

New cave-dwelling pseudocyclopiids (Copepoda, Calanoida, Pseudocyclopiidae) from the Balearic, Canary, and Philippine archipelagos

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Two new copepods are described from anchialine and littoral caves on the Balearic and Philippine archipelagos. *Thompsonopia* gen. nov. is erected to accommodate the Balearic taxon, and two species of *Pseudocyclopia* T. Scott, 1892 are transferred to the new genus, viz. *P. stephoides* Thompson, 1895 and *P. muranoi* Ohtsuka, 1992. A new species from the Philippines is assigned to *Stygocyclopia* Jaume & Boxshall, 1995, and the amazing discovery of *S. balearica* Jaume & Boxshall, 1995 in anchialine environments on Lanzarote is reported and discussed. The swimming habits of the latter taxon are briefly described. The diagnoses of *Pseudocyclopia*, *Stygocyclopia*, and of the family Pseudocyclopiidae T. Scott, 1892 are emended.

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INTRODUCTION

Calanoids in the family Pseudocyclopiidae T. Scott, 1892 are primarily marine hyperbenthic and for that reason are rarely reported. Their mode of life as opportunistic feeders closely tied to shallow-water, loose or muddy substrates, makes them excellent candidates to colonise the subterranean environment (Stock 1986; Botosaneanu & Holsinger 1991). In fact, all three genera currently composing the family have representatives in anchialine habitats (sensu Stock & al. 1986).

The seven species of *Pseudocyclopia* T. Scott, 1892 are found on muddy substrates in shallow seas (50-120 m depth) around the coasts of Britain and Norway (Scott 1892, 1894; Sars 1901-1903, 1919-1921), and in near-bottom shallow waters of the tropical Atlantic (Andronov 1986) and the NW Pacific (Ohtsuka 1992). There are two cave records (as *Pseudocyclopia* sp.) from the Croatian flooded coastal karst (Sket 1986).

The other two genera are monotypic and stygobiont: *Paracyclopia* Fosshagen, 1985 is known from Bermudian anchialine caves, and *Stygocyclopia* Jaume & Boxshall, 1995, from similar environments on the Balearic Islands (Fosshagen & Iliffe 1985; Jaume & Boxshall 1995).

We introduce here the description of a new genus of pseudocyclopiid calanoid to accommodate a new

taxon from Mediterranean caves. Two species of *Pseudocyclopia*, viz. *P. stephoides* Thompson, 1895 and *P. muranoi* Ohtsuka, 1992 are transferred to the new genus, and *Pseudocyclopia* is consequently redefined. The paper provides also the description of a new species of *Stygocyclopia* from an anchialine cave on the Philippines, and the amazing discovery of *S. balearica* Jaume & Boxshall, 1995 in both a flooded lava tube and a coastal well on the Canary Islands is also reported and discussed. The swimming habits of the latter species are concisely described. Observations made on these three genera of Pseudocyclopiidae contribute to an improved diagnosis of the family.

DESCRIPTION OF THE CAVES

Cova de na Mitjana is in Capdepera, Mallorca (Balearic Islands), UTM coordinates: 539010 / 4390710. It is a fossil littoral cave excavated in Triassic fissured limestone, with a subaerial entrance at 7 m above sea level. A topographic profile of the cavity is available in Ginés & al. (1975). It harbours a shallow lake (depth < 0.5 m) subjected to direct marine influence, with a sandy bottom, a slight swell, and a clearly marine fauna (*Conger conger* L., *Palaemon serratus* (Pennant), crabs, Cumacea, Chaetognatha, Ophiuroidea). The cave harbours also stygobiont taxa such as the superornatire-



mid harpacticoids *Neoechinophora xoni* Jaume, *Superornatiremis mendai* Jaume, and *Intercrusia garciai* Jaume, and also the janirid isopod *Troglolaniropsis lloberai* Jaume (Jaume 1995, 1997).

Panglao Island is situated in the south central Philippines about 500 km south of Manila at 9°35'N, 123°50'E. This low limestone island, which is located only 1 km off the southwest corner of Bohol Island, has numerous anchialine caves and sinkholes. Calingoob Cave is located in the bush on the northern side of Panglao Island. It consists of a single collapse chamber with an anchialine pool, partially in darkness, reaching depths to 6 m. Although salinity was not measured in this cave, other similar caves on Panglao Island have surface salinities ranging from 4 to 8 psu. In addition to copepods, one crab and one shrimp were collected.

