 1C) do not show any difference in the type of setae (apart from slight variations in length) and shape of furcal rami from their male counterparts or from adult males (copepodid IV and V females can easily be recognized and distinguished from male copepodids by their typical P5). Obviously, the transformation in the females takes place with the last moult and must be regarded under the aspect of sexual maturity and reproduction. No female copepodid of any other *Scottopsyllus*-species has been described so far. Therefore it cannot be said if e. g. in females of *S. (S.) minor* the transformation of furcal rami and setation (Table III) described by Mielke (1975) takes place with the final moult, too.

The long terminal setae in female copepodids of *S. (S.) praecipuus* are, as in adult and copepodid males, dorsally deflected due to their position in a dorsal depression in the furcal rami. This may deter adult males from trying to clasp females dorsally as is reported for some Cletodidae, Harpacticidae and Tachidiidae (Lang 1948) and described in detail for *Tachidius discipes* (Dürbaum 1997). One pre-moult copepodid V female has been observed already exhibiting the reduced setation of the furcal rami under the old cuticle. Up to now the role of bulbously transformed furcal rami in adult females as opposed to elliptical ones in males cannot be explained. Only life observations of mating pairs will help in elucidating these morphological differences.

Table III shows the variability in shape of furcal rami and modifications of setae IV and V within the genus *Scottopsyllus*. Apart from *S. (S.) praecipuus* sexual dimorphism in shape and size of furcal rami is known only from *Scottopsyllus (S.) minor* with swollen elliptical furcal rami in females and conically shaped ones in males (Mielke 1975). Most of the species of the subgenus *Scottopsyllus* carry only one strongly developed terminal seta V, with seta IV being tiny and hairlike [e.g. *S. (S.) minor*, drawing by Mielke (1975) and *S. (S.) pararobertsoni*, drawing by Lang (1965)] or forming a very short spine [*S. (S.) langi*, drawing by Mielke (1984)]. Sexual dimorphism exists in the modification of seta V : e.g. females' seta shorter than males' [*S. (S.) minor*, drawing by Mielke (1975)] or thorn-like with short filamentous outgrowth in the females and a long seta in the males [*S. (S.) langi*, drawing by Mielke (1984) and *S. (S.) langi continentalis*, drawing by Kunz (1992)]. Only *S. (S.) herdmani* with two well developed terminal setae in the known females (Thompson & A. Scott 1899, Marinov 1971, Mielke 1975) and the new species *S. (S.) praecipuus* with no well developed terminal setae in females and two unmodified long terminal setae in males are exceptions within the subgenus *Scottopsyllus*.

For the species of the subgenera *Intermedopsyllus* and *Wellsopsyllus* two well developed setae are the rule in both sexes (Tab. 3). Except *S. (I.) intermedius* (T. & A. Scott, 1895) with only one spine-like seta in both sexes (T. & A. Scott 1895b, Mielke 1975). Apart from *S. (I.) minutus* (Nicholls, 1939) and *S. (W.) abyssalis* (Becker, Noodt & Schriever, 1979) the furcal rami of which are described as being elliptical resembling those of most species of the subgenus *Scottopsyllus*, all other species of the subgenera in question bear stout or cylindrical furcal rami.

In conclusion it can be said, that up to now *S. (S.) praecipuus* sp. n. is the only species of its genus known to reduce both terminal setae IV and V to mere tubercles in adult females. While in the males the same setae remain unmodified thus resulting in distinctness between adult females and males in the number of well developed terminal setae (female : 0; male : 2) and shape of furcal rami. This particularity again underlines the special position of *S. (S.) praecipuus* sp. n. within the genus *Scottopsyllus* which, indeed, is in need of a revision.

HABITAT AND ECOLOGY

Scottopsyllus (S.) praecipuus sp. n. are comparatively large harpacticoids and can only be found in low abundances in the sediments (Fig. 9) of the transects 1 and 2 in Potter Cove. Only *Pseudotachidius jubanyensis* Veit-Köhler & Willen, 1999 being sympatric with *S. (S.) praecipuus*, has larger adults (Veit-Köhler & Willen 1999). In all samples the number of adult males of the new species exceeds the number of adult females. Due to the high parental input into each offspring (all ovigerous females found carried only four big and yolky eggs), only low numbers of copepodids can be found compared with the numbers of adults. Obviously, *Scottopsyllus (S.) praecipuus* has to be regarded as a K-selected species. This is no exception within its genus, and even within the whole Paramesochridae the production of few but

