

Japan (Tanaka, 1967; Ohtsuka, 1985; Ohtsuka & Mitsuzumi, 1990; Ohtsuka et al., 1991), Australia (McKinnon & Kimmerer, 1985), and New Zealand (Othman & Greenwood, 1992). Records of species far from their ordinary ranges, such as those of *Paramisophria cluthae* T. Scott, 1897 from the Mediterranean (Sars, 1924-1925) and the western Pacific (Tanaka, 1967), or that of *P. ammophila* Fosshagen, 1968 from the Mediterranean (Carola et al., 1995), should be considered with caution since they are based on females only, and the major diagnostic characters at the species level rely on male morphology.

In this paper, we describe three new species of *Paramisophria* from the Spanish zone of the Mediterranean, where they apparently follow an allopatric depth zonation pattern extending from the upper littoral to depths in excess of 1200 m. Additionally, the discovery of deep-water species has provided new evidence relevant to the deep-sea / shallow-water controversy on the origin of anchialine cave faunas (see Stock, 1986) from our analysis of the phylogenetic relationships between *Paramisophria* species and of the type of habitat exploited by each.

## Material and methods

The copepods studied were gathered in two different habitats: (1) near-bottom water layers above the bathyal floor, and (2) littoral caves (sensu Stock et al., 1986).

The deep-water hyperbenthic material was collected from R/V 'García del Cid' on the continental slope off Barcelona using a Macer-GIROQ type sledge (see Cartes et al., 1994). This gear has three superimposed nets (mesh size: 500 µm; 40 x 80 cm rectangular aperture) that sample the near-bottom water layers between 0.1 and 1.5 m above the bottom. Only the lowest net trapped *Paramisophria*. Sampling in Balearic caves was carried out using a hand-held plankton net or with baited traps left for several days in the cave lakes.

Drawings were prepared using a camera lucida on an Olympus BH-2 microscope equipped with differential interference contrast. Terminology used in descriptions follows Huys & Boxshall (1991) and Huys et al. (1996) (latter, for integumental and armature ornament elements). The use of the terms 'fused' for compound segments, or 'loss of proximal articulation to segment' for armature elements completely incorporated into their respective segments does not imply any phylogenetic significance, since we lack the developmental data that would be necessary to distinguish between segments or armature elements that remain undifferentiated through development and

those that secondarily fuse (see Karaytug & Boxshall, 1996).

The material is deposited in the Museu de la Naturalesa de les Illes Balears, Palma de Mallorca (MNCM). Material preserved in permanent glass slides is mounted in lactophenol sealed with nail varnish.

## Systematics

Subclass Copepoda H. Milne Edwards, 1840

Order Calanoida G.O. Sars, 1903

Family Arietellidae G.O. Sars, 1902

Genus *Paramisophria* T. Scott, 1897

*Paramisophria mediterranea* sp. nov.

(Figs. 1-9)

Material examined. – 'Cova de na Mitjana' (Capdepera, Mallorca, Balearic Is.). UTM coordinates: 53910 / 439095-7. Fossil littoral cave excavated in Triassic fissured limestone, 5 m from shoreline, harbouring sandy bottom, shallow lake (depth < 0.5 m) subjected to direct marine influence. Topography of cave in Ginés et al. (1975). Holotype: adult male 0.75 mm dissected on 6 slides; urosome preserved separately in 70 % ethanol [MNCM 356]. Paratype: adult female 0.78 mm dissected on 7 slides; urosome in 70 % ethanol [MNCM 357]. Collected by G.A. Boxshall & D. Jaume, 24 July 1997.

Adult male. – Body (Fig. 1A-B) compact and extremely asymmetrical: left side of prosome compressed, almost straight in outline from dorsal aspect. Rostrum (Fig. 8B) fused to cephalosome, asymmetrical, ventrally directed, with pair of rostral filaments on tip; right filament implanted anterior to left. Cephalosome and first pedigerous somite separate. Fourth and fifth pedigerous somites completely fused, with pair of pointed dorsolateral processes and row of tiny dorsolateral outgrowths visible in dorsal aspect only, just behind each process; ventrolateral processes absent. Urosome 5-segmented, with genital somite slightly asymmetrical: single gonopore opening ventrolaterally on right side at posterior margin, closed off by narrow lappet (Fig. 5A). Anal somite (Fig. 2C) with scarcely developed, smooth, anal operculum. Caudal rami (Fig. 2C) symmetrical, about 1.6 times longer than wide, armed with 7 setae; setae symmetrical. Seta I vestigial; seta VII smooth, displaced to distomedial angle of ramus; setae II to VI well developed, plumose; seta II located at about three quarters of distance along outer margin. Outer

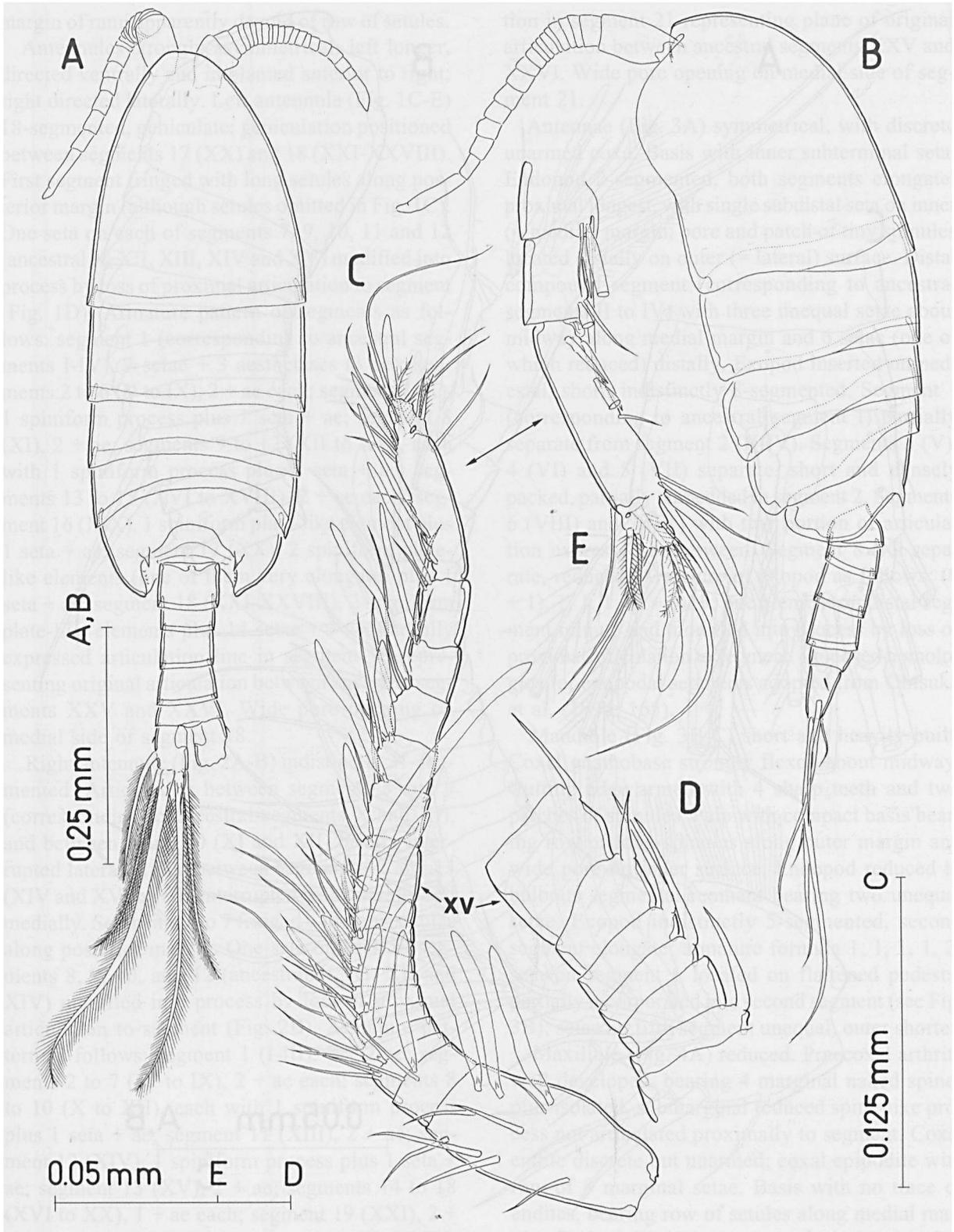


Fig. 1. *Paramisophria mediterranea* sp. nov., adult male. A, body, dorsal; B, same, lateral; C, left antennule, medial (row of setules on first segment omitted); D, detail of segments X to XV showing spiniform processes, lateral; E, detail of distal segments, medial.

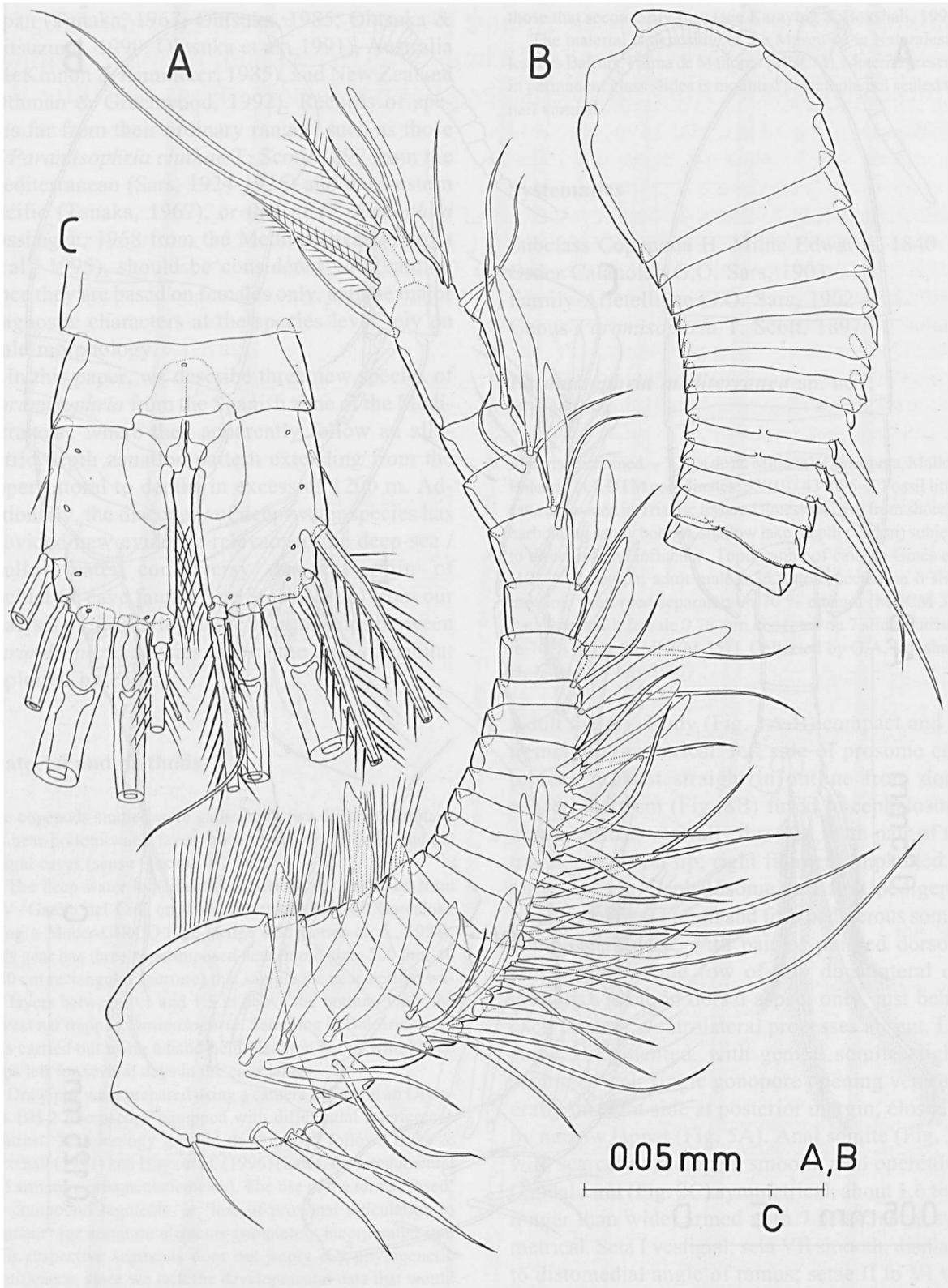


Fig. 2. *Paramisophria mediterranea* sp. nov., adult male. A, right antennule, medial; B, detail of proximal segments showing spiniform processes, lateral; C, anal somite and caudal rami, dorsal.

margin of rami apparently devoid of row of setules.

Antennules strongly asymmetrical: left longer, directed ventrally and implanted anterior to right; right directed laterally. Left antennule (Fig. 1C-E) 18-segmented, geniculate; geniculation positioned between segments 17 (XX) and 18 (XXI-XXVIII). First segment fringed with long setules along posterior margin (although setules omitted in Fig. 1C). One seta on each of segments 7, 9, 10, 11 and 12 (ancestral X, XII, XIII, XIV and XV) modified into process by loss of proximal articulation to segment (Fig. 1D). Armature pattern of segments as follows: segment 1 (corresponding to ancestral segments I-IV), 7 setae + 3 aesthetascs (3 ae); segments 2 to 6 (V to IX), 2 + ae each; segment 7 (X), 1 spiniform process plus 1 seta + ae; segment 8 (XI), 2 + ae; segments 9 to 12 (XII to XV), each with 1 spiniform process plus 1 seta + ae; segments 13 to 15 (XVI to XVIII), 2 + ae each; segment 16 (XIX), 1 spiniform plate-like element plus 1 seta + ae; segment 17 (XX), 2 spiniform plate-like elements (one of them very elongate) plus 1 seta + ae; segment 18 (XXI-XXVIII), 2 spiniform plate-like elements plus 14 setae + 3 ae; partially expressed articulation line in segment 18 representing original articulation between ancestral segments XXV and XXVI. Wide pore opening on medial side of segment 18.

Right antennule (Fig. 2A-B) indistinctly 21-segmented. Articulation between segments 8 and 9 (corresponding to ancestral segments X and XI), and between 9 and 10 (XI and XII) briefly interrupted laterally; that between segments 12 and 13 (XIV and XV) briefly interrupted both laterally and medially. Segments 1 to 7 fringed with long setules along posterior margin. One seta on each of segments 8, 9, 10, and 12 (ancestral X, XI, XII and XIV) modified into process by loss of proximal articulation to segment (Fig. 2B). Armature pattern as follows: segment 1 (I-III), 7 + 2 ae; segments 2 to 7 (IV to IX), 2 + ae each; segments 8 to 10 (X to XII), each with 1 spiniform process plus 1 seta + ae; segment 11 (XIII), 2 + ae; segment 12 (XIV), 1 spiniform process plus 1 seta + ae; segment 13 (XV), 2 + ae; segments 14 to 18 (XVI to XX), 1 + ae each; segment 19 (XXI), 2 + ae; segment 20 (XXII), 1 seta; segment 21 (XXIII-XXVIII), 12 + 2 ae; partially expressed articula-

tion in segment 21 representing plane of original articulation between ancestral segments XXV and XXVI. Wide pore opening on medial side of segment 21.

Antennae (Fig. 3A) symmetrical, with discrete unarmed coxa. Basis with inner subterminal seta. Endopod 2-segmented, both segments elongate, proximal longest, with single subdistal seta on inner (= medial) margin; pore and patch of tiny spinules located distally on outer (= lateral) surface. Distal compound segment (corresponding to ancestral segments II to IV) with three unequal setae about midway along medial margin and 6 setae (one of which reduced) distally. Exopod inserted on pedestal, short, indistinctly 8-segmented. Segment 1 (corresponding to ancestral segment I) partially separate from segment 2 (II-IV). Segments 3 (V), 4 (VI) and 5 (VII) separate, short and densely packed, partially embedded in segment 2. Segments 6 (VIII) and 7 (IX) with tiny portion of articulation expressed in between. Segment 8 (X) separate, reduced. Armature of exopod as follows: (0 + 1), 1, 1, 1, (1 + 0), 3; one element on distal segment minute and modified into process by loss of proximal articulation to segment. Proposed homologies for exopodal segments adopted from Ohtsuka et al. (1994: 165).

Mandible (Fig. 3B-C) short and heavily built. Coxal gnathobase strongly flexed about midway. Cutting edge armed with 4 sharp teeth and two patches of spinules. Palp with compact basis bearing row of long spinules along outer margin and wide pore on inner surface. Endopod reduced to bulbous segmental remnant bearing two unequal setae. Exopod indistinctly 5-segmented, second segment elongate; armature formula 1, 1, 1, 1, 2; seta on segment 1 located on flattened pedestal partially incorporated into second segment (see Fig. 3B); setae on fifth segment unequal, outer shorter.

Maxillule (Fig. 4A) reduced. Praecoxal arthrite well developed, bearing 4 marginal naked spines plus isolated, submarginal reduced spine-like process not articulated proximally to segment. Coxal endite discrete but unarmed; coxal epipodite with row of 8 marginal setae. Basis with no trace of endites, bearing row of setules along medial margin. Endopod reduced, unsegmented, with two unequal setae distally. Exopod incorporated into

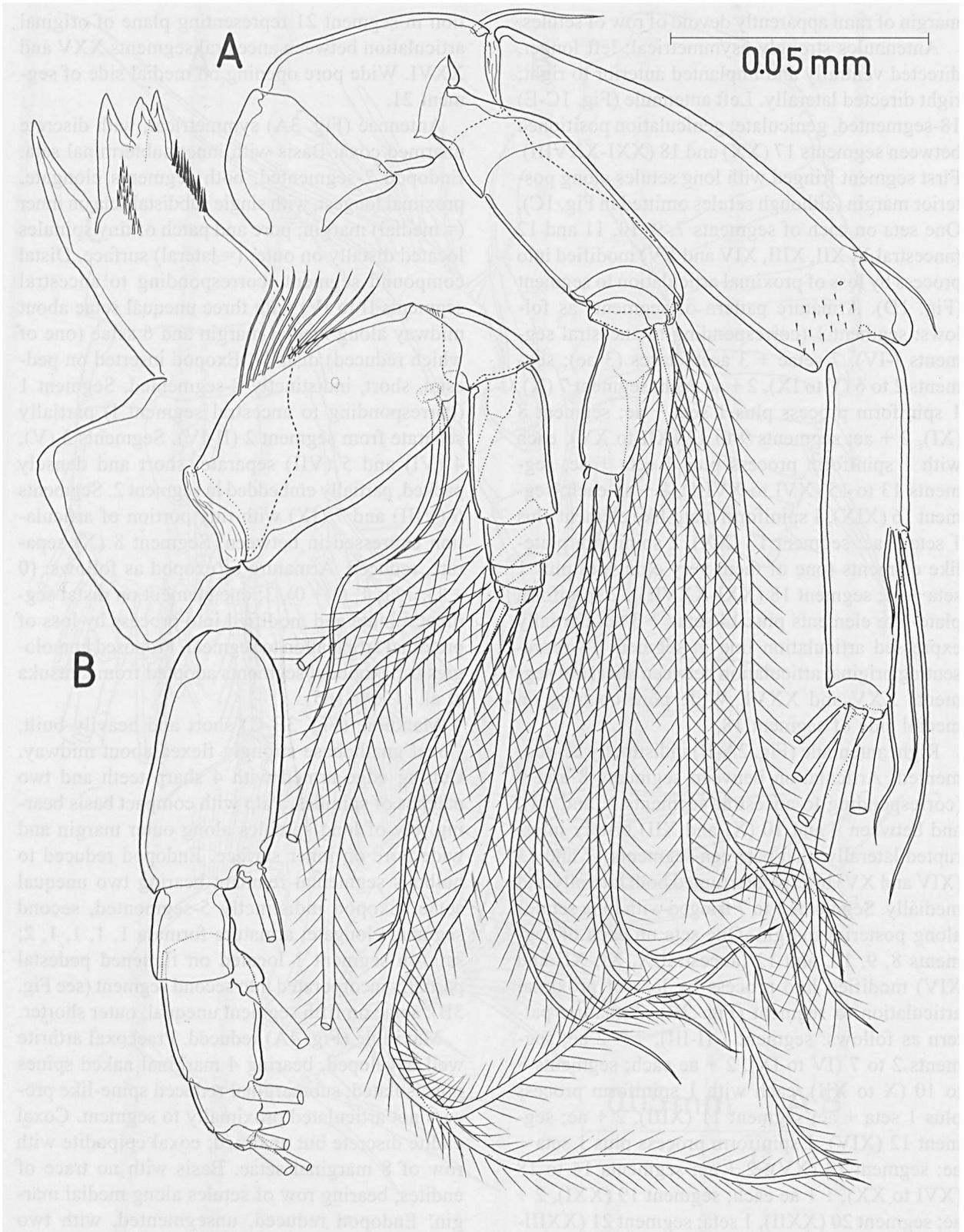


Fig. 3. *Paramisophria mediterranea* sp. nov., adult male. A, antenna, lateral; B, mandible; mandibular palp, anterior.