Cueva de los Lagos is a segment of one of the world's longest lava tubes located on Lanzarote in the Canary Islands. The tube begins at the base of the volcano Monte Corona, extends 7 km down the slope of the mountain to the coastline where it continues a further 1.4 km out to sea. Cueva de los Lagos is the farthest inland point to which seawater penetrates. About 300 m from the cave entrance, the Jameo de los Lagos is a series of shallow, 1-2 m deep, pools that extend over a horizontal distance of about 150-200 m. Water in these pools is flushed by the tides as evidenced by a diurnal change in water level. At the seaward end of this section, the tube becomes submerged and extends underwater toward the coast in the direction of the Jameos del Agua.

One of the most common species found in the Cueva de los Lagos is the gastropod *Littorina saxatilis* (Oliv). Additionally, the polychaete *Gesiella jameensis* (Hartmann-Schröder), the gastropod *Peringiella epidaurica* (Brusina), the amphipod *Spelaeonicippe buchi* (Andres), the mysid *Heteromydoides cotti* (Calman), the ostracod *Danielopolina wilkensi* Hartmann, the remipede *Speleonectes ondinae* (García-Valdecasas), and the copepods *Speleophriopsis canariensis* Jaume & Boxshall, *Expansophria dimorpha* Boxshall & Iliffe, and *Muceddina multispinosa* Jaume & Boxshall have been observed (Wilkens & al. 1993; Jaume & Boxshall 1996a, 1996b).

The Túnel de Atlántida is a 1.4 km long, totally submerged section of the lava tube that extends seaward from the Jameos del Agua. The entrance to this part of the tube is a small pool at the seaward end of the Jameos del Agua. Average passage size is about 10 m in diameter. The cave continues in a straight line out to sea before ending at 57 m depth. Salinity in the cave is slightly below that of seawater.

Common species in the water column of the Túnel de Atlántida include the amphipods *Liagoceradocus*

acutus Andres and *Spelaeonicippe buchi*, the thermosbaenacean *Halosbaena fortunata* Bowman & Iliffe, the copepods *Dimisophria cavernicola* Boxshall & Iliffe, *Expansophria dimorpha*, and *Palpophria aestheta* Boxshall & Iliffe, the ostracods *Danielopolina phalanx* Kornicker & Iliffe, *D. wilkensi*, and *Eupolycope pnyx* Kornicker & Iliffe, the remipede *Speleonectes ondinae*, the polychaete *Gesiella jameensis*, and the archiannelid *Protodrilus* sp. (Wilkens & Parzefall 1974; Iliffe & al. 1984; Wilkens & al. 1986; Iliffe & al., in press).

METHODS

Samples were taken using a hand-held plankton net (60 µm mesh size) with an extensible (to 3 m) handle, or with a plankton net (93 µm mesh) towed through the water column of cave lakes.

Specimens were examined with a differential interference contrast microscope (Olympus BH-2). The terminology used in descriptions follows Huys & Boxshall (1991). Material is deposited in The Natural History Museum, London (BMNH) and in Museu de la Naturalesa de les Illes Balears, Palma de Mallorca (MNCM).

TAXONOMIC PART

Family Pseudocyclopiidae T. Scott, 1892 (emend.)

Diagnosis. Body compact, with prosome laterally compressed. Rostrum simple. First pedigerous somite incorporated into cephalothorax in adult, free during copepodid stages. Second pedigerous somite with dorsal integumental fold in anterior half. Third pedigerous somite with hypertrophied sensilla on lateral margin. Fourth and fifth pedigerous somites fused. Urosome 4-segmented in female, 5-segmented in male; urosomal somites profusely adorned with lamellar spinules. Caudal rami carrying seven setae; seta I tiny; seta II carried on biarticulate socle, as seta VII; seta VII located on ventromedial side of ramus. Antennules of both sexes with one sensilla on ancestral segments I, II and V; compound segments II-IV and XXVII-XXVIII present. Male antennule lacking geniculation. First two proximal segments of antennary exopod corresponding, respectively, to ancestral segments I and at least II-IV. Maxilla displaying soft lobe of uncertain homology between praecoxal endites; free endopod unsegmented or 2-segmented, with seven setae. Swimming legs 1 and 2 with endopods 1 and 2-segmented, respectively. Leg 3 displaying stout, hypertrophied inner coxal spine; first exopod segment of *Pseudocyclopia* and *Paracyclopia* frequently with accessory spine sub-marginally on pos-