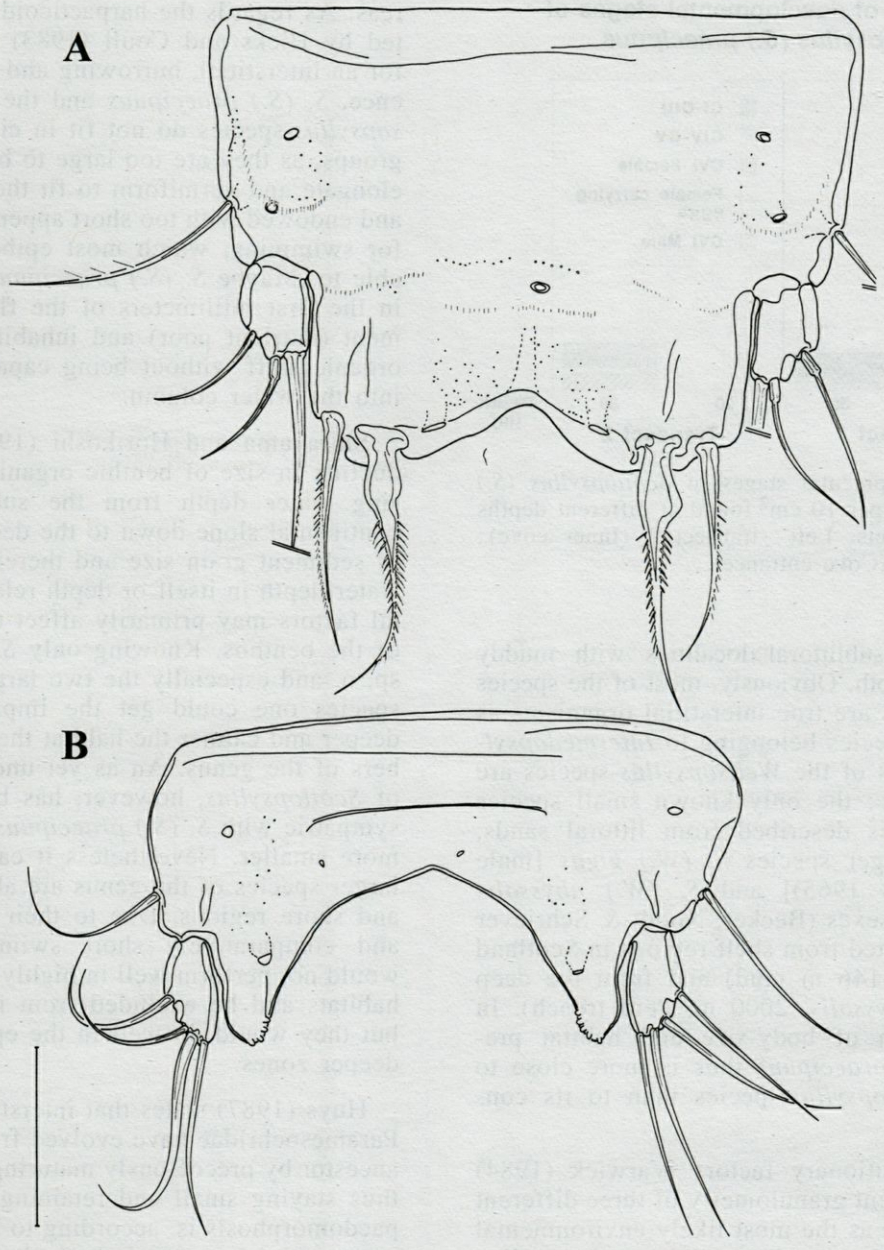

Fig. 8. – *Scottopsyllus (S.) praecipuus* sp. n. A. Female P5 (paratype); B. Male P5 (paratype). Scale bar = 0.03 mm.

large eggs seems to be the rule (T. & A. Scott 1895a, 1895b; Letova 1982).

Scottopsyllus (S.) praecipuus sp. n. prefers muddy sediments in the deeper calm and unexposed areas of Potter Cove. As shown in fig. 9, along both transects the species was not found at the 5 m and 10 m stations. In transect 1 the first individuals are found at a depth of 20 m, in transect 2 at 30 m. As the transects are from two very distinct sites (transect 1 in the calm inner cove and transect 2 in the highly disturbed cove entrance) the grain size distribution along each is different (Veit-Köhler & Willen 1999). But in no case the mean diameter of grain size exceeds 40 µm and the sediments are poorly to very poorly sorted (calculated after Giere, Eleftheriou & Murison 1988).