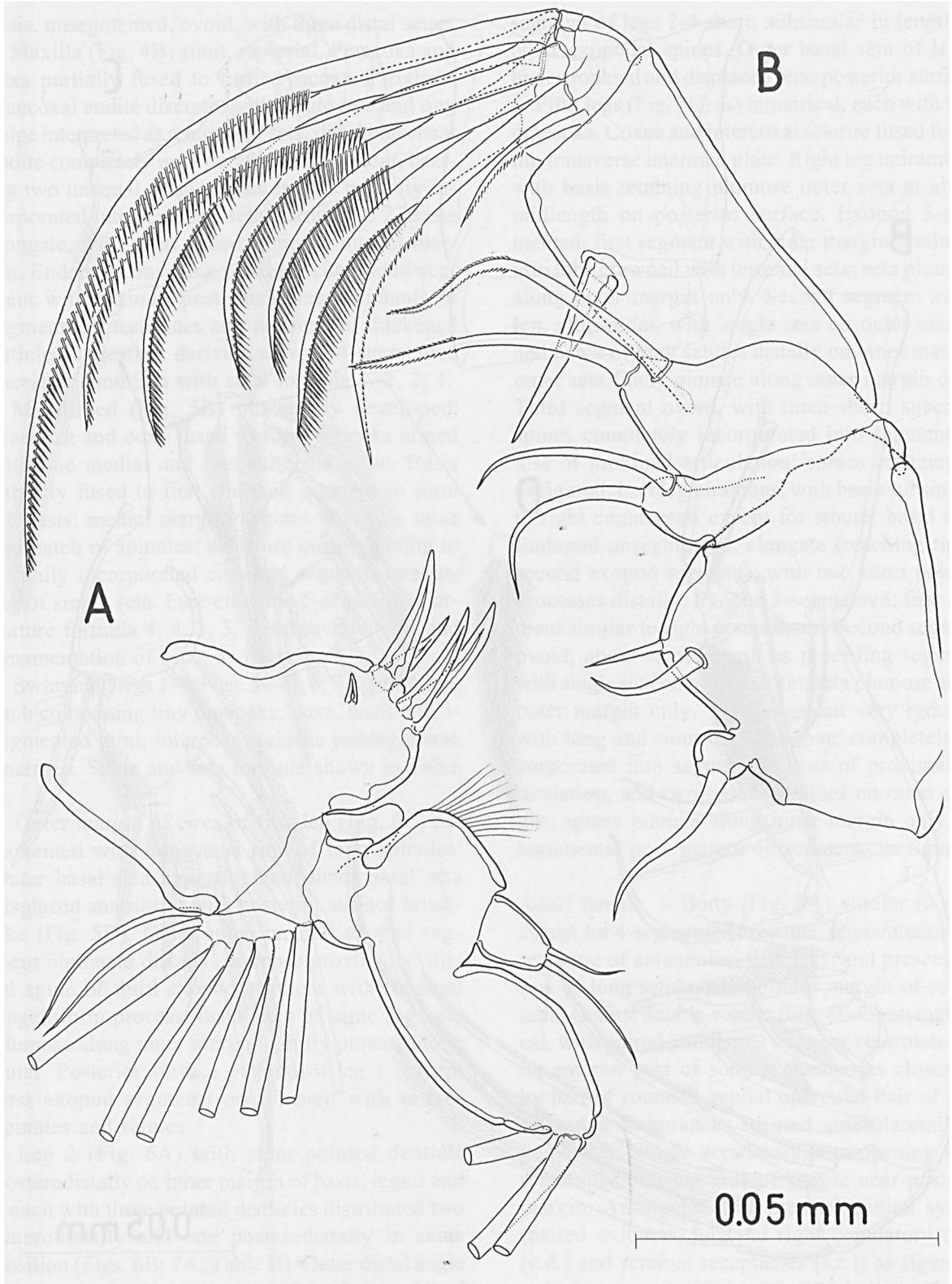


Fig. 4. *Paramisophria mediterranea* sp. nov., adult male. A, maxillule; B, maxilla.

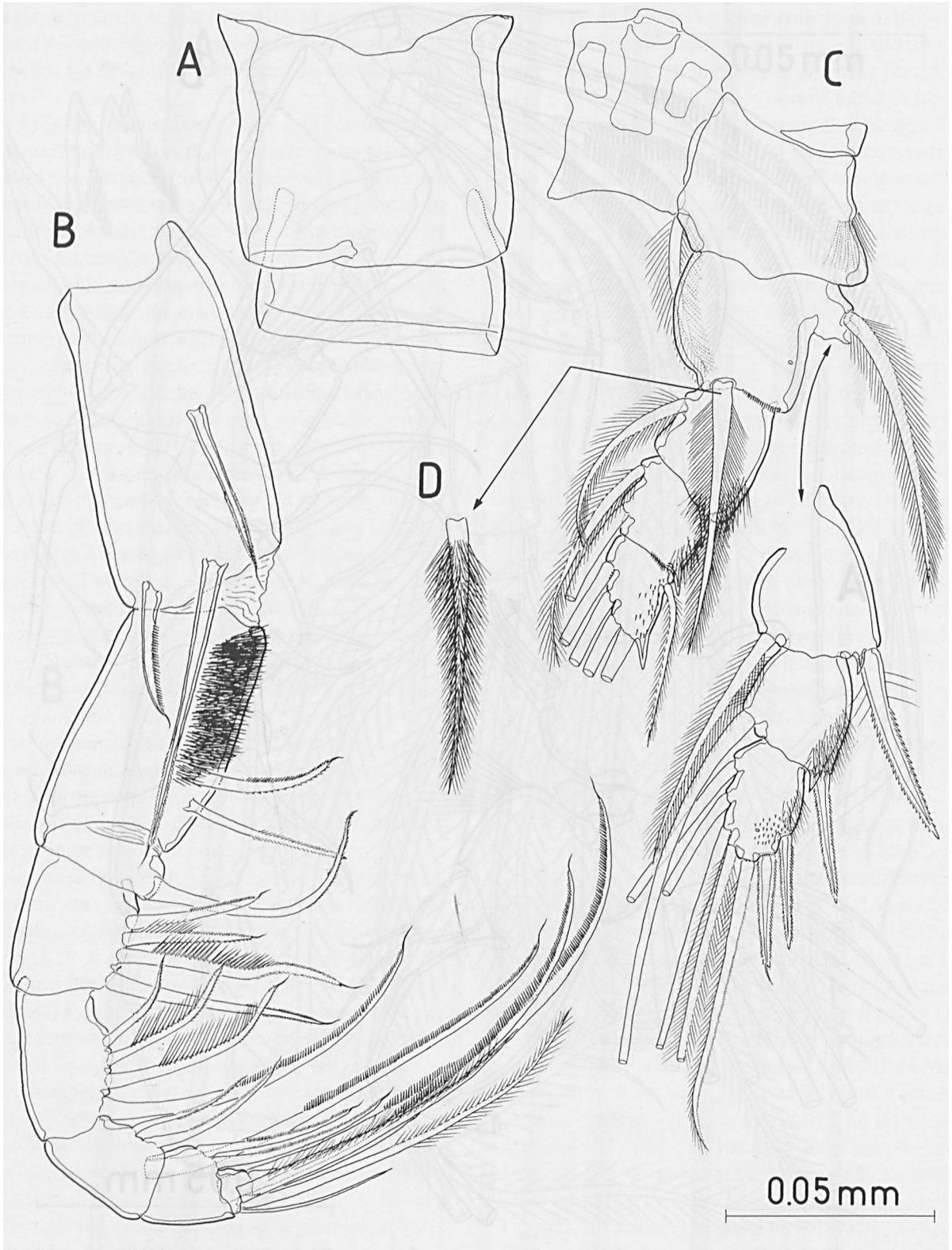


Fig. 5. *Paramisophria mediterranea* sp. nov., adult male. A, genital and first abdominal somites, ventral; B, maxilliped; C, first leg, anterior; D, inner basal seta, posterior.

basis, unsegmented, ovoid, with three distal setae.

Maxilla (Fig. 4B) stout, raptorial. Praecoxa and coxa partially fused to form syncoxa. Proximal praecoxal endite discrete, with single seta and tiny bulge interpreted as remnant of seta; distal praecoxal endite completely incorporated into segment, bearing two unequal setae. Coxal endites partially incorporated into segment, setal formula 2, 2. Basis elongate, with stout naked spine on medial margin. Endopod consisting of single compound segment with 8 stout, pectinate setae; remnants of segmental suture lines and portions of thickened cuticle suggesting derivation from 4-segmented ancestral condition with setal formula 1, 2, 2, 3.

Maxilliped (Fig. 5B) powerfully developed. Praecoxa and coxa fused to form syncoxa armed with one medial and two subdistal setae. Basis partially fused to first endopod segment to form allobasis; medial margin of basis with two setae and patch of spinules; armature corresponding to partially incorporated endopod segment consisting of single seta. Free endopod 5-segmented, armature formula 4, 4, 3, 3, 4; relative lengths and ornamentation of setae as figured.

Swimming legs 1-4 (Figs. 5C-D; 6; 7A) biramous, each comprising tiny praecoxa, coxa, basis and 3-segmented rami; intercoxal sclerite joining coxae unarmed. Spine and seta formula shown in Table I.

Outer margin of coxa of first leg (Fig. 5C) ornamented with transverse row of long spinules. Outer basal seta hypertrophied; inner basal seta displaced anteriorly, with posterior surface brush-like (Fig. 5D). Outer spine on first exopod segment bipinnate distally, plumose proximally; distal spine of third exopod segment with terminal flagelliform process; distal seta of same segment plumose along inner margin, faintly pinnate along outer. Posterior surface of rami of leg 1 (except first exopod segment) ornamented with microspinules and setules.

Leg 2 (Fig. 6A) with stout pointed denticle posterodistally on inner margin of basis; legs 3 and 4 each with three pointed denticles distributed two anterodistally and one posterodistally in same position (Figs. 6B; 7A; Table II). Outer distal angle of second endopod segment of legs 2-4 produced into acute process. Distal spine of third exopod

segment of legs 2-4 short, subsimilar in length to other exopodal spines. Outer basal seta of leg 4 hypertrophied and displaced onto posterior surface.

Fifth legs (Fig. 7C) asymmetrical, each with tiny praecoxa. Coxae and intercoxal sclerite fused forming transverse unarmed plate. Right leg uniramous, with basis retaining plumose outer seta at about midlength on posterior surface. Exopod 3-segmented; first segment with outer margin produced into lobe crowned with terminal seta; seta plumose along outer margin only. Second segment swollen, ellipsoidal, with single seta on outer margin and patch of long setules distally on inner margin; outer seta finely pinnate along outer margin only. Third segment ovoid, with three short, subequal spines completely incorporated into segment by loss of proximal articulation; spines ornamented as figured. Left leg biramous, with basis subsimilar to right counterpart except for stouter basal seta. Endopod unsegmented, elongate (reaching tip of second exopod segment), with two short pointed processes distally. Exopod 3-segmented; first segment similar to right counterpart. Second segment ovoid, about same length as preceding segment, with single seta on outer margin; seta plumose along outer margin only. Third segment very reduced, with long and stout terminal spine completely incorporated into segment by loss of proximal articulation, and two reduced spines on outer margin; spines pinnate along inner margin only. Integumental pore pattern on segments as figured.

Adult female. – Body (Fig. 8A) similar to male except for 4-segmented urosome, segmentation and armature of antennules, fifth legs, and presence of row of long setules along outer margin of caudal rami. Genital double-somite (Fig. 8F-G) asymmetrical, with paired gonopores opening ventrolaterally on anterior part of somite; gonopores closed off by pair of rounded genital opercula. Pair of sclerotized protuberances located anterolaterally to gonopores. Single copulatory pore opening ventrolaterally on right side of somite near posterior margin. Arrangement of internal genital system (paired oviducts, left and right copulatory ducts [c.d.] and seminal receptacles [s.r.]) as figured.

Left antennule (Figs. 8E; 9B) indistinctly 21-segmented, with articulation between segments 8

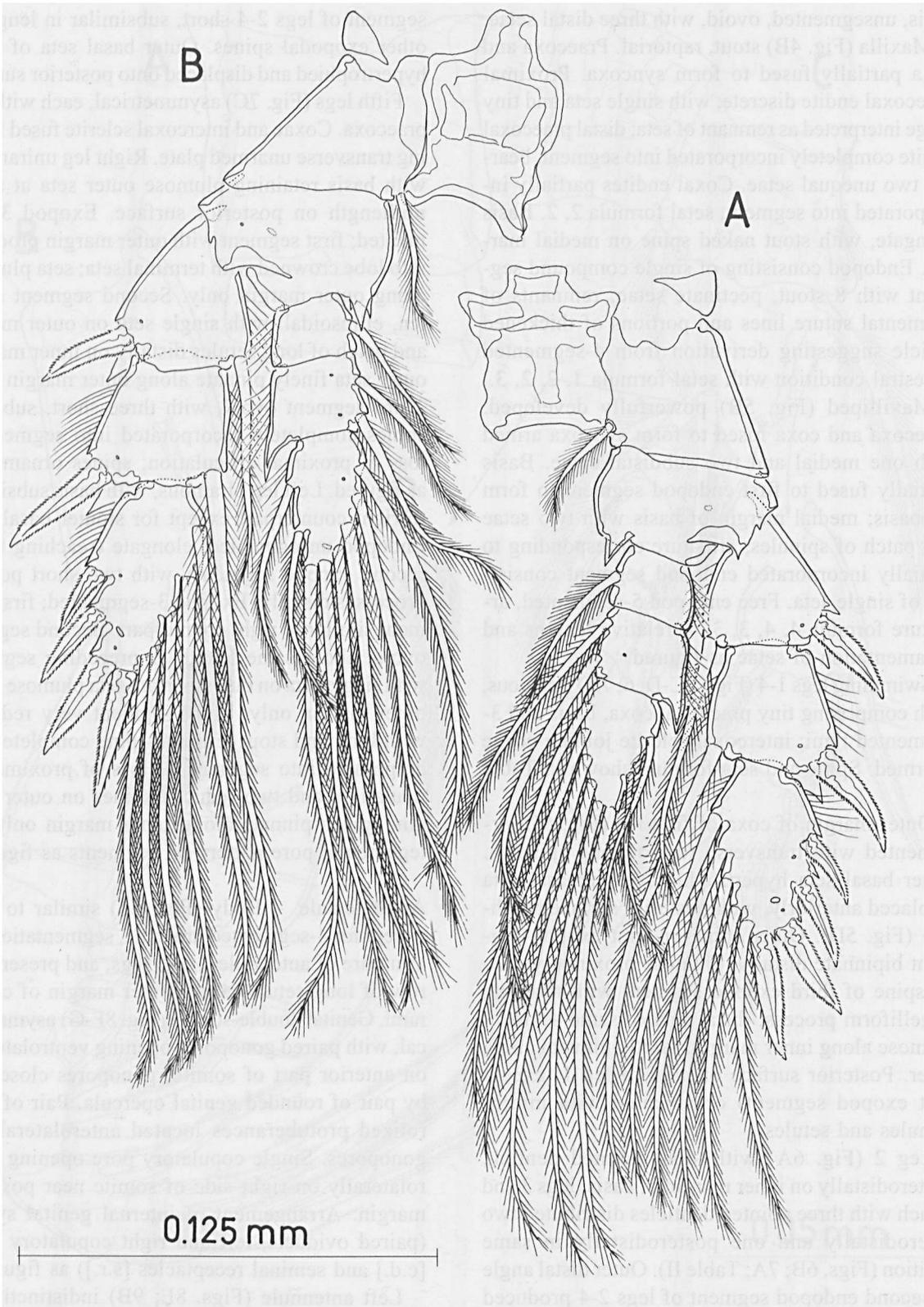


Fig. 6. *Paramisophria mediterranea* sp. nov., adult male. A, second leg, posterior; B, third leg, posterior.

Table I. Armature formula of swimming legs of *Paramisophria mediterranea* sp. nov.

	Coxa	Basis	Exopod segment	Endopod segment
Leg 1	0-1	1-1	I-1; I-1; II,1,4	0-1; 0-2; 1,1,3
Legs 2 & 3	0-1	0-0	I-1; I-1; III,1,5	0-1; 0-2; 2,2,4
Leg 4	0-0	1-0	I-1; I-1; III,1,5	0-1; 0-2; 2,2,3

Table II. Arrangement of distal denticles on the inner margin of basis of legs 2-4 of the three new *Paramisophria* species.

		<i>P. mediterranea</i> sp. nov.	<i>P. bathyalis</i> sp. nov.	<i>P. intermedia</i> sp. nov.
LEG 2	anterodistal	0	0	0
	distal	0	1	1
	posterodistal	1	0	0
LEG 3	anterodistal	2	1	1
	distal	0	1	1
	posterodistal	1	1	0
LEG 4	anterodistal	2	1	1
	distal	0	1	1
	posterodistal	1	0	0

and 9 (ancestral segments X and XI), 9 and 10 (XI and XII), and 12 and 13 (XIV and XV) briefly interrupted laterally. Segments 1 and 2 fringed with long setules along posterior margin. One of setae on each of segments 8, 9, 10, and 12 (ancestral X, XI, XII and XIV) modified into process by loss of proximal articulation to segment (Fig. 8E). Segmentation pattern and armature as follows: segment 1 (ancestral I-III), 7 setae + 3 ae; segment 2 (IV), 2 setae; segment 3 (V), 2 + ae; segment 4 (VI), 2 setae plus tiny process interpreted as teratologic aesthetasc; segment 5 (VII), 2 + ae; segment 6 (VIII), 2 + teratologic ae; segment 7 (IX), 2 + ae; segments 8 to 10 (X to XII), each with 1 spiniform process plus 1 seta + ae (aesthetasc on

segments 8 and 10 abnormal); segment 11 (XIII), 2 + ae; segment 12 (XIV), 1 very slender spiniform process plus 1 seta + ae; segments 13 to 17 (XVI to XX), 2 + ae each. Homology and armature of segments 18 to 21 unresolved due to damage to antennule caused during dissection.

Right antennule (Figs. 8D; 9A) as in male except for absence of aesthetasc on segment 2 (IV), presence of long setules along posterior margin of segment 8 (X), and complete separation of segments 12 and 13 (XIV and XV).

Fifth legs (Fig. 7B) apparently symmetrical (the posterolateral seta of left basis, which is ordinarily more stout than its right counterpart, is accidentally missing in the single specimen available), each retaining reduced praecoxa. Both coxae and intercoxal sclerite fused to form unarmed compound segment. Basis and endopod completely fused to form basoendopod, with single plumose basal seta posterolaterally; endopodal lobe incorporated posterodistally into medial margin of basis, with single plumose seta and stout denticle terminally. Exopod unsegmented, ellipsoidal, about 2.2 times longer than wide, with three short spines along outer margin, one distal spine, and one short subdistal spine on inner margin; distal spine twice length of other spines; spines flanged at insertion with large, sharp denticles. Stout, basally-bifid denticle with serrate margins positioned between terminal spine and subdistal inner spine, almost equal to length of latter. Integumental pores on segments as figured.