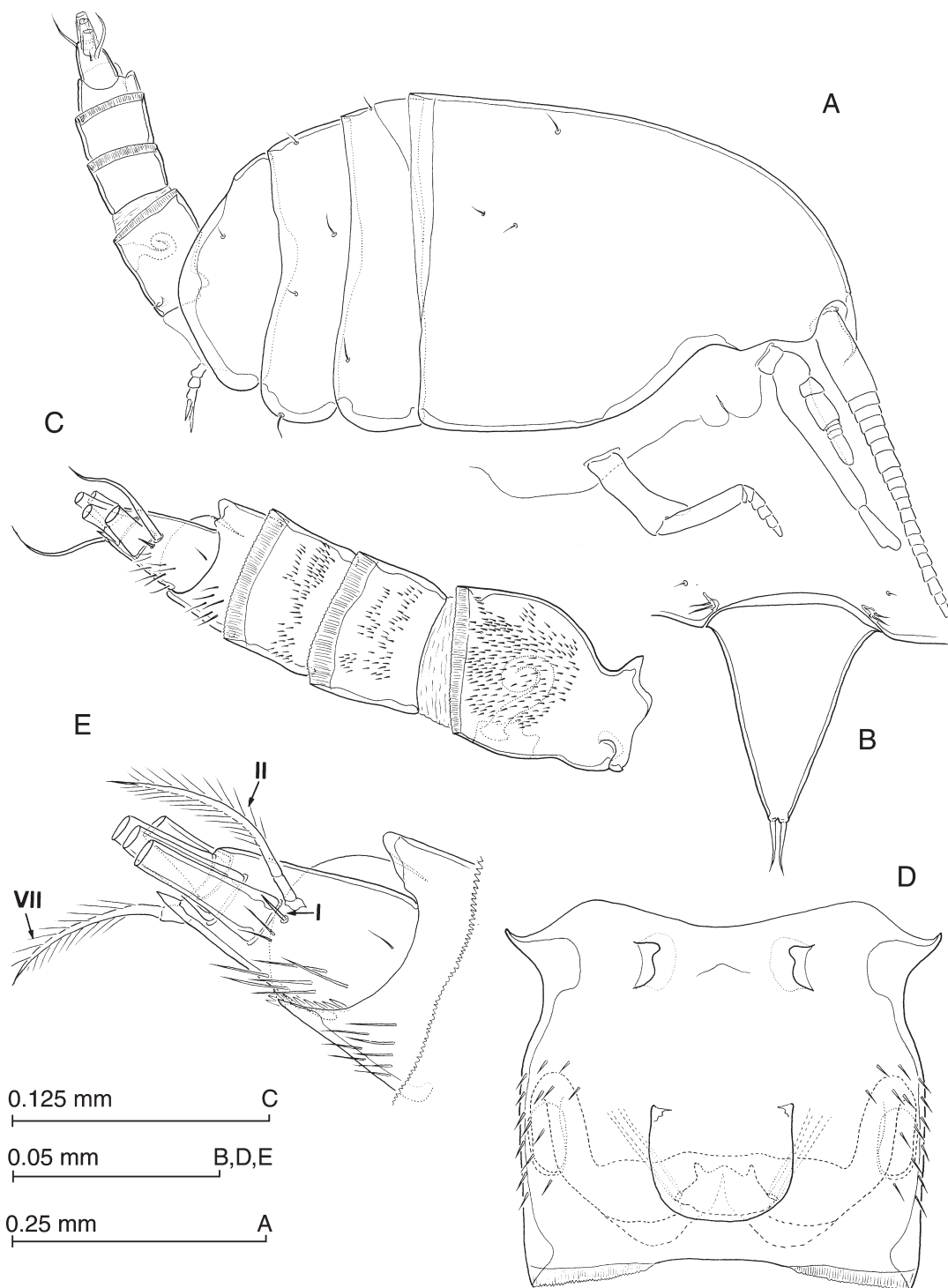


Fig. 1. *Thompsonopia mediterranea* gen. et sp. nov., adult ♀. A, habitus, lateral; B, rostrum; C, urosome, lateral; D, genital double-somite, ventral; E, detail of right caudal ramus, lateral.



terior surface of segment, near to distal end of outer margin. Female fifth legs uniramous, reduced, 3-segmented, ending in two or three points. Male fifth legs asymmetrical.