All other species of the subgenus *Scottopsyllus* have been described from sandy sediments (Table III). They have been reported from tide pools, samples of coarse sand, clean sand, shell sand and fine sand on shores and beaches. Their body-sizes range from 0.32 mm in the male of *S.(S.) langi continentalis* (Kunz, 1992) to 0.63 mm in the females of *S. (S.) robertsoni* (T. & A. Scott, 1895a). Only *S. (S.) herdmani*, the hitherto largest species of the subgenus (Table III), was reported by Apostolov and Marinov (1988) from the intertidal,

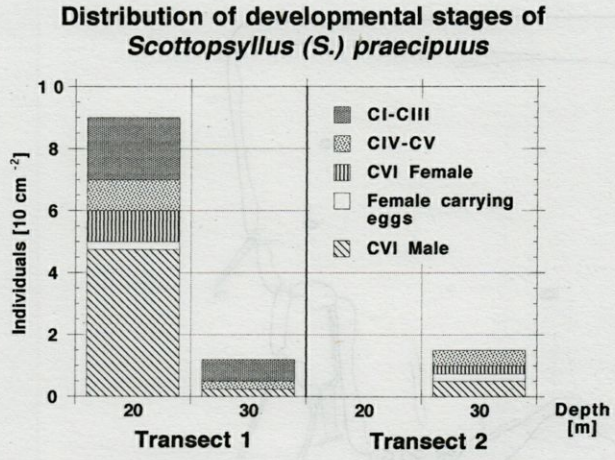

Fig. 9. – Developmental stages of *Scottopsyllus (S.) praecipuus* sp. n. per 10 cm^2 found at different depths along two transects. Left : transect 1 (Inner cove); right : transect 2 (Cove entrance).

but also from sublittoral localities with muddy sand at 20 m depth. Obviously, most of the species of this subgenus are true interstitial organisms as are the small species belonging to *Intermedopsyllus*. The habitats of the *Wellsopsyllus*-species are clearly different : the only known small species *S. (W.) runtzi* is described from littoral sands, whereas the larger species *S. (W.) gigas* [male 0.8 mm (Wells 1965)] and *S. (W.) abyssalis* [0.95 mm both sexes (Becker, Noodt & Schriever 1979)] are reported from shelf regions in Scotland (*S. (W.) gigas*, 146 m mud) and from the deep sea (*S. (W.) abyssalis*, 2000 m, Peru trench). In the combination of body-size and habitat preference *S. (S.) praecipuus* thus is more close to the large *Wellsopsyllus*-species than to its consubgeners.

Besides evolutionary factors Warwick (1984) discusses sediment granulometry of three different sandy sediments as the most likely environmental constraint on body-size. Depending on the median diameter of the sand particles, colonization of the interstices is possible for meiofaunal species of all sizes in coarse sands, of only small sizes in finer sands and of either very small interstitial species or sufficiently large burrowers able to displace sand grains in very fine sand. Schwinghamer (1981) argues that there is an upper limit of body-size of interstitial meiofauna, followed by a shift in size from interstitial to burrowing lifestyle with a class of intermediate sized animals capable of neither. But he observed no restriction on size in organisms capable of burrowing in fluid muds. The muds encountered in Potter Cove are very fluid and the RPD layer was never observed in the sampled upper 3 cm of the sediment. So *S. (S.) praecipuus* may burrow there but probably is not large or strong enough to burrow in the consolidated sandy sediments of the shallower areas. As regards the harpacticoid body forms stated by Hicks and Coull (1983) as being typical for an interstitial, burrowing and epibenthic existence, *S. (S.) praecipuus* and the two large *Wellsopsyllus*-species do not fit in either of the three groups, as they are too large to be interstitial, too elongate and vermiform to fit the burrowing type and endowed with too short appendages unsuitable for swimming, which most epibenthic forms are able to. Maybe *S. (S.) praecipuus* partly burrows in the first millimeters of the fluid muddy sediment (nutrient poor) and inhabits the epibenthic organic fluff without being capable of emerging into the water column.

Shirayama and Horikoshi (1989) report a reduction in size of benthic organisms with increasing water depth from the sublittoral via the continental slope down to the deep-sea regardless of sediment grain size and therefore propose that water depth in itself or depth related environmental factors may primarily affect the size structure of the benthos. Knowing only *S. (S.) praecipuus* sp. n. and especially the two large *Wellsopsyllus*-species one could get the impression, that the deeper and calmer the habitat the larger the members of the genus. An as yet undescribed species of *Scottopsyllus*, however, has been found to be sympatric with *S. (S.) praecipuus* and to be much more smaller. Nevertheless it can be stated, that larger species of the genus are absent from beach and shore regions. Due to their larger body-size and comparatively short swimming legs they would not perform well in highly disturbed littoral habitats and be excluded from interstitial spaces but they would do well in the epibenthic fluff of deeper zones.

Huys (1987) states that interstitial forms of the Paramesochridae have evolved from an epibenthic ancestor by precociously maturing at a larval stage thus staying small and retaining short legs. This paedomorphosis is, according to him, increasingly expressed in a morphological series within the *Scottopsyllus*-group sensu Huys (1987). As the three large species of *Scottopsyllus* still show this reduced state especially in the swimming-legs their enlargement must be secondary phylogenetically so that they may well have had interstitial ancestors.

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