**Etymology.** – Species name derived from its type locality, the Mediterranean Sea.

**Remarks.** – This is a dwarf *Paramisophria* – the remaining representatives of the genus, with the exception of *P. spooneri* Krishnaswamy, 1959 (but see below), have body sizes larger than 1 mm. It is characterized by the extreme asymmetry of the body, with the left margin of the prosome straight in dorsal aspect and the left antennule implanted more frontally than the right. Within the genus, only *P. platysoma* Ohtsuka & Mitsuzumi, 1990 exhibits such extreme body asymmetry (see Ohtsuka & Mitsuzumi, 1990). Nevertheless, these species can be distinguished by the morphology of the fifth

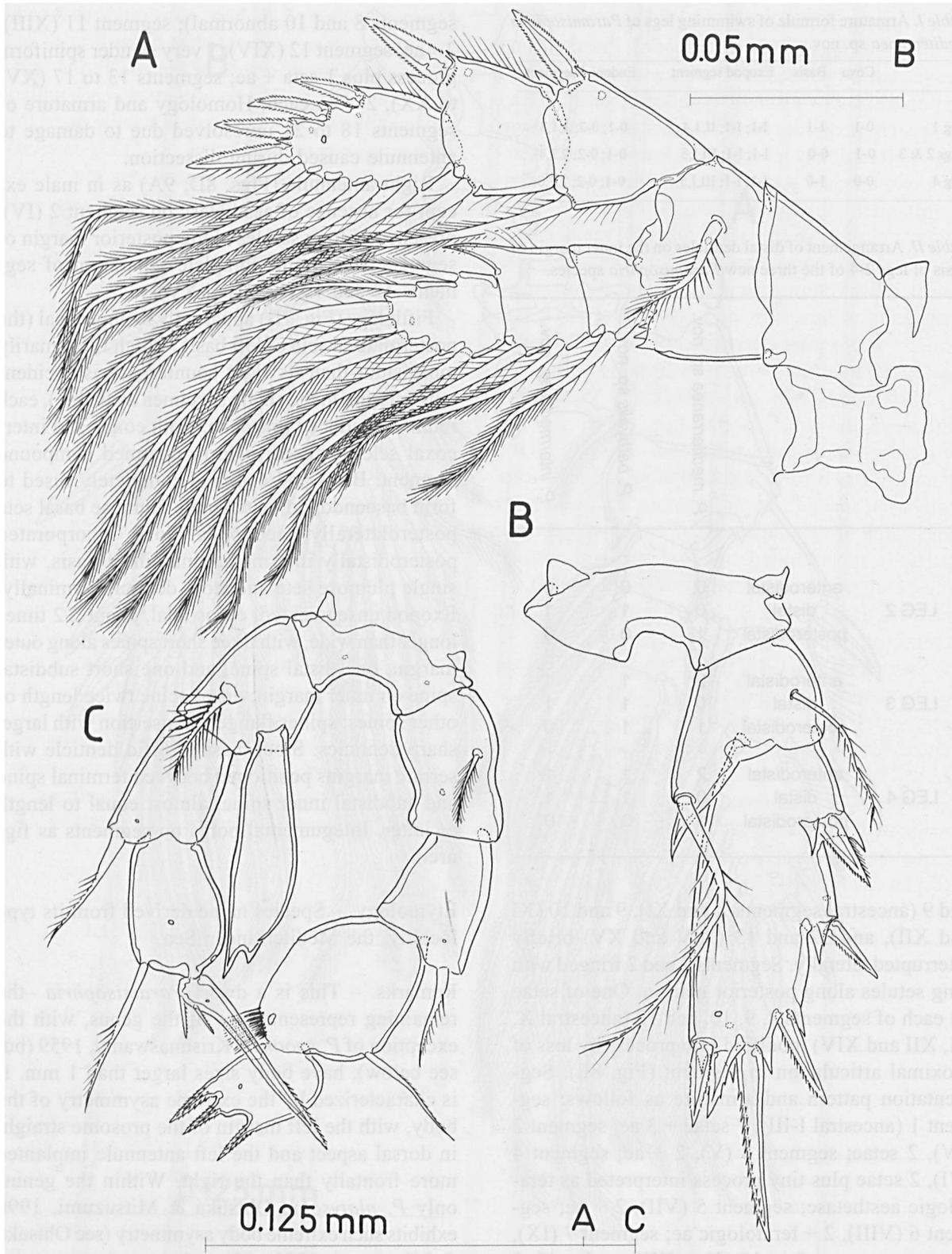


Fig. 7. *Paramisophria mediterranea* sp. nov. A, female fourth leg, posterior; B, female right fifth leg, posterior; C, male fifth legs, posterior.

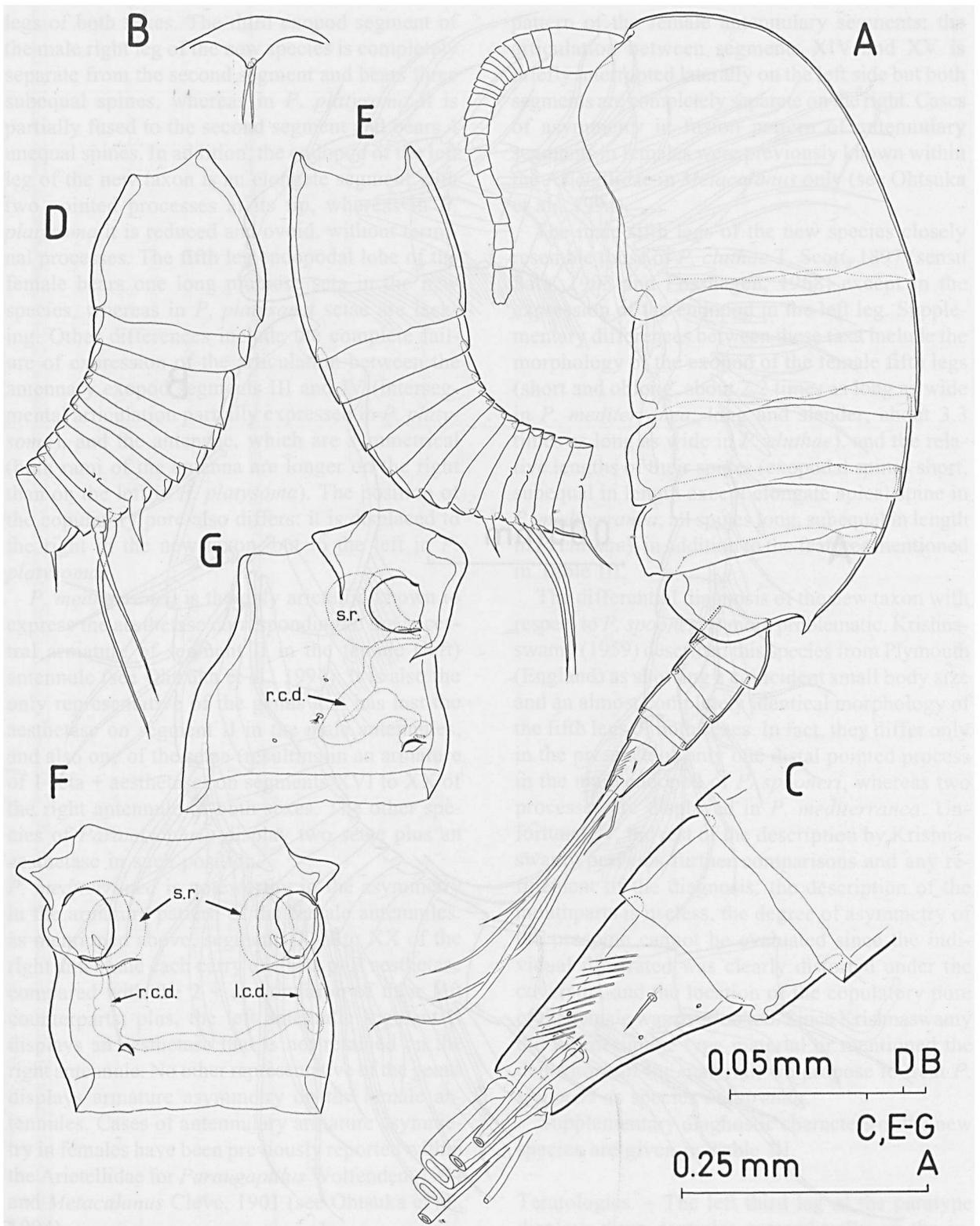


Fig. 8. *Paramisophria mediterranea* sp. nov., adult female. A, body, lateral; B, rostrum, anteroventral; C, anal somite and left caudal ramus, lateral; D, detail of proximal segments of right antennule showing spiniform processes, lateral; E, same of left antennule; F, genital double-somite, ventral; G, right side of same, lateral.

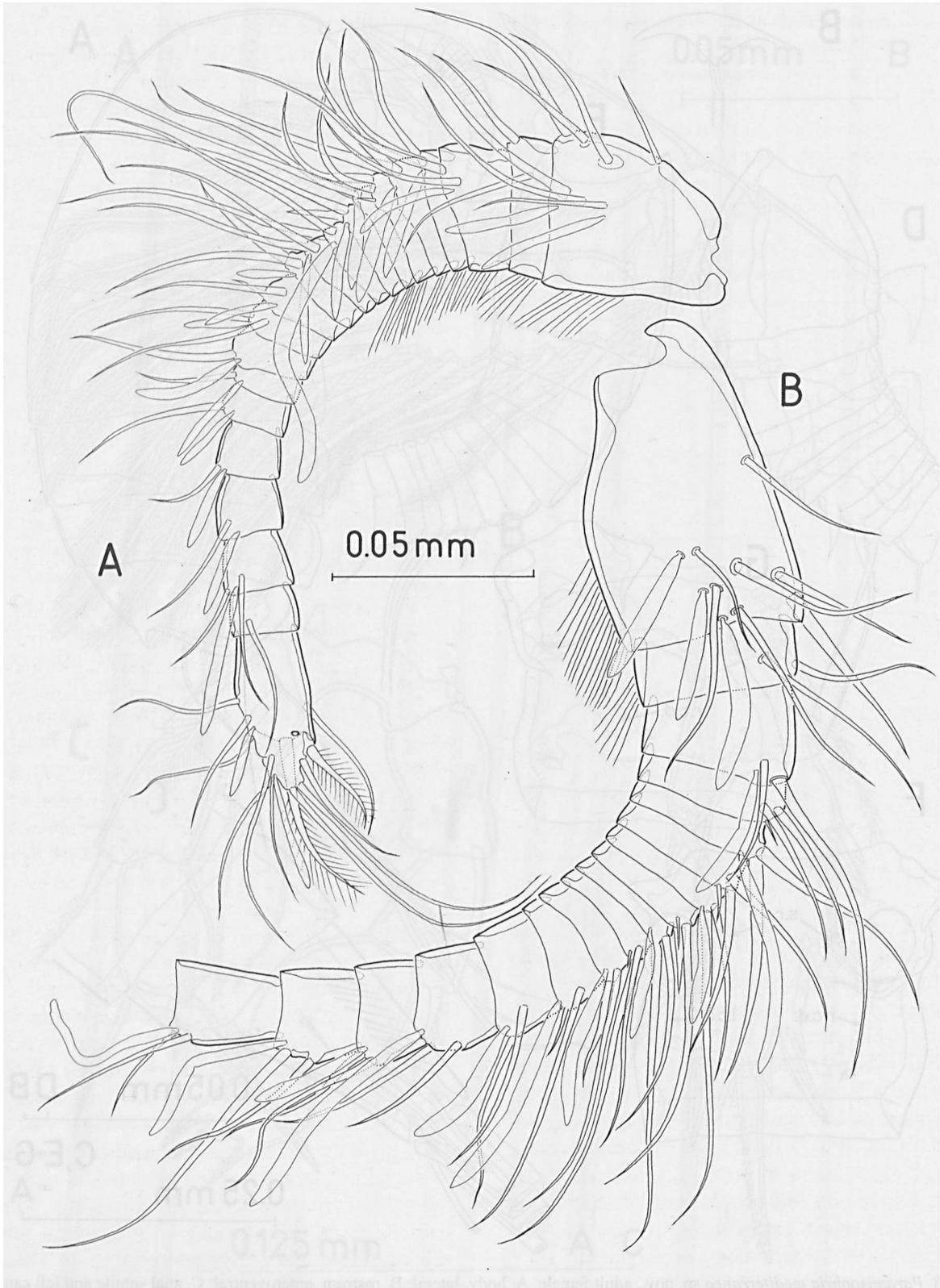


Fig. 9. *Paramisophria mediterranea* sp. nov., adult female. A, right antennule, medial; B, left antennule, medial (4 distal segments omitted).

legs of both sexes. The third exopod segment of the male right leg of the new species is completely separate from the second segment and bears three subequal spines, whereas in *P. platysoma* it is partially fused to the second segment and bears 4 unequal spines. In addition, the endopod of the left leg of the new taxon is an elongate segment with two pointed processes at its tip, whereas in *P. platysoma* it is reduced and ovoid, without terminal processes. The fifth leg endopodal lobe of the female bears one long plumose seta in the new species, whereas in *P. platysoma* setae are lacking. Other differences include the complete failure of expression of the articulation between the antennary exopod segments III and IV (intersegmental articulation partially expressed in *P. platysoma*), and the antennae, which are symmetrical (both rami of the antenna are longer on the right than on the left in *P. platysoma*). The position of the copulatory pore also differs: it is displaced to the right in the new taxon, but to the left in *P. platysoma*.

*P. mediterranea* is the only arietellid known to express the aesthetasc corresponding to the ancestral armature of segment II in the female (left) antennule (see Ohtsuka et al., 1994). It is also the only representative of the genus that has lost the aesthetasc on segment II in the male antennules, and also one of the setae (resulting in an armature of 1 seta + aesthetasc) on segments XVI to XX of the right antennule of both sexes. The other species of *Paramisophria* display two setae plus an aesthetasc in such position.

*P. mediterranea* is noteworthy in the asymmetry in the armature pattern of the female antennules: as mentioned above, segments XVI to XX of the right antennule each carry one seta plus aesthetasc compared with the 2 + ae condition of their left counterparts; plus, the left antennule segment II displays an aesthetasc that is not retained on the right antennule. No other representative of the genus displays armature asymmetry on the female antennules. Cases of antennular armature asymmetry in females have been previously reported within the Arietellidae for *Paraugaptilus* Wolfenden, 1904 and *Metacalanus* Cleve, 1901 (see Ohtsuka et al., 1994).

*P. mediterranea* is also the only representative of the genus displaying asymmetry in the fusion

pattern of the female antennular segments: the articulation between segments XIV and XV is briefly interrupted laterally on the left side but both segments are completely separate on the right. Cases of asymmetry in fusion pattern of antennular segments in females were previously known within the Arietellidae in *Metacalanus* only (see Ohtsuka et al., 1994).

The male fifth legs of the new species closely resemble those of *P. cluthae* T. Scott, 1897 (sensu Sars, 1903 and Fosshagen, 1968) except in the expression of the endopod in the left leg. Supplementary differences between these taxa include the morphology of the exopod of the female fifth legs (short and oblong, about 2.2 times as long as wide in *P. mediterranea*; long and slender, about 3.3 times as long as wide in *P. cluthae*), and the relative lengths of their spines (exopodal spines short, subequal in length except elongate apical spine in *P. mediterranea*; all spines long, subequal in length in *P. cluthae*), in addition to the features mentioned in Table III.

The differential diagnosis of the new taxon with respect to *P. spooneri* is more problematic. Krishnaswamy (1959) described this species from Plymouth (England) as showing a coincident small body size and an almost completely identical morphology of the fifth legs of both sexes. In fact, they differ only in the presence of only one distal pointed process in the male endopod of *P. spooneri*, whereas two processes are displayed in *P. mediterranea*. Unfortunately, the rest of the description by Krishnaswamy prevents further comparisons and any refinement of the diagnosis: the description of the mouthparts is useless, the degree of asymmetry of the prosome cannot be evaluated since the individual illustrated was clearly distorted under the coverslip, and the location of the copulatory pore of the female was overlooked. Since Krishnaswamy did not designate type material or mentioned the depository of the material, we propose to treat *P. spooneri* as species *inquirenda*.

Supplementary diagnostic characters of the new species are given in Table III.

Teratologies. – The left third leg of the paratype displays three denticles anterodistally on the inner margin of the basis instead of the ordinary two.

Table III. Character set permitting the differentiation of the 13 species of *Paramisophria*. All characters refer to adult specimens. A1: antennule; art.: articulation; end-: endopod segment; exp-: exopod segment; seg.: segment.

	<i>P. ammophila</i> Fosshagen, 1968	<i>P. bathyalis</i> sp. nov.	<i>P. cluthae</i> T. Scott, 1997	<i>P. fosshageni</i> Ohtman & Greenwood, 1992	<i>P. galapagensis</i> Ohtsuka, Fosshagen & Iliffe, 1993	<i>P. giselae</i> (Campaner, 1977)	<i>P. intermedia</i> sp. nov.	<i>P. itoi</i> Ohtsuka, 1985	<i>P. japonica</i> Ohtsuka, Fosshagen & Go, 1991	<i>P. mediterranea</i> sp. nov.	<i>P. platysoma</i> Ohtsuka & Mitsuzumi, 1990	<i>P. reducta</i> Ohtsuka, fosshagen & Iliffe, 1993	<i>P. variabilis</i> McKinnon & Kimmerer, 1985
♂ body size (mm)	1.08-1.18	1.73-1.74	1.10	1.22-1.30	1.50	1.73-	1.79	1.30	1.41-1.64	0.75	1.03	1.60	1.42
♀ body size (mm)	1.21-1.39	-	1.20	1.45-1.50	-	2.55-2.60	-	1.61	1.85-2.08	0.78	1.08	1.71	1.64
Prosoma left side (Convex / nearly Straight in dorsal aspect)	C	C	C	C	C	C	C	C	C	S	S	C	C
Position of ♀ copulatory pore (Ventromedially / Left side / Right side)	-	-	L	-	-	R	-	L	V	R	L	V	-
Dorsolateral processes on last prosomal somite (Absent / Present)	P	P	P	P	A	P	P	P	P	P	P	A	P
Ventrolateral processes on last prosomal somite (Absent / Present)	P	P	P	P	A	P	P	P	P	A	P	A	P
Art. between antennary exopodal segs. III-IV (Partially / Not expressed)	-	N	-	P	P	P	P	P	N	N	P	P	N
Armature of maxillulary praecoxal arthrite	5+1	5+1	5+1	4+1	4+1	5+1	4+1	4+1	5+1	4+1	4+1	5+1	4+1
Maxillulary coxal endite (Armed / Unarmed)	U	U	A	-	U	A	U	U	A	U	U	U	-
Maxillulary basal seta (Present / Absent)	A	A	A	A	A	P	A	A	P	A	A	A	A
Number of setae on proximal praecoxal endite of maxilla	1	1	1	1	1	2	1	1	1	1	1	1	1
Inner margin of outer spine on exp-1 of leg 1 (Pinnate / PLumose)	-	PL	-	-	PL	PL	PL	PL	PL	P	P	PL	-
Number of setae on inner margin of end-3 of legs 2 & 3	4	4	4	4	3	4	4	4	4	4	4	4	4
Number of setae on inner margin of end-3 of leg 4	3	3	3	3	2	3	3	3	3	3	3	3	3
♂ left A1 intersegmental art. XXIII-XXIV (Fully / Partially / Not expressed)	N	F	N	N	N	-	N	N	F	N	F	P	N
♂ left A1 intersegmental art. XXV-XXVI (Fully / Partially expressed)	P	F	P	F	F	-	F	F	P	P	P	P	P
Aesthetasc on ♂ antennulary seg. II (Present / Absent)	-	P	P	-	P	-	P	-	P	A	-	P	-
Armature on each of ♂ antennulary segs. XVI to XX	-	2+ae	-	-	-	-	2+ae	-	2+ae	1+ae	-	-	-
Number of spines/setae on exp-3 of ♂ left leg 5	3	4	3	3	3	-	3	3	3	3	4	3	4
Endopod of ♂ left leg 5 (well Developed / Reduced / Absent)	R	R	A	R	R	-	D	R	R	D	R	D	R
Art. between exp-2 and 3 of ♂ right leg 5 (Fully / Partially / Not expressed)	P	P	P	N	P	-	P	N	N	F	P	F	P
Remnant of inner seta on exp-2 of ♂ right leg 5 (Present / Absent)	-	P	-	A	A	-	P	A	A	A	P	A	A
Number of spines/setae on exp-3 of ♂ right leg 5	3	3	3	3	3	-	4	3	4	3	4	3	3
♀ A1 intersegmental art. XXIII-XXIV (Fully / Partially / Not expressed)	-	-	N	-	-	-	-	N	F	N	N	P	-
Aesthetasc on ♀ left antennulary seg. II (Present / Absent)	-	-	-	-	-	A	-	-	A	P	-	P	-
Armature of each of ♀ right antennulary segs. XVI to XX	-	-	-	-	-	-	-	-	2+ae	1+ae	-	2+ae	-
Articulation between exp-1 and 2 of ♀ leg 5 (Fully / Not expressed)	N	-	N	N	-	N	-	F	F	N	N	N	N
Number of spines on exopod of ♀ leg 5	5	-	5	5	-	5	-	5	5	5	5	4	5
Number of setae on endopod of ♀ leg 5	1	-	1	1	-	2	-	1	2	1	0	1	1

*Paramisophria bathyalis* sp. nov.