Thompsonopia gen. nov.

Diagnosis. Pseudocyclopiidae. Rostrum pointed, movable, not fused to cephalosome, with two terminal filaments. Antennules of both sexes 20-segmented, displaying characteristic compound segment X-XIV. Female antennule with segment I completely incorporated into II-IV, and with segments XXII and XXIII separate. Male antennules with segment I separate; articulation between segments XXII and XXIII partially expressed in right antennule, not expressed in left; quadrithe on segment VII. First antennary endopod segment fully incorporated into basis. Maxillary endopod unsegmented. First leg with outer basal spine; endopod with five setae. First exopod segment of leg 3 lacking accessory spine on outer margin. Fourth legs armature sexually dimorphic, with male lacking inner coxal spine and with two proximal segments of endopod bearing ordinary setae; those of female bearing inner coxal spine and with armature on two proximal endopod segments transformed into robust spines. Female fifth legs 3-segmented, uniramous, each ending in three points. Male fifth legs asymmetrical, uniramous, with basis of left leg swollen posteriorly; right leg elongate, filiform. Female genital double-somite symmetrical.

Etymology. Genus named in honour of the British marine biologist Isaac C. Thompson, who first noticed the peculiar segmentation of the antennule in the species of *Pseudocyclopia* now transferred to the new genus. The suffix “-opia” is the typical termination of names of pseudocyclopiid genera.

Type species. *Thompsonopia mediterranea* sp. nov., here designated.

Other species in the genus. *T. muranoi* (Ohtsuka, 1992) and *T. stephoides* (Thompson, 1895).

Thompsonopia mediterranea sp. nov.
(Figs 1-8)

Material examined. Cova de na Mitjana (Capdepera, Mallorca, Balearic Islands). Holotype: adult ♀ 0.88 mm partially dissected on 5 slides; mounted in lactophenol sealed with nail varnish [MNCM. 350]. Paratypes: adult ♂ 0.76 mm, adult ♀ 0.86 mm and 3 copepodids

[MNCM. 350]. Collected by D. Jaume and G.A. Boxshall, 21 August 1997.

Comparative material examined. *Pseudocyclopia stephoides* Thompson, 1895. Ospøy (Norway), 27-10 m depth, with Ockelmann epibenthic sledge (see Ockelmann 1964). Five adult ♂♂ and adult ♀ [BMNH reg. nos. 1998.2633-2638]. Collected by A. Fosshagen, 18 January 1968.

Adult female. Eyes absent. Body (Fig. 1A) compact, with prosome laterally compressed. Rostrum (Fig. 1B) movable, tapering, with pair of apical filaments. First pedigerous somite incorporated into cephalosome conforming cephalothorax. Fourth and fifth pedigerous somites completely fused. Sensillae distributed on prosomal somites as figured.

Urosome (Fig. 1C) 4-segmented, with surface of somites richly ornamented with both ordinary and lamellar spinules, latter easily lost when manipulating animals. Genital double-somite (Fig. 1D) symmetrical. Internal genital system not fully resolved: both seminal receptacles developed, forming dorsal lobe at each side, with serpentiform receptacle ducts; pair of oviducts emptying into separate gonopores also discerned. Ducts and gonopores opening into common mid-ventral atrium closed off by quadrangular operculum. Two sac-like sclerotized folds similar to those displayed by *Crassarietellus huyi* Ohtsuka, Boxshall & Roe, 1994 (see Ohtsuka & al. 1994, fig. 2a) positioned ventrolaterally near anterior margin of double-somite. Anal somite (Fig. 2A) with weakly developed, unarmed operculum. Caudal rami (Figs 1E; 2A, B) symmetrical, short, with medial margin covered with setules; armature consisting of seven setae. Setae III to VI implanted distally, very thick, with internal tissue finely granulated. Seta I tiny, positioned laterally near insertion of seta II (arrowed in Fig. 1E). Setae II and VII reduced; seta II implanted dorsolaterally, seta VII displaced ventromedially.