(Figs. 10-16)

Material examined. – Catalan Sea (western Mediterranean), 40°4.2'N / 2°06.3'E; 1258 m depth; habitat: bathyal muddy bottoms with hemipelagic pteropod shells. Holotype: adult male 1.73 mm dissected on 9 slides [MNCM. 351]. Paratype: adult male 1.74 mm dissected on 4 slides [MNCM 352]. Collected by J.E. Cartes, 9 December 1991.

Adult male. – Body similar to *P. mediterranea* except for nearly symmetrical prosome, not compressed on left side (see Fig. 10A-B), more slender rostrum (Fig. 10C), and rounded ventrolateral processes on last prosomal somite. Caudal rami (Fig. 10D) with row of setules along inner margin; row apparently absent along outer margin; caudal setae symmetrical in length.

Antennules strongly asymmetrical as in *P. mediterranea*, but both implanted at same level. Left antennule (Fig. 11A) indistinctly 20-segmented. Segmentation pattern and armature of segments proximal to geniculation almost identical to *P. mediterranea*: differences include presence of additional aesthetasc on segment 1 (corresponding to armature of segment II), and incomplete expression of articulation between segments 8 to 12. Latter features variable: holotype displaying articulation between segments 8 and 9, and between 11 and 12 both with brief interruptions laterally, and articulation between segments 9 and 10, and between 10 and 11 both with brief interruptions medially (see Fig. 14D); paratype displaying segments 8 and 9, and 11 and 12 completely separated. Additional difference being the presence of long setules flanging posteriorly segments 1 to 7 in *P. bathyalis*, setules apparently present only on segment 1 in *P. mediterranea*. Armature pattern of segments distal to geniculation as follows: segment 18 (compound XXI-XXIII), 2 plate-like spini-form processes, 2 setae + aesthetasc; segment 19 (XXIV-XXV), 4 + ae; segment 20 (XXVI-XXVIII), 8 + ae. Wide pore opening on medial side of segment 20.

Right antennule (Fig. 11B) differing from *P. mediterranea* in presence of aesthetasc on segment II and in armature of segments 14 to 18 (2 setae + aesthetasc per segment whereas only 1 + ae in *P. mediterranea*). Articulation between segments 8

and 9, and between 9 and 10 with brief interruptions both laterally and medially (see Fig. 14E; these articulations with brief interruptions laterally only, in *P. mediterranea*). Finally, posterior margin of segment 8 flanged with long setules (this margin lacks setules in *P. mediterranea*).

Antenna, mandibular palp, maxilla and maxilliped (Figs. 13A; 15B; 12A-B) as in *P. mediterranea*.

Mandibular coxal gnathobase characterised by possession of accessory reduced tooth between second and third dorsalmost major teeth, which is absent in other representatives of the genus (see Fig. 15C).

Maxillule (Fig. 16C) differing from *P. mediterranea* in armature of praecoxal arthrite, comprising 5 marginal spines plus submarginal process, instead of 4 + 1 arrangement; in addition, submarginal process not reduced in size.

Legs 1-4 (Figs. 14A-B; 15A; 13B; 16A-B) with same segmentation and armature formula as *P. mediterranea*, but outer spine of first exopod segment of leg 1 with outer margin uniformly pinnate, inner margin uniformly plumose, and submarginal row of pinnules along posterior surface of spine near inner margin. In *P. mediterranea* this spine plumose on both sides in proximal quarter, and pinnate in distal three quarters. Distal spine of third exopod segment lacking terminal flagelliform process as present in *P. mediterranea*. Same spine on legs 2-4 clearly longer than remaining exopodal spines; in *P. mediterranea* this spine subsimilar in length to others. Arrangement of distal denticles on inner margin of basis of legs 2-4 differing between species (see Table II).

Fifth legs (Fig. 14C) similar to *P. mediterranea* except for segmentation and armature of rami. Right exopod indistinctly 3-segmented, with second and third segments partially fused posteromedially; first segment with outer margin produced posterodistally into lobe crowned with terminal seta; seta finely pinnate along outer margin. Second segment swollen, with single, finely pinnate seta on outer margin, and patch of densely set setules covering two small bulges located distally on inner margin; soft, pointed process (interpreted here as remnant of seta) located subdistally on inner margin. Third segment ovoid, with distal margin bearing one slender in-

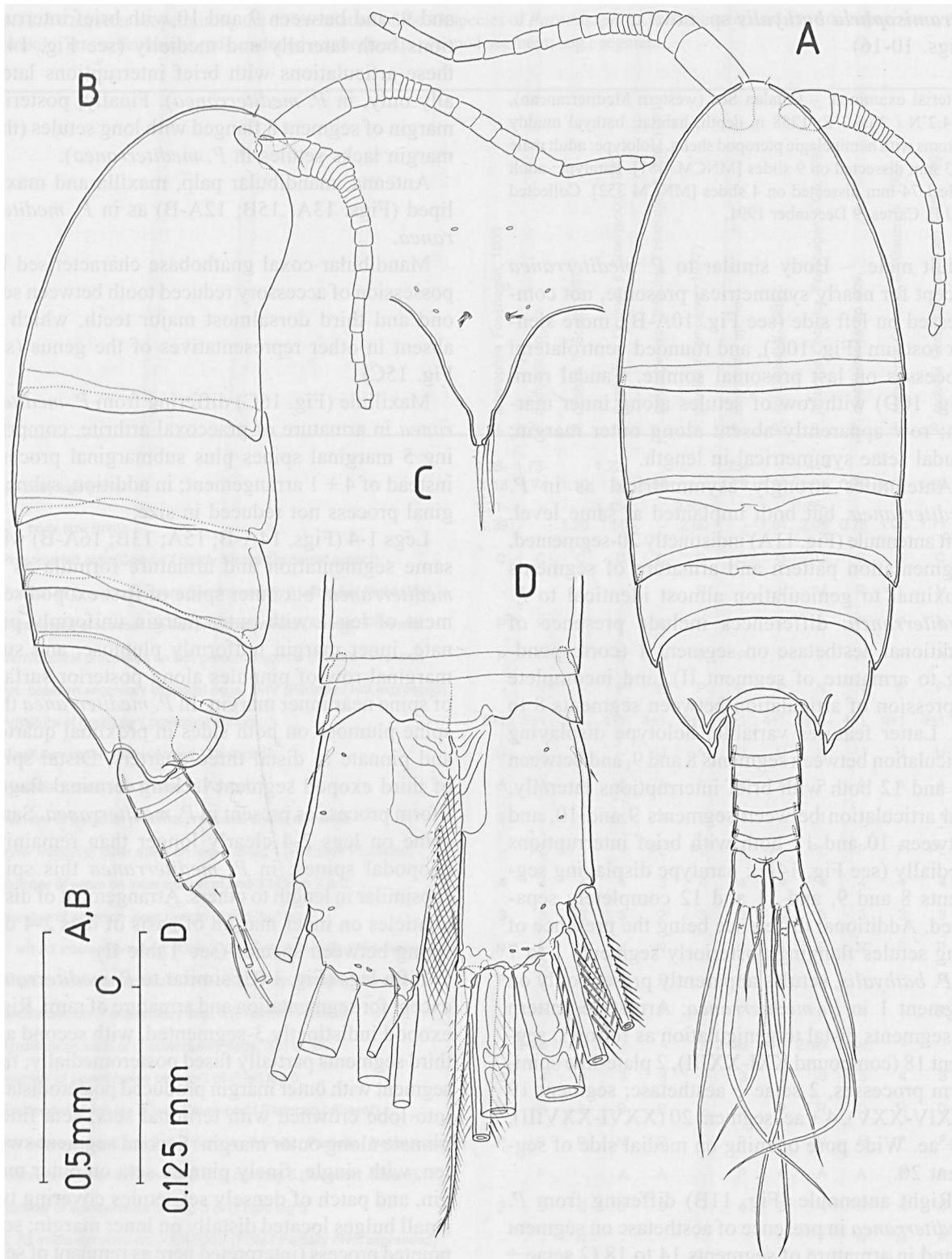


Fig. 10. *Paramisophria bathyalis* sp. nov., adult male. A, body, dorsal.; B, same, lateral; C, rostrum, anteroventral; D, detail of caudal rami, dorsal.

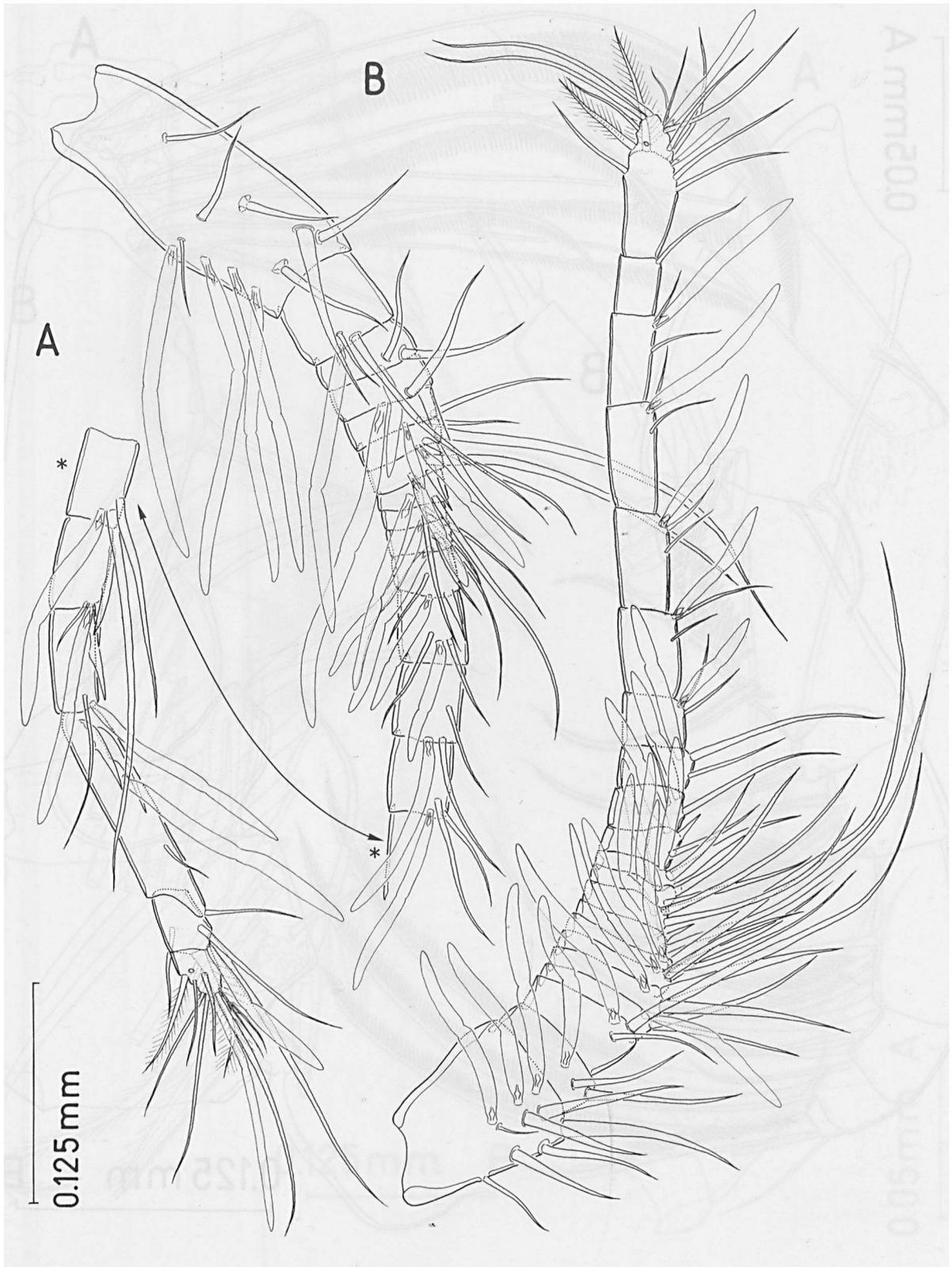


Fig. 11. *Paramisophria bathyalis* sp. nov., adult male. A, left antennule, medial; B, right antennule, medial.

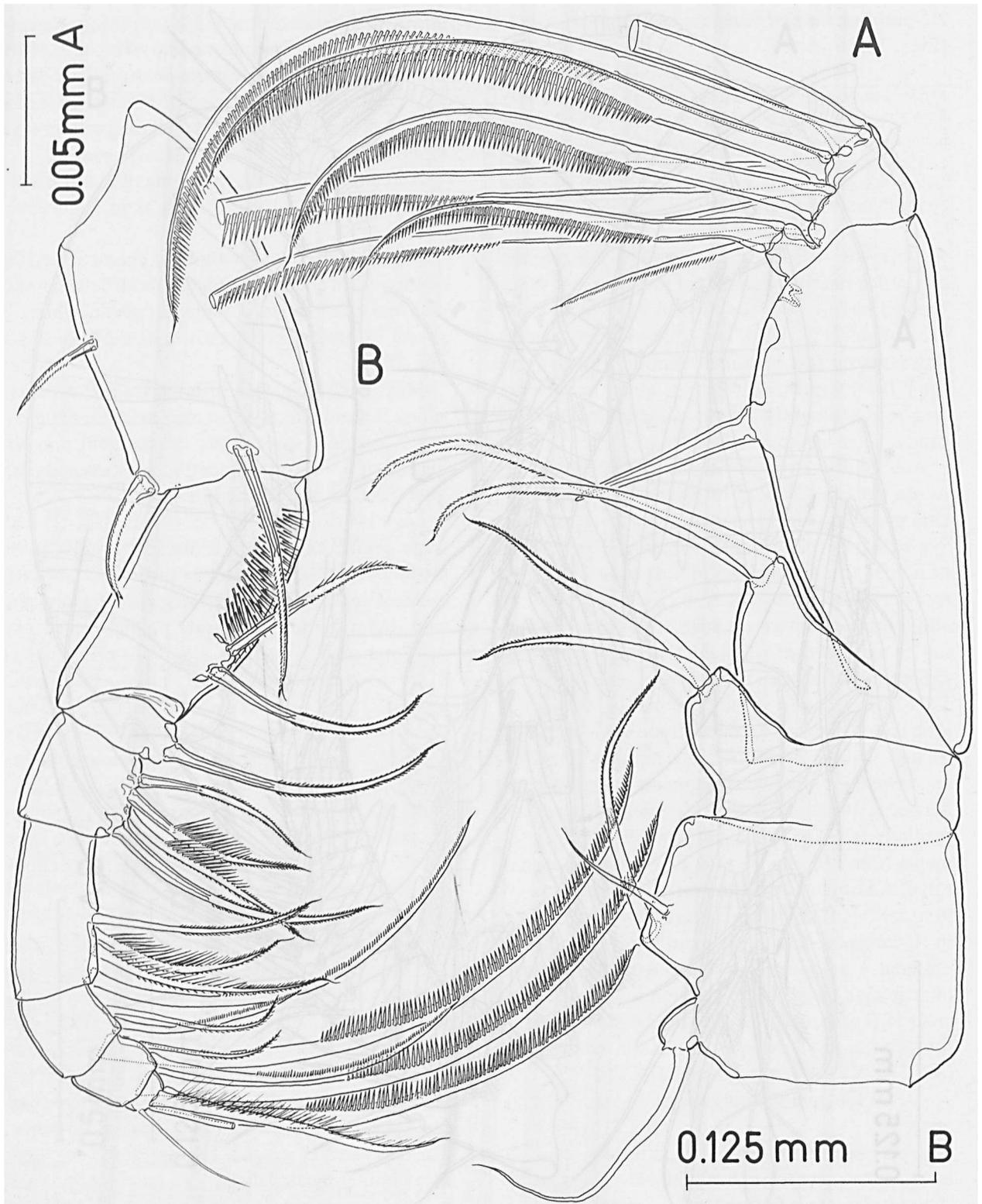


Fig. 12. *Paramisophria bathyalis* sp. nov., adult male. A, maxilla; B, maxilliped (note syncoxa accidentally rotated 180° with respect to ordinary relative position).

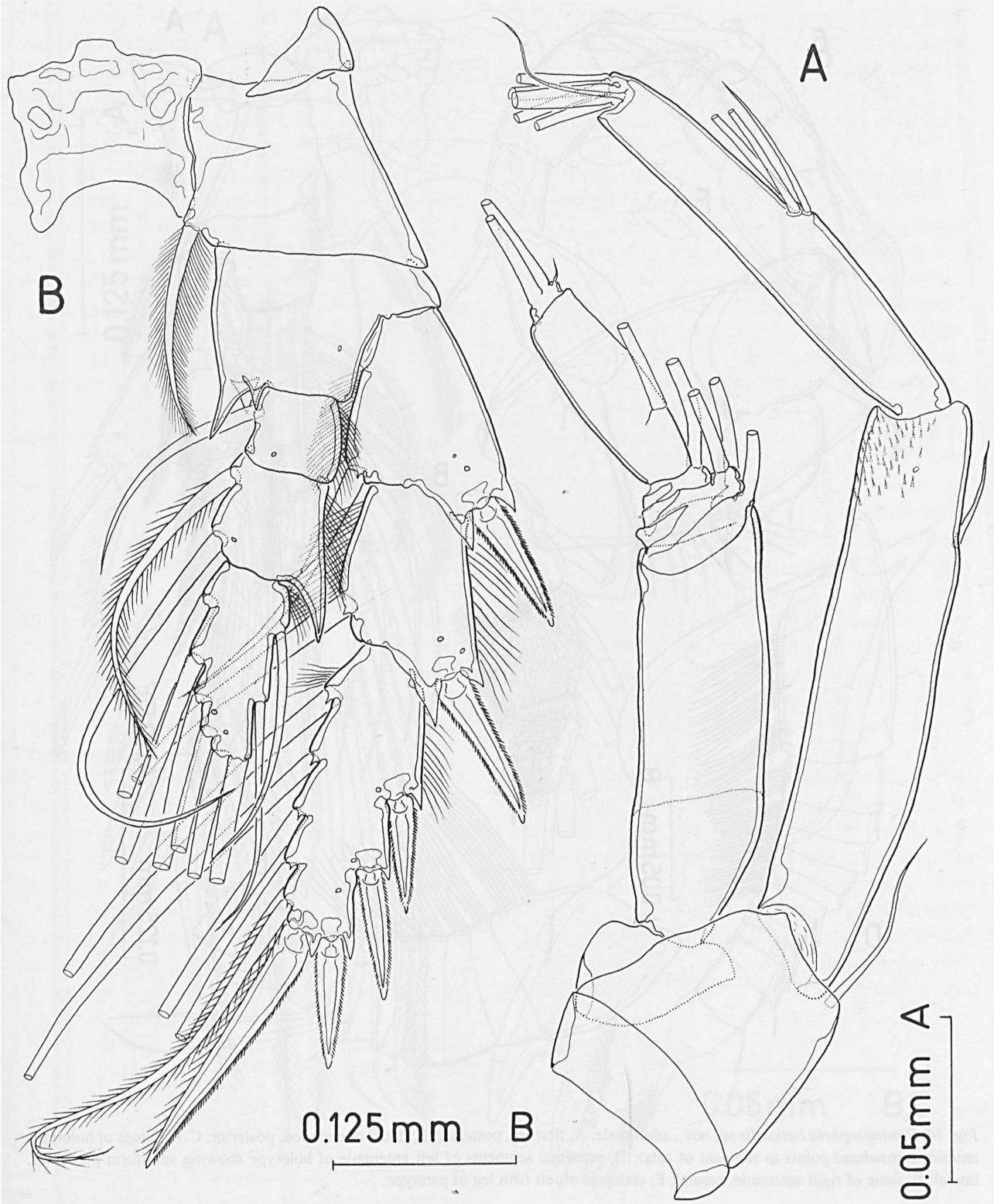


Fig. 13. *Paramisophria bathyalis* sp. nov., adult male. A, antenna; B, third leg, anterior.

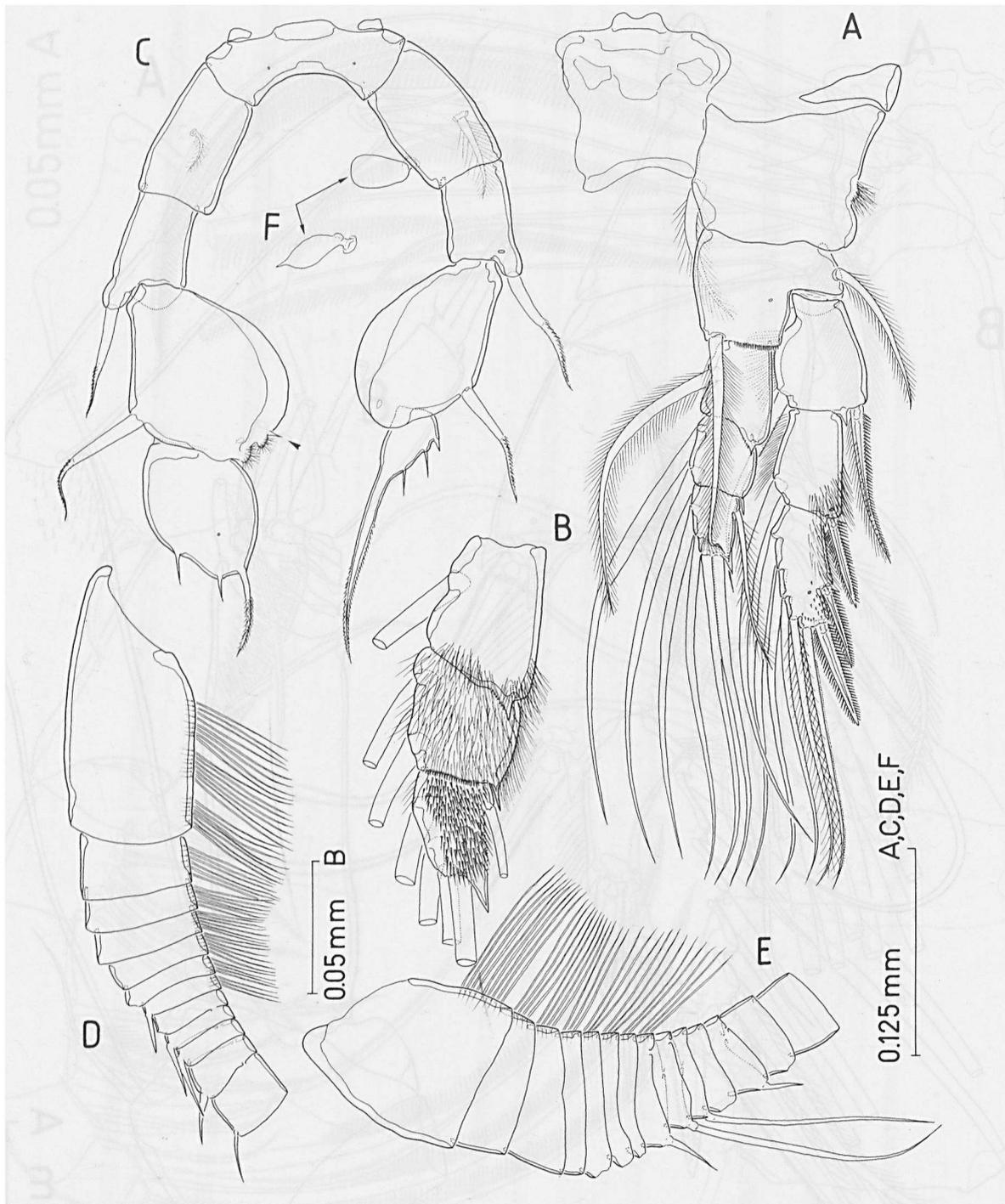


Fig. 14. *Paramisophria bathyalis* sp. nov., adult male. A, first leg, posterior; B, detail of endopod, posterior; C, fifth legs of holotype, anterior (arrowhead points to remnant of seta); D, proximal segments of left antennule of holotype showing spiniform processes, lateral; E, same of right antennule, medial; F, endopod of left fifth leg of paratype.

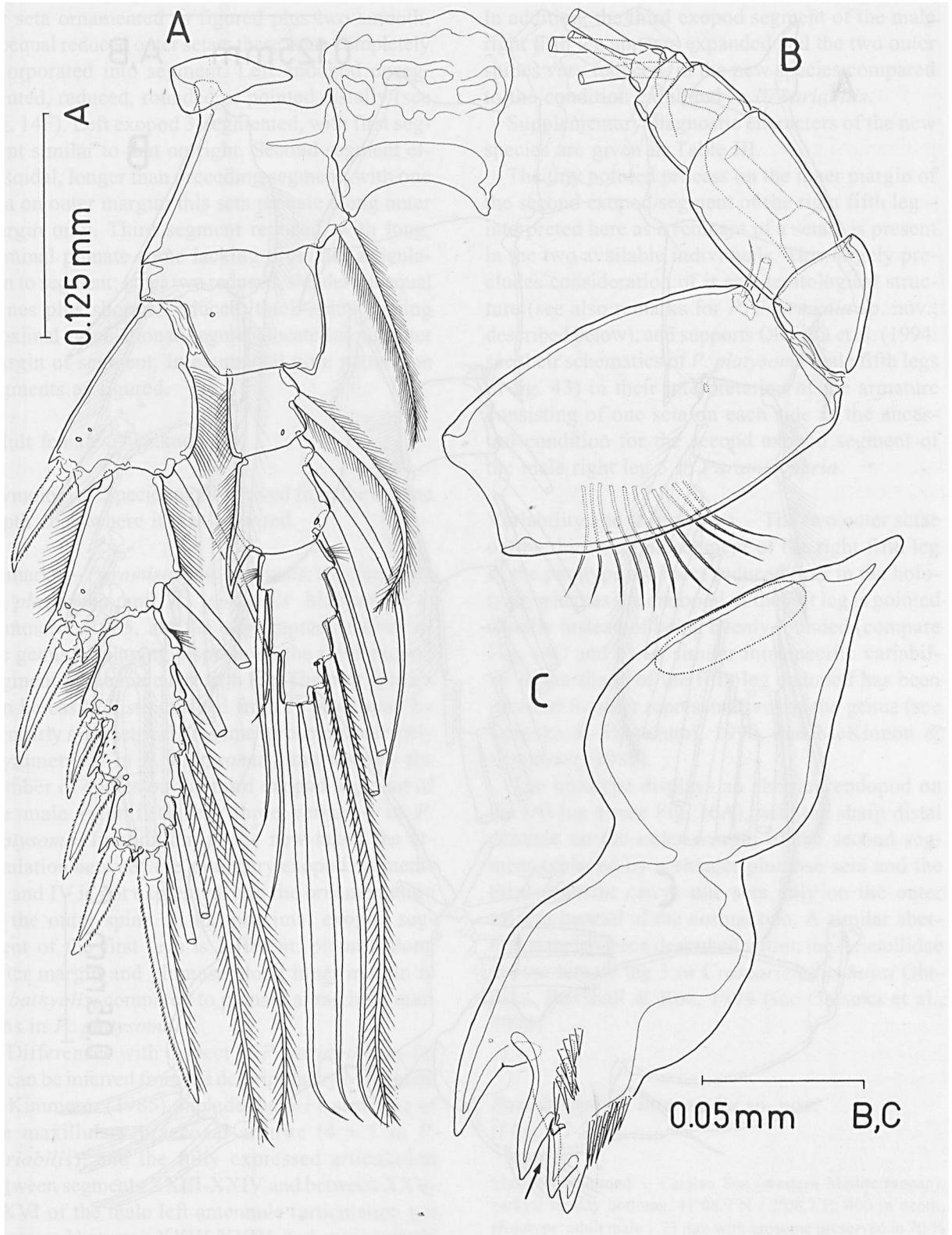


Fig. 15. *Paramisophria bathyalis* sp. nov., adult male. A, second leg, anterior; B, mandibular palp; C, mandibular coxal gnathobase (arrow pointing to reduced accessory tooth).

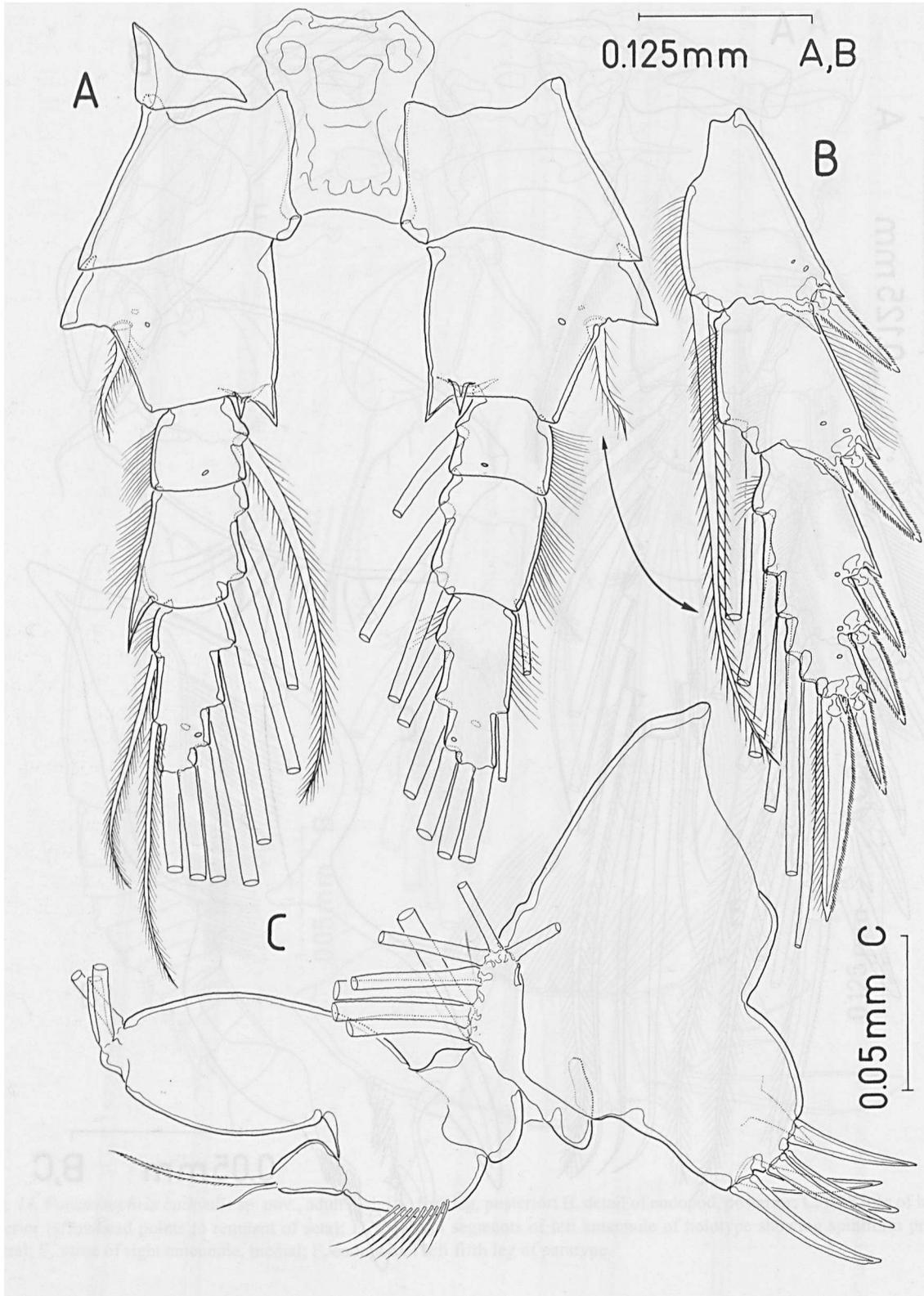


Fig. 16. *Paramisophria bathyalis* sp. nov., adult male. A-B, fourth legs of holotype, anterior (note teratologic armature of distal segments of left endopod); C, maxillule.

ner seta ornamented as figured plus two smooth, subequal reduced outer setae; these setae completely incorporated into segment. Left endopod unsegmented, reduced, rounded or pointed distally (see Fig. 14F). Left exopod 3-segmented, with first segment similar to that on right. Second segment ellipsoidal, longer than preceding segment, with one seta on outer margin; this seta pinnate along outer margin only. Third segment reduced, with long, terminal pinnate spine lacking proximal articulation to segment; other two reduced, slender subequal spines plus shorter, reduced, thick spine lacking proximal articulation to segment located along outer margin of segment. Integumental pore pattern on segments as figured.

Adult female. – Unknown.

Etymology. – Species name derived from the marine depth zone where it was captured.

Remarks. – *Paramisophria bathyalis*, together with *P. platysoma* and *P. variabilis* McKinnon & Kimmerer, 1985, are the only representatives of the genus displaying 4 spines on the third exopod segment of the male left fifth leg. The new species can be easily distinguished from *P. platysoma* by its nearly symmetrical prosome (prosome extremely asymmetrical in *P. platysoma*), and also by the number of spines on the third exopod segment of the male right fifth leg: three versus 4 in *P. platysoma*. In addition, in the new taxon the articulation between the antennary exopod segments III and IV is not expressed, and the ornamentation of the outer spine on the proximal exopod segment of the first legs is different: pinnate along outer margin and plumose along inner margin in *P. bathyalis*, compared to pinnate along both margins in *P. platysoma*.

Differences with respect to *P. variabilis*, as far as can be inferred from the description by McKinnon & Kimmerer (1985), include the 5 + 1 armature of the maxillulary praecoxal arthrite (4 + 1 in *P. variabilis*), and the fully expressed articulation between segments XXIII-XXIV and between XXV-XXVI of the male left antennule (articulation not expressed between XXIII-XXIV, and only partially expressed between XXV-XXVI in *P. variabilis*).

In addition, the third exopod segment of the male right fifth leg appears expanded and the two outer spines very reduced, in the new species compared to the condition exhibited in *P. variabilis*.

Supplementary diagnostic characters of the new species are given in Table III.

The tiny pointed process on the inner margin of the second exopod segment of the right fifth leg – interpreted here as a remnant of a seta – is present in the two available individuals. This largely precludes consideration of it as a teratological structure (see also remarks for *P. intermedia* sp. nov., described below), and supports Ohtsuka et al. (1994: see their schematics of *P. platysoma* male fifth legs in fig. 43) in their interpretation of the armature consisting of one seta on each side as the ancestral condition for the second exopod segment of the male right leg 5 in *Paramisophria*.

Variability and teratologies. – The two outer setae on the third exopod segment of the right fifth leg of the paratype are more reduced than in the holotype, whereas the endopod of the left leg is pointed distally instead of being evenly rounded (compare Fig. 14C and F). A similar intraspecific variability in the shape of the fifth leg endopod has been reported in other representatives of the genus (see Ohtsuka & Mitsuzumi, 1990, and McKinnon & Kimmerer, 1985).

The holotype displays an aberrant endopod on the left leg 4 (see Fig. 16A), with the sharp distal denticle on the outer margin of the second segment replaced by a slender plumose seta and the third segment carries one seta only on the outer margin instead of the normal two. A similar aberrant state has been described within the Arietellidae for the female leg 3 of *Crassarietellus huysi* Ohtsuka, Boxshall & Roe, 1994 (see Ohtsuka et al., 1994).

#### *Paramisophria intermedia* sp. nov.

(Figs. 17-23)

Material examined. – Catalan Sea (western Mediterranean), bathyal muddy bottoms. 41°08.9'N / 2°08.7'E; 400 m depth. Holotype: adult male 1.73 mm with urosome preserved in 70 % ethanol; rest dissected on 9 slides [MNCM 353]. – 41°05.8'N / 2°08.5'E; 552 m depth. Adult male 1.73 mm dissected on 7

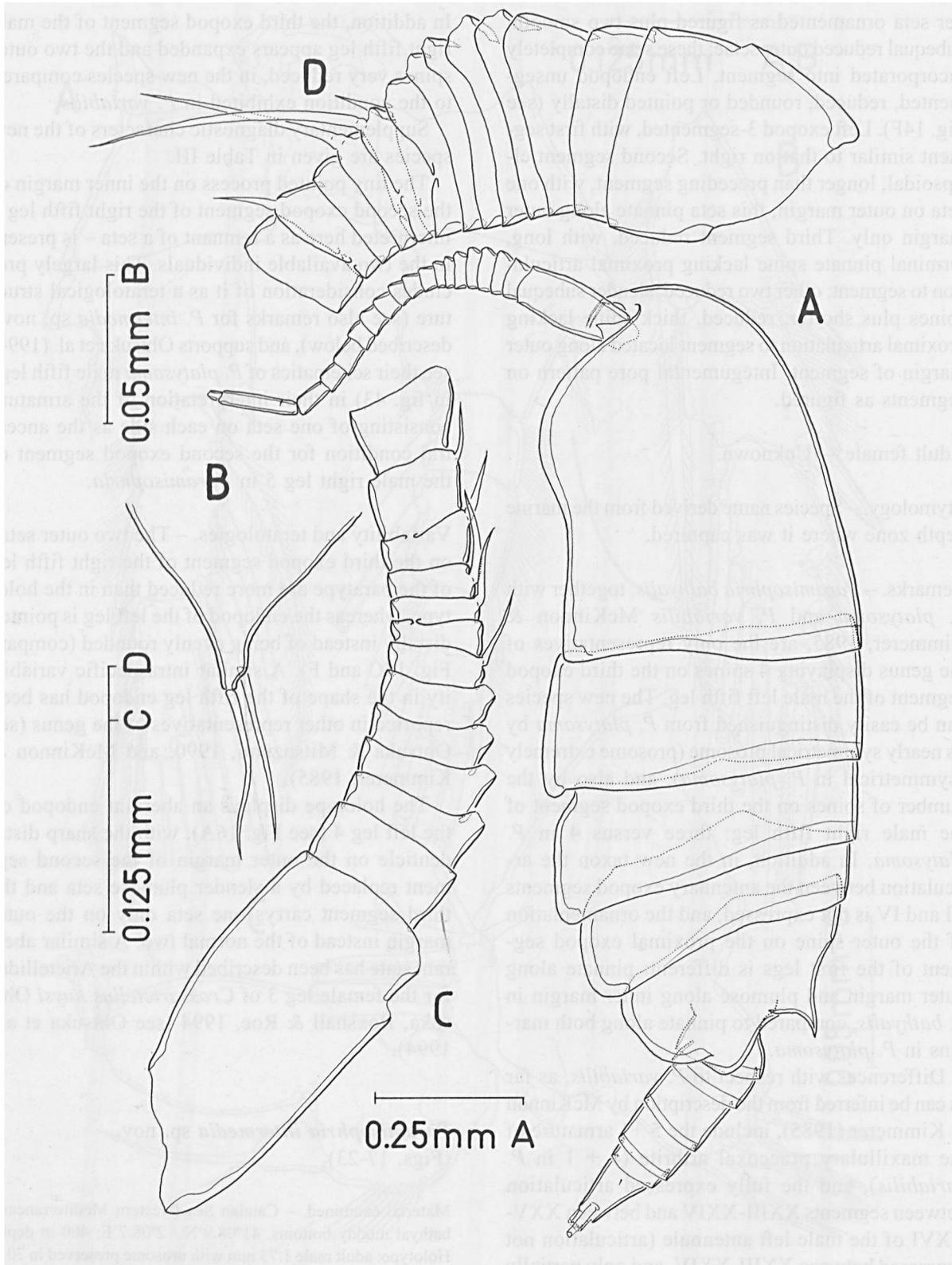


Fig. 17. *Paramisophria intermedia* sp. nov., adult male. A, body, lateral; B, rostrum, anteroventral; C, detail of proximal segments of left antennule showing spiniform processes, lateral; D, same of right antennule, medial.

slides [MNCM 354]. Both samples collected by J.E. Cartes, 9 December 1991. – 41°05.56'N / 2°09.09'E; between 602-594 m depth. Adult male 1.79 mm with prosome dissected on 5 slides; urosome preserved separately in 70 % ethanol [MNCM 355]. Collected by J.E. Cartes, 13 October 1996.