Antennules (Fig. 3A) short, symmetrical, 20-segmented, directed ventrally, not reaching distal end of cephalothorax. First segment largest, representing ancestral segments I to IV. Other compound segments involving ancestral segments X-XIV and XXVII-XXVIII. Armature pattern as follows: segment 1 (I-IV), 5 setae; segments 2 and 3 (V and VI), 2 setae each; segment 4 (VII), 2 setae + aesthetasc; segment 5 (VIII), 1 seta; segment 6 (IX), 2 setae; segment 7 (X-XIV), 6 setae + ae; segment 8 (XV), 1 seta; segment 9 (XVI), 1 seta + ae; segments 10 to 13 (XVII to XX), 1 seta each; segment 14 (XXI), 1 seta + ae; segments 15 and 16 (XXII and XXIII), 1 seta each; segments 17 to 19 (XXIV to XXVI), 2 setae each; segment 20 (XXVII-XXVIII), 5

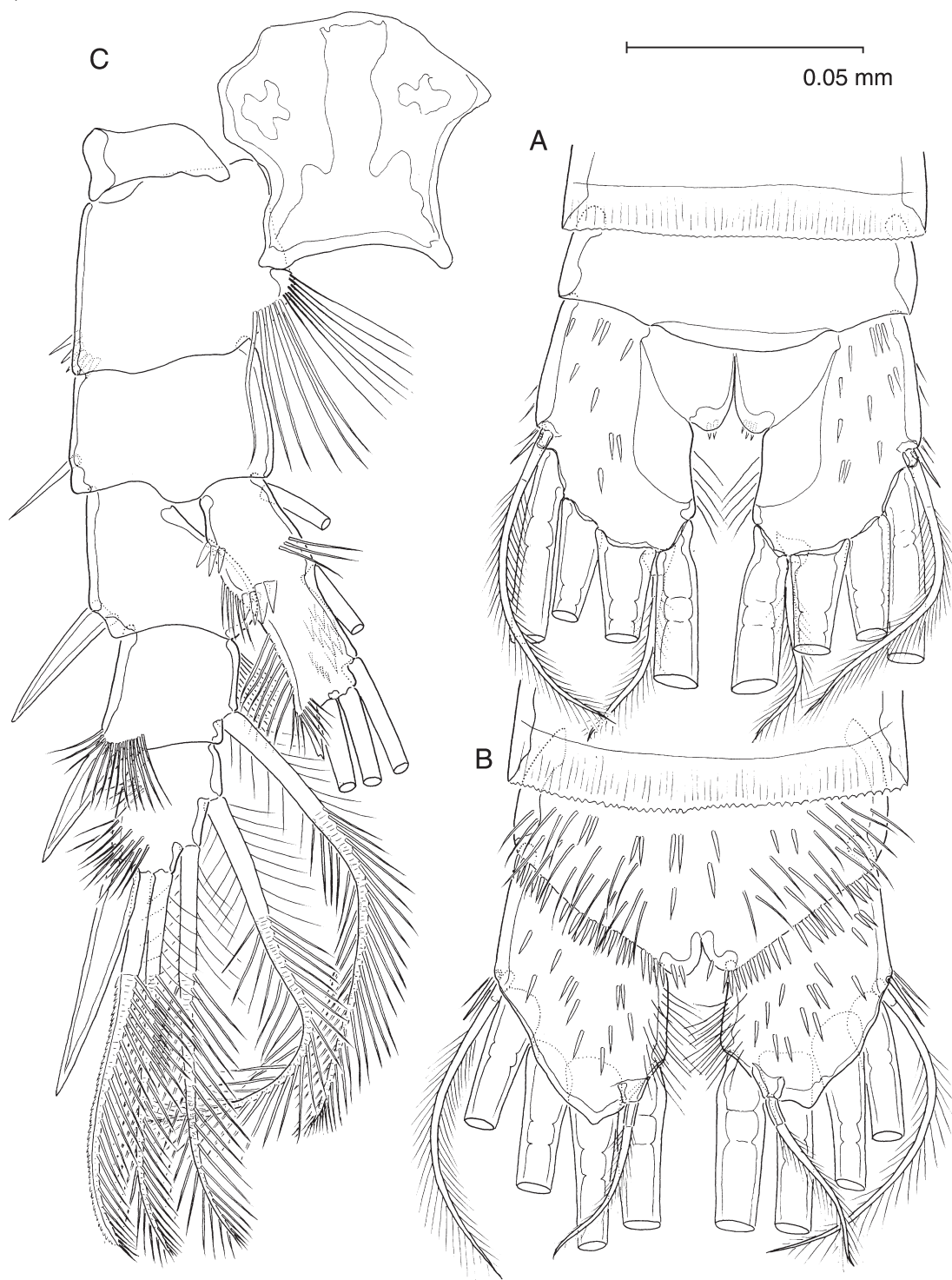


Fig. 2. *Thompsonopia mediterranea* gen. et sp. nov., adult ♀. A, anal somite and caudal rami, dorsal; B, same, ventral; C, first leg, anterior.