Adult male. – Body (Fig. 17A), right antennule (Figs. 17D; 18B), mandibular palp (Fig. 19B), maxilla (Fig. 21A-C), maxilliped (Fig. 21D-F), and legs 1, 2, and 4 (Figs. 22; 23B) similar to *P. bathyalis*. Symmetry in length of caudal setae unconfirmed.

Left antennule (Fig. 18A) indistinctly 19-segmented, with segments proximal to geniculation displaying same pattern as in *P. bathyalis* except for segments 9, 10 and 11, being completely separate (see Fig. 17C). Articulations between segments 8 and 9, and between 11 and 12 briefly interrupted laterally (Fig. 17C). Armature pattern of segments distal to geniculation as follows: segment 18 (compound XXI-XXV), 2 plate-like spiniform processes, 6 setae + 2 aesthetascs; partial suture line in segment 18 representing articulation between ancestral segments XXI and XXII; segment 19 (compound XXVI-XXVIII), 8 + ae. Wide pore opening on medial side of segment 19.

Antenna (Fig. 20A) differing from *P. bathyalis* only in partial expression of articulation between exopodal segments III and IV.

Mandibular coxal gnathobase (Fig. 19A) lacking accessory reduced tooth described for *P. bathyalis*.

Maxillule (Fig. 20B) similar to *P. bathyalis* except for armature of praecoxal arthrite, comprising 4 marginal spines plus submarginal process instead of 5 + 1 arrangement, and in presence of patch of tiny spinules near insertion of endopod.

Leg 3 (Fig. 23A) as in *P. bathyalis* except for absence of posterodistal denticle on inner margin of basis (see Table II).

Fifth legs (Fig. 19C-D) differing from *P. bathyalis* in segmentation and armature of rami. Right exopod indistinctly 3-segmented, with second and third segments partially fused posteromedially; first segment with outer margin produced posterodistally into lobe bearing terminal seta finely pinnate along outer margin. Second segment produced medially into lobe, armed with finely pinnate seta on outer margin, patch of densely set setules distally on the

inner margin and soft pointed process (interpreted here as remnant of seta) positioned subdistally on inner margin. Third segment displaying patch of spinules proximally on medial margin and three well developed, finely pinnate spines completely incorporated into segment, distalmost longest; tiny pointed process, interpreted as remnant of seta, located on lateral margin of segment immediately adjacent to outer spine. Left endopod unsegmented, elongate (although not reaching tip of second exopod segment), and bearing two short pointed processes distally plus oblique, partial articulation line at about mid-length. Left exopod 3-segmented, with first segment similar to right counterpart. Second segment ellipsoidal, longer than preceding segment, with single smooth seta on outer margin. Third segment reduced and bearing long terminal spine plus two unequal, shorter spines on outer margin; all three spines pinnate, their size increasing medially, and all lacking proximal articulation with segment. Integumental pore pattern on segments as figured.

Adult female. – Unknown.

Etymology. – The species name is derived from the intermediate water depth range it apparently occupies compared to the other two new species described above.

Remarks. – The new species, together with *P. japonica* Ohtsuka, Fosshagen & Go, 1991 and *P. platysoma*, are the only representatives of the genus possessing 4 armature elements on the third exopod segment of the male right leg 5. It can be easily differentiated from *P. platysoma* by its symmetrical prosome, the ornamentation of the outer spine on the proximal exopod segment of the first legs (pinnate along the outer margin and plumose along the inner, compared with pinnate along both margins in *P. platysoma*), the well-developed endopod of the male left fifth leg (reduced in *P. platysoma*), and the presence of only three armature elements on the third exopod segment of the male left fifth leg (4 are present in *P. platysoma*).

Significant differences between the new species and *P. japonica* are the partial expression of the articulation between segments III and IV of the

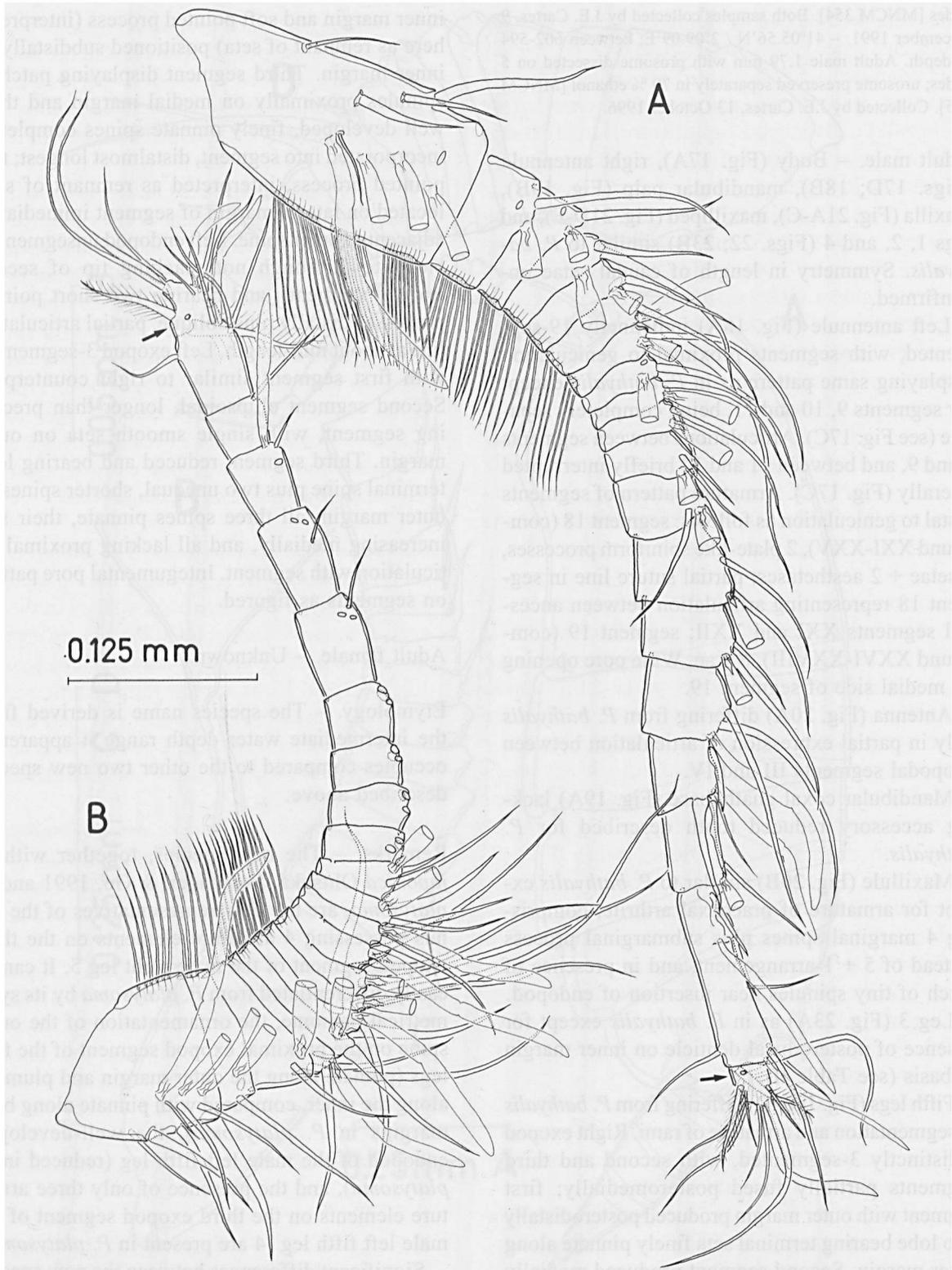


Fig. 18. *Paramisophria intermedia* sp. nov., adult male. A, left antennule, medial (insertion of accidentally lost setae on segments 1 to 3, 5 and 8 outlined in figure). B, right antennule, medial (insertion of accidentally lost armature elements on segments 2 and 13 to 19 outlined in figure). Arrows indicate pore on distal segment of each antennule.

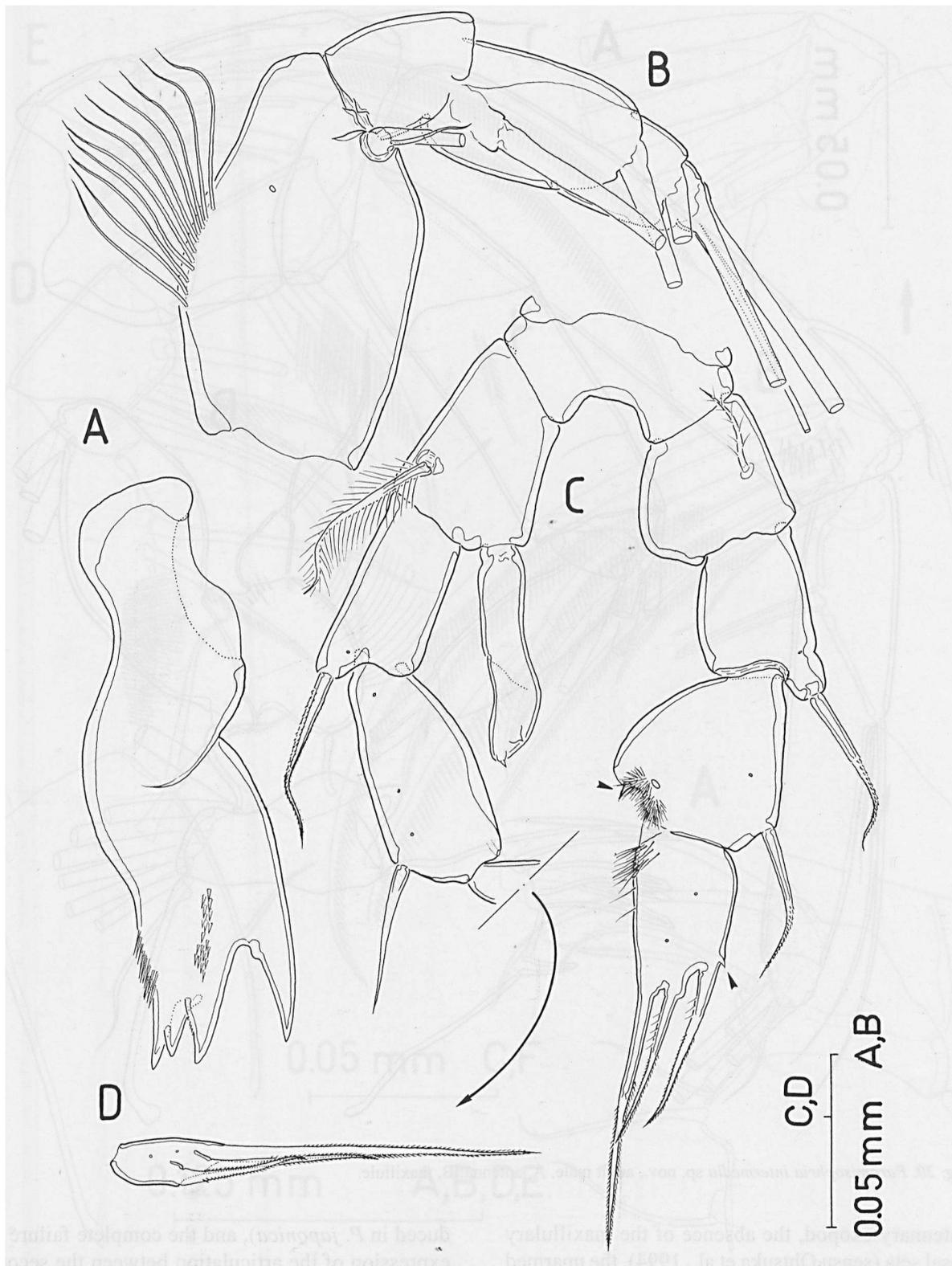


Fig. 19. *Paramisophria intermedia* sp. nov., adult male. A, mandibular coxal gnathobase; B, mandibular palp, medial; C, fifth legs, posterior (arrowheads pointing to remnants of setae); D, detail of third exopod segment of left fifth leg.

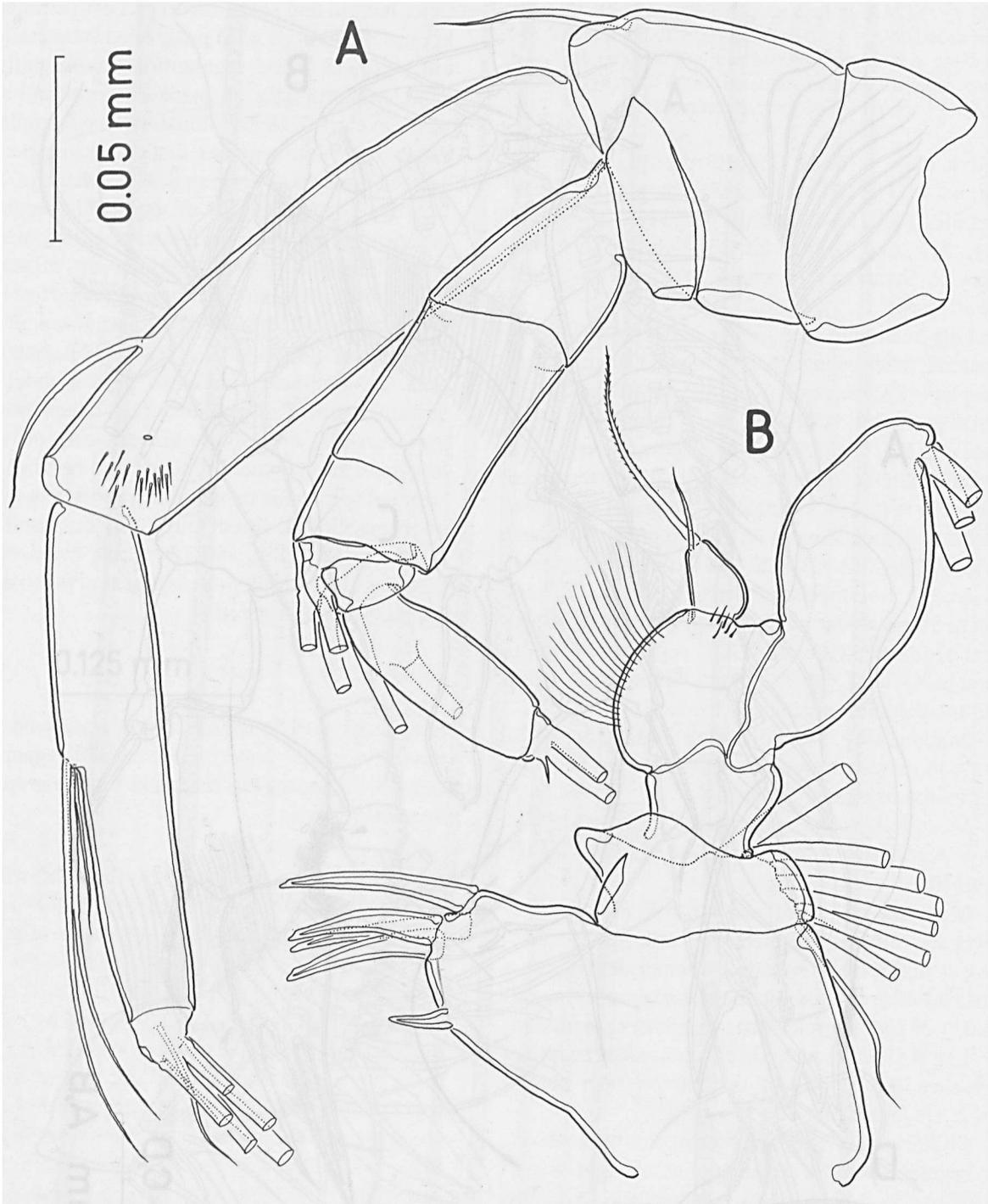


Fig. 20. *Paramisophria intermedia* sp. nov., adult male. A, antenna; B, maxillule.

antennary exopod, the absence of the maxillulary basal seta (sensu Ohtsuka et al., 1994), the unarmed condition of the maxillulary basal endite, the well developed endopod of the male left fifth leg (re-

duced in *P. japonica*), and the complete failure of expression of the articulation between the second and third exopod segments of the male right fifth leg in *P. japonica*, which has the spines correspond-

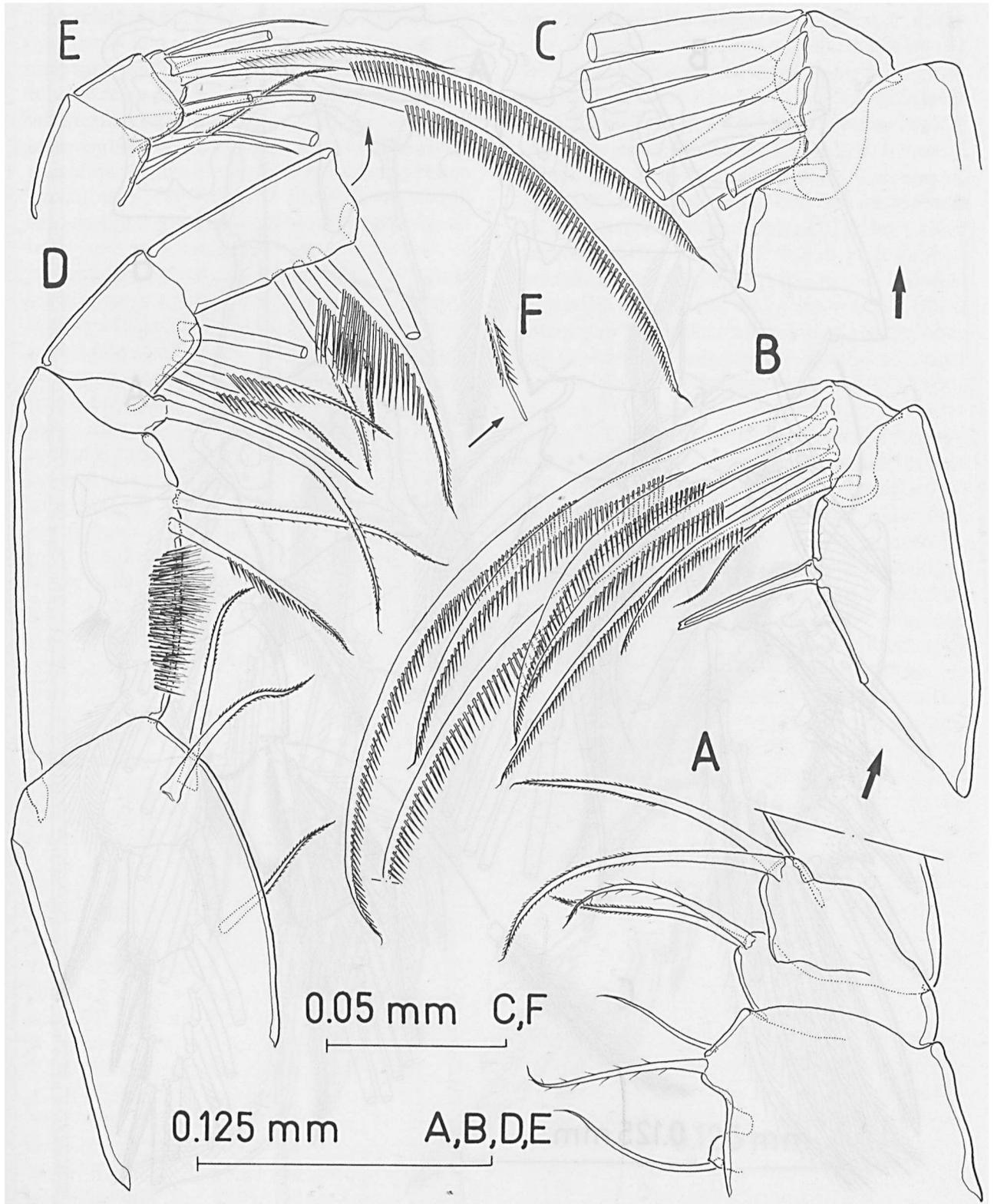


Fig. 21. *Paramisophria intermedia* sp. nov., adult male. A-B, maxilla; C, detail of maxillary endopod; D-E, maxilliped; F, detail of tip of one seta of maxilliped.

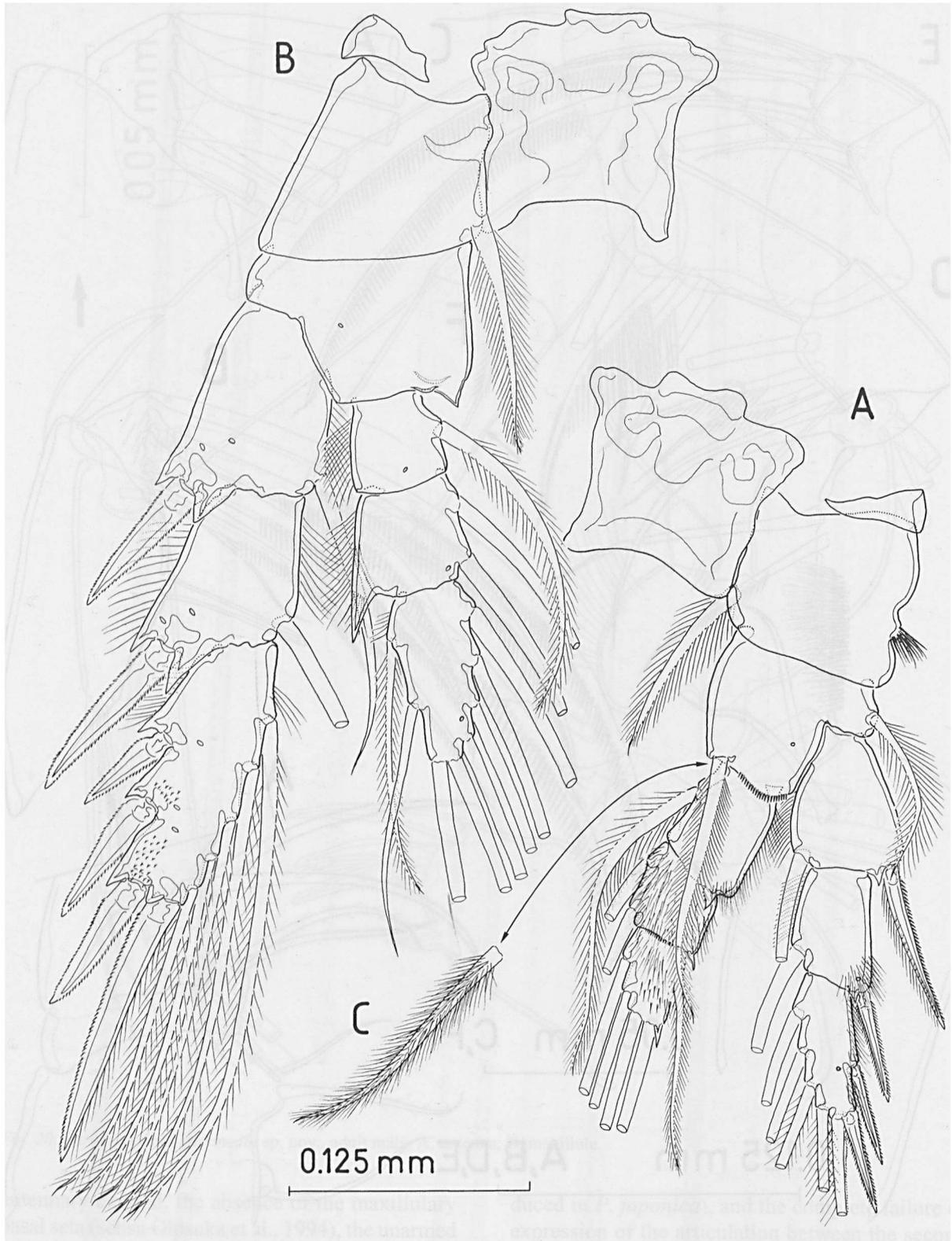


Fig. 22. *Paramisophria intermedia* sp. nov., adult male. A, first leg, posterior; B, second leg, anterior; C, detail of ornamentation on posterior surface of inner basal seta of first leg.

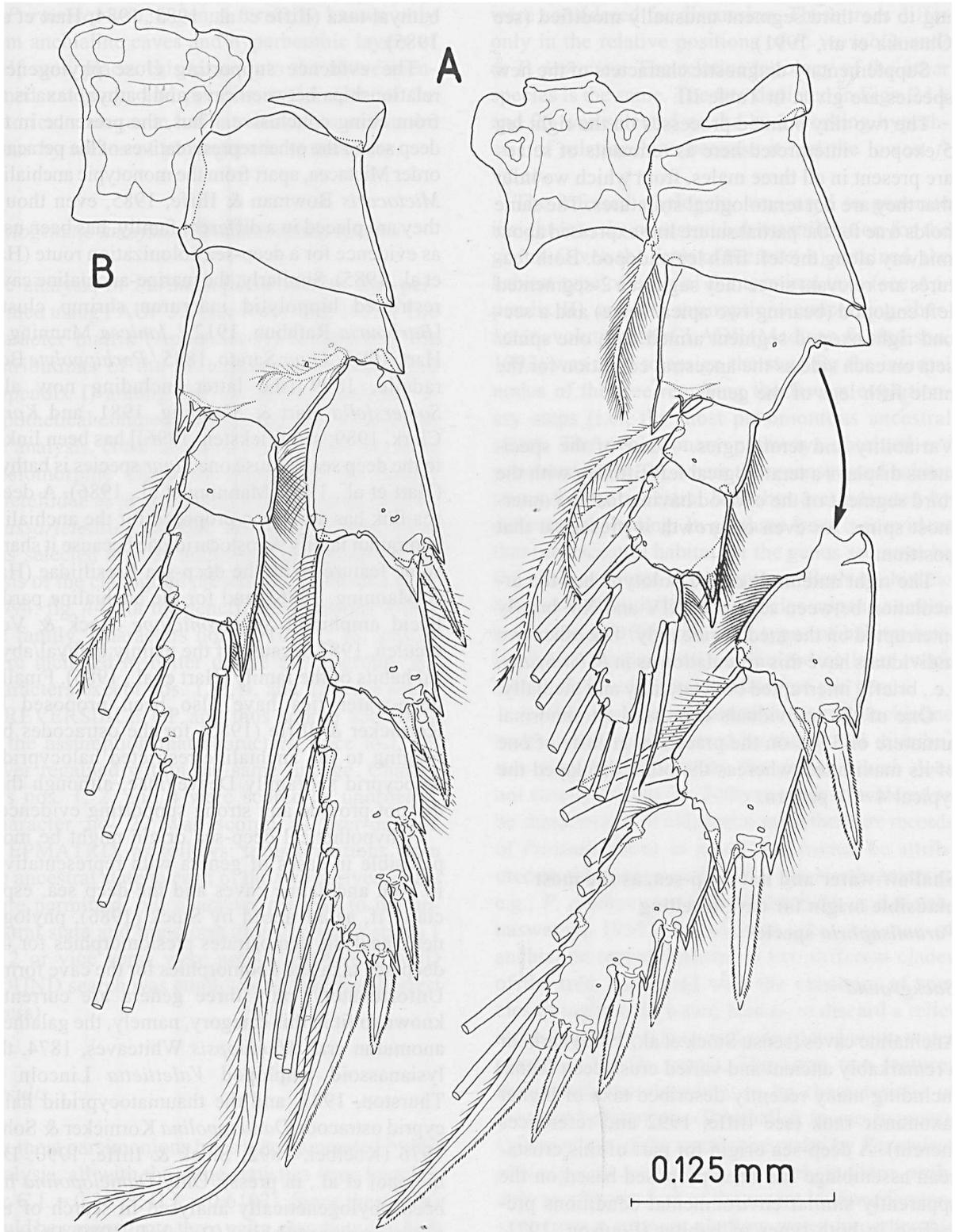


Fig. 23. *Paramisophria intermedia* sp. nov., adult male. A, third leg, anterior; B, fourth leg, anterior.

ing to the third segment unusually modified (see Ohtsuka et al., 1991).

Supplementary diagnostic characters of the new species are given in Table III.

The two tiny pointed processes on the right leg 5 exopod –interpreted here as remnants of setae– are present in all three males, from which we infer that they are not teratological structures. The same holds true for the partial suture line expressed about midway along the left fifth leg endopod. Both features are relevant since they suggest a 2-segmented left endopod (bearing two apical setae) and a second right exopod segment armed with one spine/seta on each side as the ancestral condition for the male fifth legs of the genus.

Variability and teratologies. – One of the specimens displays a teratological left fifth leg with the third segment of the exopod having lost the outermost spine. An even outgrowth is present at that position.

The right antennule of the holotype has the articulation between segments XIV and XV briefly interrupted on the medial side only. The other two individuals have this articulation as in *P. bathyalis*, i.e., briefly interrupted both laterally and medially.

One of the individuals expressed an abnormal armature of 5 + 1 on the praecoxal arthrite of one of its maxillules, whereas the other displayed the typical 4 + 1 pattern.

### Shallow-water and not deep-sea, as the most plausible origin for cave-dwelling *Paramisophria* species

#### Background

Anchialine caves (sensu Stock et al., 1986) harbour a remarkably ancient and varied crustacean fauna, including many recently described taxa of higher taxonomic rank (see Iliffe, 1992 and references therein). A deep-sea origin for part of this crustacean assemblage has been proposed based on the apparently similar environmental conditions prevailing in both types of habitat (Poulson, 1971; Margalef, 1976), and the supposed close phylogenetic relationship existing between some cave and

bathyal taxa (Iliffe et al., 1983; 1984; Hart et al., 1985).

The evidence supporting close phylogenetic relationships between cave and bathyal taxa is far from being conclusive. Thus, the presence in the deep sea of the other representatives of the peracarid order Mictacea, apart from the monotypic anchialine *Mictocaris* Bowman & Iliffe, 1985, even though they are placed in a different family, has been used as evidence for a deep-sea colonization route (Hart et al., 1985). Similarly, the marine-anchialine cave-restricted hippolytid macruran shrimp cluster [*Barbouria* Rathbun, 1912 / *Janicea* Manning & Hart, 1984 / *Ligur* Sarato, 1885 / *Parhippolyte* Borradaile, 1899 (the latter including now also *Somersiella* Hart & Manning, 1981, and *Koror* Clark, 1989; see Wicksten, 1996)] has been linked to the deep sea because one *Ligur* species is bathyal (Hart et al., 1985; Manning et al., 1986). A deep-sea link has also been proposed for the anchialine anomuran family Agostocarididae because it shares some features with the deep-sea Bresiliidae (Hart & Manning, 1986), and for the anchialine pardaliscid amphipod *Spelaonicippe* Stock & Vermeulen, 1982 because of the mainly bathyal/abysal habits of the family (Hart et al., 1985). Finally, deep-water ties have also been proposed by Kornicker & Iliffe (1985) for the ostracodes belonging to the anchialine-restricted halocypridid halocyprid subfamily Deevyinae, although they did not provide any strong supporting evidence.

A hypothetical deep-sea origin might be more plausible in cases of genera with representatives in both anchialine caves and the deep sea, especially if, as advanced by Stock (1986), phylogenetic analysis demonstrates plesiomorphies for the deep-sea taxa and apomorphies for the cave forms. Unfortunately, only three genera are currently known to fit in this category, namely, the galatheid anomuran crab *Munidopsis* Whiteaves, 1874, the lysianassoid amphipod *Valettietta* Lincoln & Thurston, 1983, and the thaumatocypridid halocyprid ostracode *Danielopolina* Kornicker & Sohn, 1976 (Koelbel, 1892; Stock & Iliffe, 1990; Danielopol et al., in press). Only *Danielopolina* has been phylogenetically analysed in search of the generic primary habitat (Boxshall, 1989; Baltanás & Danielopol, 1995; Danielopol et al., in press).

The discovery here of bathyal representatives

of *Paramisophria*, a genus formerly known only from anchialine caves and hyperbenthic layers of shelf seas, places this taxon into the above-mentioned category, and permits exploration of the historical changes in habitat utilization within the genus by means of phylogenetic systematics.

#### *Phylogenetic analysis of Paramisophria species*

The analysis of *Paramisophria* species was performed using PAUP 3.1 (see Swofford, 1993). The character matrix (Appendix II) summarizes the distributions of the 22 characters included (see Appendix I) among the 13 species analysed. A hypothetical composite out-group was included in the analysis, constructed on the basis of the most plesiomorphic character states for the family Arietellidae as presented by Ohtsuka et al. (1994). *Crassarietellus* Ohtsuka, Boxshall & Roe, 1994 was selected also as additional out-group on the basis of the cladogram presented by Ohtsuka et al. (1994: fig. 44) for the generic relationships within the family. Characters nos. 6, 10, 17, 18, and 21 were included to better define the in-group. All characters except nos. 1, 2, 4, and 22 were set as IRREVERSIBLE UP and thus scored according to the assumption that characters, once lost, are never regained within the same lineage. Characters nos. 1, 2, and 4 were scored as unordered. Character no. 22 was scored as user-defined STEPMATRIX as follows: transformations from the ancestral state to each of the two derived states were permitted, but character reversal to the ancestral state and transformations between states 1 to 2 or vice versa were not. A BRANCH AND BOUND search was employed to find the shortest tree(s).

#### *Results*

Six most parsimonious trees were generated by the analysis, all with the same statistics (tree length = 59; C.I. = 0.3898; H.I. = 0.6102). Since these trees could be grouped into three pairs, members of which differed only in the relative position occupied by the two out-groups, only three topologies (Fig. 24)

were considered for discussion. These trees differ only in the relative positions of *P. variabilis* and/or *P. japonica*. The relative topology of the other species is the same. The tree depicted in Figs. 24A and 25 was selected as the best working hypothesis of relationships because it had the lowest *f*-value.

The inferred phylogeny was used to generate insight into the ancestral habitat utilization for the genus. Given the form of the tree(-s) obtained, the habitat type of each of the terminal taxa (see Appendix II), and the assumptions concerning character evolution, McCLADE (Madison & Madison, 1992) was used to assign the state for the internal nodes of the tree requiring the fewest evolutionary steps (i.e., the most parsimonious ancestral state). The evolutionary pathways obtained are presented in Fig. 24, where the reconstructed habitat states for the ancestral branches are indicated by differential shading. In all three trees it is evident that the ancestral habitat for the genus seems to be the shallow water hyperbenthos. Both anchialine and bathyal hyperbenthic species appear as relatively recent offshoots, both types of habitat having been independently colonized at least twice during the evolutionary history of the genus.

A relatively recent penetration into the anchialine realm could be supported by the global distribution pattern exhibited by the genus, which does not strictly fit into the Tethyan track considered to be characteristic of old marine taxa (there are records of *Paramisophria* in zones that cannot be attributed to the Tethys realm, like the North Atlantic, e.g., *P. cluthae*; see Sars, 1924-1925, and Krishnaswamy, 1959). In addition, the presence of anchialine representatives in two different clades of the tree, combined with the existence of species living in cold water, lead us to discard a relict status for the cave taxa, and a restricted warm water condition for the genus. The latter two features are considered elsewhere to be characteristic of the truly Tethyan taxa (Boxshall & Jaume, in press). Colonization of the anchialine realm by *Paramisophria* species seems to be relatively modern, probably as a by-product of the recent landward extension from a primary shallow-water hyperbenthic habitat.

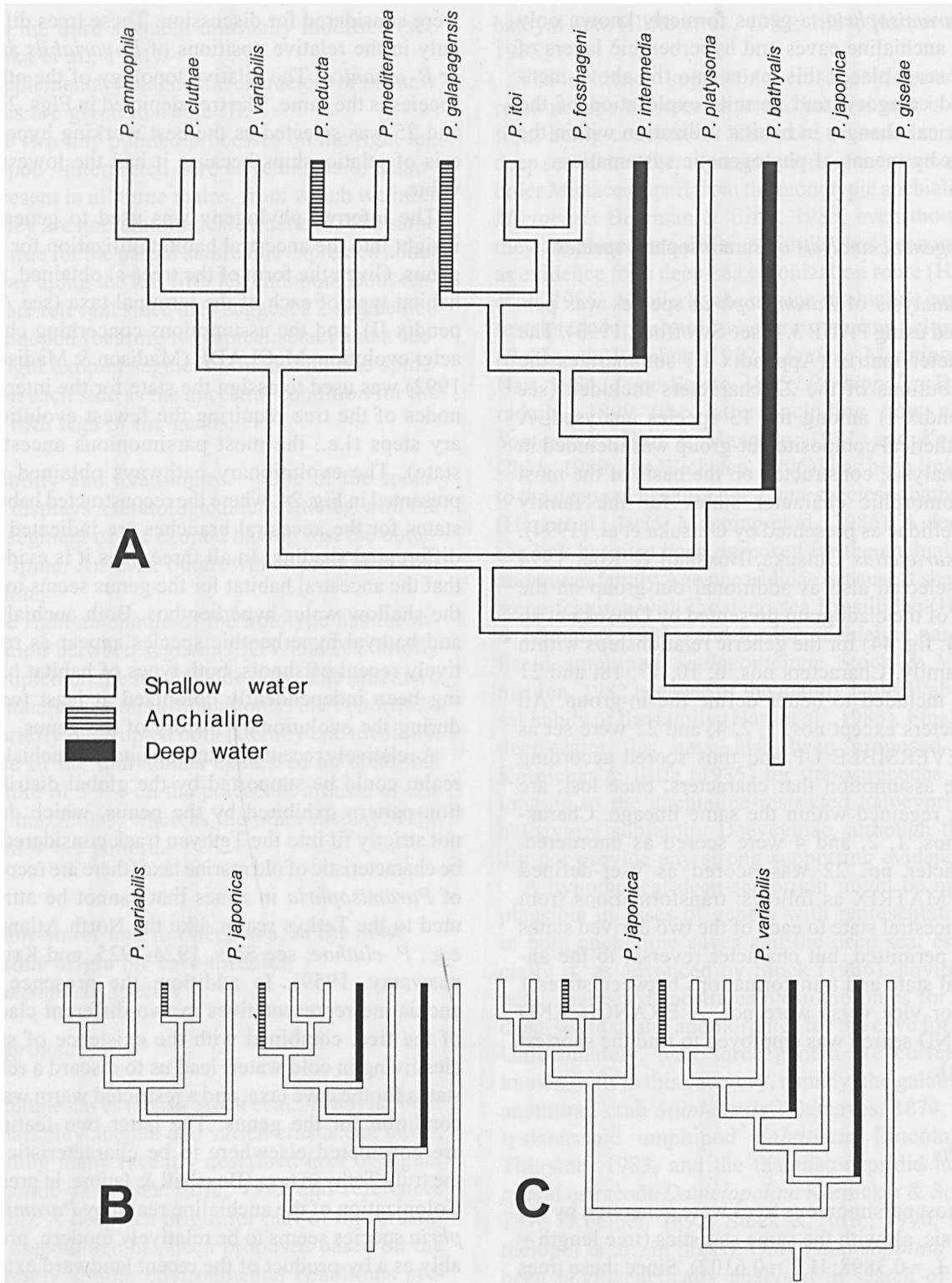


Fig. 24. Three most-parsimonious cladograms produced by the cladistic analysis of *Paramisophria* species. A, tree with  $f$ -value = 516; B, tree with  $f$ -value = 616; C, tree with  $f$ -value = 584. Shading of branches indicating inferred habitat of ancestors.

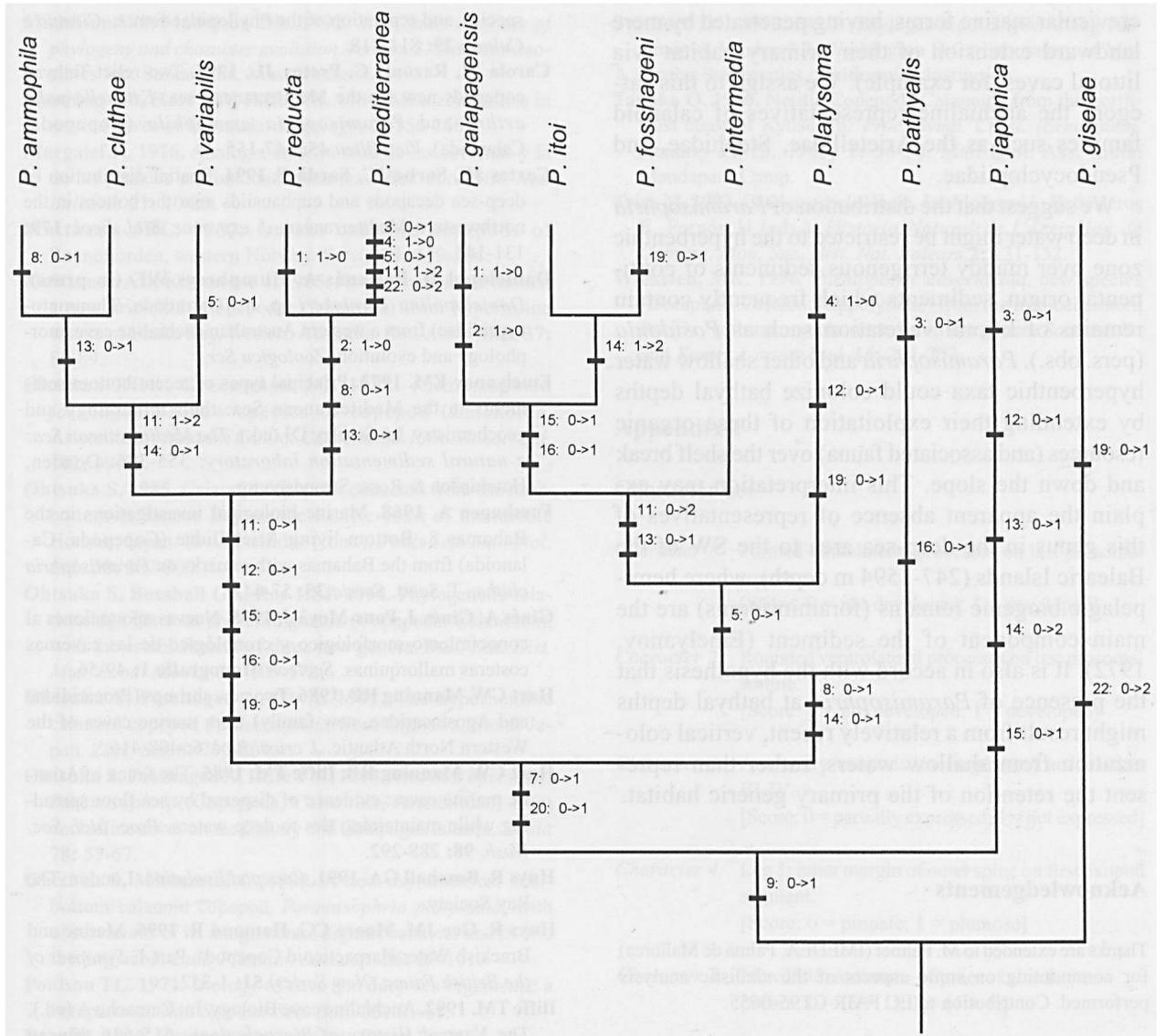


Fig. 25. Same cladogram as Fig.24A, showing character transformations.

Discussion

The analysis of *Paramisophria* species relationships supports the view already advanced in similar studies, e.g., those of Boxshall & Jaume (in press) on misosphrioid generic relationships, Stock (1986) on *Nicippe-Spelaenicippe* species, or both Baltanás & Danielopol (1995), and Danielopol et al. (in press) on *Danielopolina* species. They point to a shallow-water, and not deep-sea origin for the anchialine fauna. Evidence for the supposed deep-sea link for certain anchialine taxa is being pro-

gressively eroded as more potential examples are thoroughly analysed. Nevertheless, the deep-sea hypothesis cannot be completely rejected since cases like the anomuran *Munidopsis*, with no shallow-water representatives, remain.

The genus *Paramisophria* is illustrative of the heterogeneous age of members of the anchialine crustacean fauna: this habitat is being continuously colonized, and newcomers coexist with a basal assemblage composed of phylogenetically ancient and relictual taxa (those displaying a Tethyan pattern). These newcomers are mainly shallow-water

crevicular marine forms, having penetrated by mere landward extension of their primary habitat (via littoral caves, for example). We assign to this category the anchialine representatives of calanoid families such as the Arietellidae, Stephidae, and Pseudocyclopiidae.

We suggest that the distribution of *Paramisophria* in deep water might be restricted to the hyperbenthic zone over muddy terrigenous sediments of continental origin, sediments which frequently contain remains of littoral vegetation such as *Posidonia* (pers. obs.). *Paramisophria* and other shallow water hyperbenthic taxa could colonize bathyal depths by extending their exploitation of these organic resources (and associated fauna) over the shelf break and down the slope. This interpretation may explain the apparent absence of representatives of this genus in the deep-sea area to the SW of the Balearic Islands (247-1594 m depth), where hemipelagic biogenic remains (foraminiferans) are the main component of the sediment (Emelyanov, 1972). It is also in accord with the hypothesis that the presence of *Paramisophria* at bathyal depths might result from a relatively recent, vertical colonization from shallow waters, rather than represent the retention of the primary generic habitat.

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## References

- Andrews JN, Ginés A, Pons-Moyà J, Smart PL, Trias M. 1989. Noves dades sobre el jaciment paleontològic de la Cova de na Barxa (Capdepera, Mallorca). *Endins* 14/15: 17-26.
- Baltanás A, Danielopol D. 1995. Cladistic analysis of *Danielopolina* species (Ostracoda, Thaumatoocyprididae) and the origin of the anchialine fauna. *Mitt. hamb. zool. Mus. Inst.* 92: 315-324.
- Boxshall GA. 1989. Colonization of inland marine caves by misophrioid copepods. *J. Zool., London* 219: 521-526.
- Boxshall GA, Jaume D. (in press). Discoveries of cave misophrioids (Crustacea: Copepoda) shed new light on the origin of anchialine faunas. *Zool. Anz.* 238.
- Campaner AF. 1977. New definition of the Arietellidae (Copepoda, Calanoida) with the description of a new genus and species, and separation of the Phyllopiidae fam. n. *Ciència e Cultura* 29: 811-818.
- Carola M, Razouls C, Pretus JL. 1995. Two relict Tethyan copepods new for the Mediterranean sea: *Exumella polyarthra* and *Paramisophria ammophila* (Copepoda: Calanoida). *Vie Milieu* 45: 147-155.
- Cartes JE, Sorbe JC, Sardà F. 1994. Spatial distribution of deep-sea decapods and euphausiids near the bottom in the northwestern Mediterranean. *J. exp. mar. Biol. Ecol.* 179: 131-144.
- Danielopol D, Baltanás A, Humphreys WF. (in press). *Danielopolina kornickeri* sp. n. (Ostracoda, Thaumatoocyprididae) from a western Australian anchialine cave: morphology and evolution. *Zoologica Scr.*
- Emelyanov EM. 1972. Principal types of recent bottom sediments in the Mediterranean Sea: their mineralogy and geochemistry. In: Stanley DJ (ed.), *The Mediterranean Sea: a natural sedimentation laboratory*: 355-386. Douden, Hutchinson & Ross: Stroudsboung.
- Fosshagen A. 1968. Marine biological investigations in the Bahamas 8. Bottom-living Arietellidae (Copepoda, Calanoida) from the Bahamas with remarks on *Paramisophria cluthae* T. Scott. *Sarsia* 35: 57-64.
- Ginés A, Ginés J, Pons-Moyà J. 1975. Nuevas aportaciones al conocimiento morfológico y cronológico de las cavernas costeras mallorquinas. *Speleon Monografía* 1: 49-56.
- Hart CW, Manning RB. 1986. Two new shrimps (Procarididae and Agostocaridae, new family) from marine caves of the Western North Atlantic. *J. crust. Biol.* 6: 408-416.
- Hart CW, Manning RB, Iliffe TM. 1985. The fauna of Atlantic marine caves: evidence of dispersal by sea floor spreading while maintaining ties to deep waters. *Proc. biol. Soc. Wash.* 98: 288-292.
- Huys R, Boxshall GA. 1991. *Copepod Evolution*. London: The Ray Society.
- Huys R, Gee JM, Moore CG, Hamond R. 1996. Marine and Brackish Water Harpacticoid Copepods. Part 1. *Synopses of the British Fauna (New Series)* 51: 1-352.
- Iliffe TM. 1992. Anchialine cave Biology. In: Camacho A (ed.), *The Natural History of Biospeleology*: 615-636. Museo Nacional de ciencias Naturales: Madrid.
- Iliffe TM, Hart CW, Manning RB. 1983. Biogeography and the caves of Bermuda. *Nature* 302: 141-142.
- Iliffe TM, Wilkens H, Parzefall J, Williams D. 1984. Marine lava cave fauna: composition, biogeography and origins. *Science* 225: 309-311.
- Karaytug S, Boxshall GA. 1996. The life cycle of *Paracyclops fimbriatus* (Fischer, 1853) (Copepoda, Cyclopoida). *Bull. nat. Hist. Mus. Lond. (Zool.)* 62: 41-70.
- Koelbel K. 1892. Beiträge zur Kenntnis der Crustaceen der Canarischen Inseln. *Ann. Naturh. Hofmus. Wien* 7: 105-116.
- Kornicker LS, Iliffe TM. 1985. Deeveyinae, a new subfamily of ostracoda (Halocyprididae) from a marine cave on the Turks and Caicos Islands. *Proc. biol. Soc. Wash.* 98: 476-493.
- Krishnaswamy S. 1959. A new species of Copepoda from the Eddystone shell gravel. *J. mar. biol. Ass. U.K.* 38: 543-546.

- Maddison WP, Maddison DR. 1992.** *MacClade. Analysis of phylogeny and character evolution. Version 3.* Sinauer Associates Inc: Sunderland, Massachusetts.
- Manning RB, Hart CW, Iliffe TM. 1986.** Mesozoic relicts in marine caves of Bermuda. *Stygologia* 2: 156-166.
- Margalef R. 1976.** Analogía entre la vida de las cavernas y la de las grandes profundidades marinas. *Bol. Soc. Hist. Nat. Baleares* 21: 10-20.
- Matthews JBL. 1967.** On the calanoid copepods of Raunefjorden, western Norway. *Sarsia* 29: 159-164.
- McKinnon AD, Kimmerer J. 1985.** *Paramisophria variabilis*, a new arietellid (Copepoda: Calanoida) from hypersaline waters of Shake Bay, Western Australia. *Rec. Austr. Mus.* 37: 85-89.
- Ohtman BHR, Greenwood JG. 1992.** *Paramisophria fosshageni*, a new species of copepod (Calanoida, Arietellidae) from the Gulf of Carpentaria. *Proc. R. Soc. Qd.* 102: 49-56.
- Ohtsuka S. 1985.** Calanoid copepods collected from the near-bottom in Tanabe Bay on the Pacific coast of the middle Honshu, Japan. II. Arietellidae (cont.). *Publs Seto mar. biol. Lab.* 30: 287-306.
- Ohtsuka S, Boxshall GA, Roe HSJ. 1994.** Phylogenetic relationships between arietellid genera (Copepoda: Calanoida), with the establishment of three new genera. *Bull. Nat. Hist. Mus. Lond. (Zool.)* 60: 105-172.
- Ohtsuka S, Fosshagen A, Go A. 1991.** The hyperbenthic calanoid copepod *Paramisophria* from Okinawa, South Japan. *Zool. Sci.* 8: 793-804.
- Ohtsuka S, Fosshagen A, Iliffe TM, 1993.** Two new species of *Paramisophria* (Copepoda, Calanoida, Arietellidae) from anchialine caves on the Canary and Galápagos Islands. *Sarsia* 78: 57-67.
- Ohtsuka S, Mitsuzumi C. 1990.** A new asymmetrical near-bottom calanoid copepod, *Paramisophria platysoma*, with observations of its integumental organs, behavior and in-situ feeding habit. *Bull. Plankton Soc. Jap.* 36: 87-101.
- Poulson TL. 1971.** Biology of cave and deep sea organisms: a comparison. *Nat. Speleol. Soc. Bull.* 33: 51-61.
- Rose M. 1933.** Copépodes pélagiques. *Faune Fr.* 26: 1-374.
- Sars GO. 1901-1903.** *An account of the Crustacea of Norway, with short descriptions and figures of all the species. IV Copepoda Calanoida.* Bergen Museum: Bergen.
- Sars GO. 1924 - 1925.** Copépodes particulièrement bathypélagiques provenant des campagnes scientifiques accomplies par le Prince Albert Ier de Monaco. *Résult. Camp. Scient. Prince Albert I* 69: text (1925), 408 pp., atlas (1924), 127 pls.
- Scott T. 1897.** The marine fishes and invertebrates of Loch Fyne. *Rep. Fishery Bd for Scotl.* 15 (3): 107-174.
- Stock JH. 1986.** Deep sea origin of cave faunas: an unlikely supposition. *Stygologia* 2: 105-111.
- Stock JH, Iliffe TM. 1990.** Amphipod crustaceans from anchialine cave waters of the Galapagos Islands. *Zool. J. Linn. Soc.* 98: 141-160.
- Stock JH, Iliffe TM, Williams D. 1986.** The concept "anchialine" reconsidered. *Stygologia* 2: 90-92.
- Swofford DL. 1993.** PAUP (Phylogenetic Analysis Using Parsimony). Version 3.1. Washington D.C.: Laboratory of Molecular Systematics, Smithsonian Institution.
- Tanaka O. 1966.** Neritic Copepoda Calanoida from the north-west coast of Kyusu. In: *Proc. Symp. Crust. (Ernakulam, January 12-15, 1965)* 1: 36-50. Mar. Biol. Ass. India: Mandapam Camp.
- Trias M. 1993.** Catàleg espeleològic. In: Alcover JA, Ballesteros E, Fornós JJ (eds.), *Història Natural de l'Arxipèlag de Cabrera. Mon. Soc. Hist. Nat. Balears* 2: 131-152.
- Wicksten, MK. 1996.** *Parhippolyte cavernicola*, new species (Decapoda: Caridea: Hippolytidae) from the tropical eastern Pacific, with taxonomic remarks on the genera *Somersiella* and *Koror*. *J. crust. Biol.* 16: 201-207.

## Appendix I

### Character set

- Character 1:** Pointed dorsolateral processes on last prosomal somite.  
[Score: 0 = not developed; 1 = developed]
- Character 2:** Rounded ventrolateral processes on last prosomal somite.  
[Score: 0 = not developed; 1 = developed]
- Character 3:** Antennary exopod: intersegmental articulation III-IV.  
[Score: 0 = partially expressed; 1 = not expressed]
- Character 4:** Leg 1: inner margin of outer spine on first exopod segment.  
[Score: 0 = pinnate; 1 = plumose]
- Character 5:** Maxillule: armature of praecoxal arthrite.  
[Score: 0 = (5 + 1); 1 = (4 + 1)]
- Character 6:** Maxillule: armature of coxal epipodite.  
[Score: 0 = more than 7 setae; 1 = 6 setae]
- Character 7:** Maxillulary basal seta.  
Comments: seta named after Ohtsuka et al. (1994: 166).  
[Score: 0 = present; 1 = absent]
- Character 8:** Maxillulary coxal endite.  
[Score: 0 = retaining tiny remnant of seta; 1 = unarmed]
- Character 9:** Maxilla: distal seta on first praecoxal endite.  
[Score: 0 = present; 1 = absent]
- Character 10:** Maxillary basal seta.  
[Score: 0 = ornamented with spinules; 1 = naked]

*Character 11:* Male left antennule: intersegmental articulation XXIII-XXIV.  
[Score: 0 = fully expressed; 1 = partially expressed; 2 = not expressed]

*Character 12:* Male left antennule: intersegmental articulation XXV-XXVI.  
[Score: 0 = fully expressed; 1 = partially expressed]

*Character 13:* Male left fifth leg: number of spines/setae on third exopod segment.  
Comments: the seta alternatively retained or lost corresponds to seta 'c' in schematic presented by Ohtsuka et al. (1994: fig. 43).  
[Score: 0 = four; 1 = three]

*Character 14:* Male right fifth leg: articulation between second and third exopod segment.  
[Score: 0 = fully expressed; 1 = partially expressed; 2 = not expressed]

*Character 15:* Male right fifth leg: remnant of inner seta on second exopod segment.  
Comments: this seta corresponds to seta 'k' in schematic presented by Ohtsuka et al. (1994: fig. 43).  
[Score: 0 = present; 1 = absent]

*Character 16:* Male right fifth leg: number of spines/setae on third exopod segment.  
Comments: the seta alternatively retained or lost corresponds to seta 'c' in schematic presented by Ohtsuka et al. (1994: fig. 43).  
[Score: 0 = four; 1 = three]

*Character 17:* Female antennules.  
[Score: 0 = symmetrical; 1 = asymmetrical]

*Character 18:* Female antennules: aesthetasc on segment IV.  
[Score: 0 = present; 1 = absent]

*Character 19:* Female fifth legs: articulation between first and second exopod segment.  
[Score: 0 = expressed; 1 = not expressed]

*Character 20:* Female fifth legs: inner subapical seta on endopod.  
Comments: this seta corresponds to seta 'c' in schematic presented by Ohtsuka et al. (1994: fig. 42).  
[Score: 0 = present; 1 = absent]

*Character 21:* Female genital double-somite: copulatory pores.  
[Score: 0 = separate; 1 = fused]

*Character 22:* Female genital double-somite: arrangement of copulatory pore(s) on ventral surface.  
[Score: 0 = symmetrical; 1 = one on left side; 2 = one on right side]

## Appendix II

### Character matrix

Taxon	Characters 1-22	Habitat
Ancestral arietellid	000?000000000000000000	
<i>Crassarietellus</i>	0001010000010????001000	
<i>P. ammophila</i>	11??0011112111?11111??	(shallow water)
<i>P. cluthae</i>	11??00101112111?111111	(shallow water)
<i>P. fosshageni</i>	110?101?112012111?11??	(shallow water)
<i>P. galapagensis</i>	0001101111201111??????	(anchialine cave)
<i>P. giselae</i>	1101000001?????111012	(shallow water)
<i>P. itoi</i>	1101101111201211110111	(shallow water)
<i>P. japonica</i>	1111000011011210110010	(shallow water)
<i>P. platysoma</i>	1100101111010100111111	(shallow water)
<i>P. reducta</i>	0001001111111011111110	(anchialine cave)
<i>P. variabilis</i>	111?101?112101111?11??	(shallow water)
<i>P. bathyalis</i>	1111001111000101??????	(bathyal)
<i>P. intermedia</i>	1101101111201100??????	(bathyal)
<i>P. mediterranea</i>	1010101111211011111112	(shallow water = littoral cave)