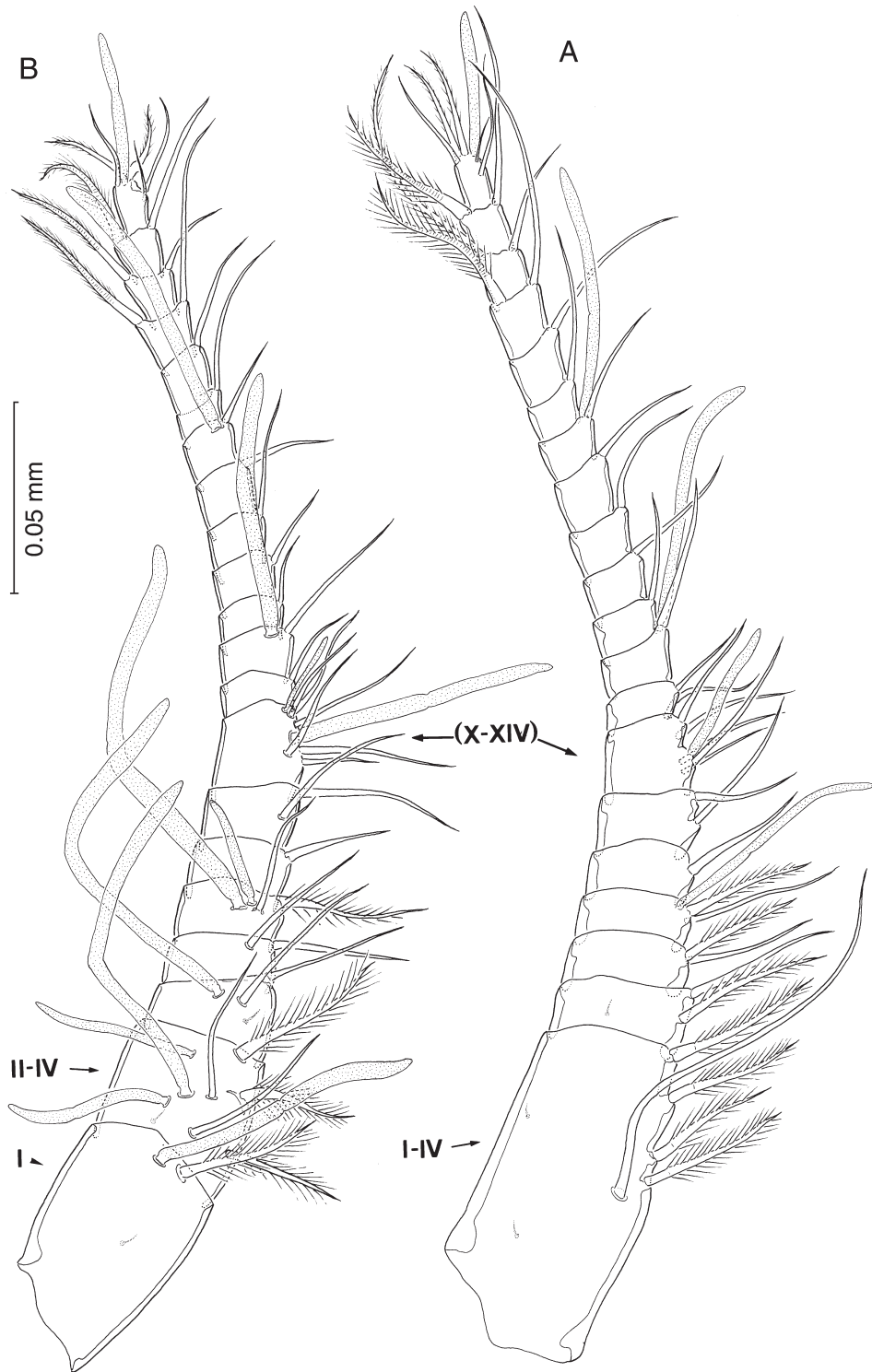


Fig. 3. *Thompsonopia mediterranea* gen. et sp. nov. A, adult ♀ right antennule, ventral; B, adult ♂ right antennule, ventral.

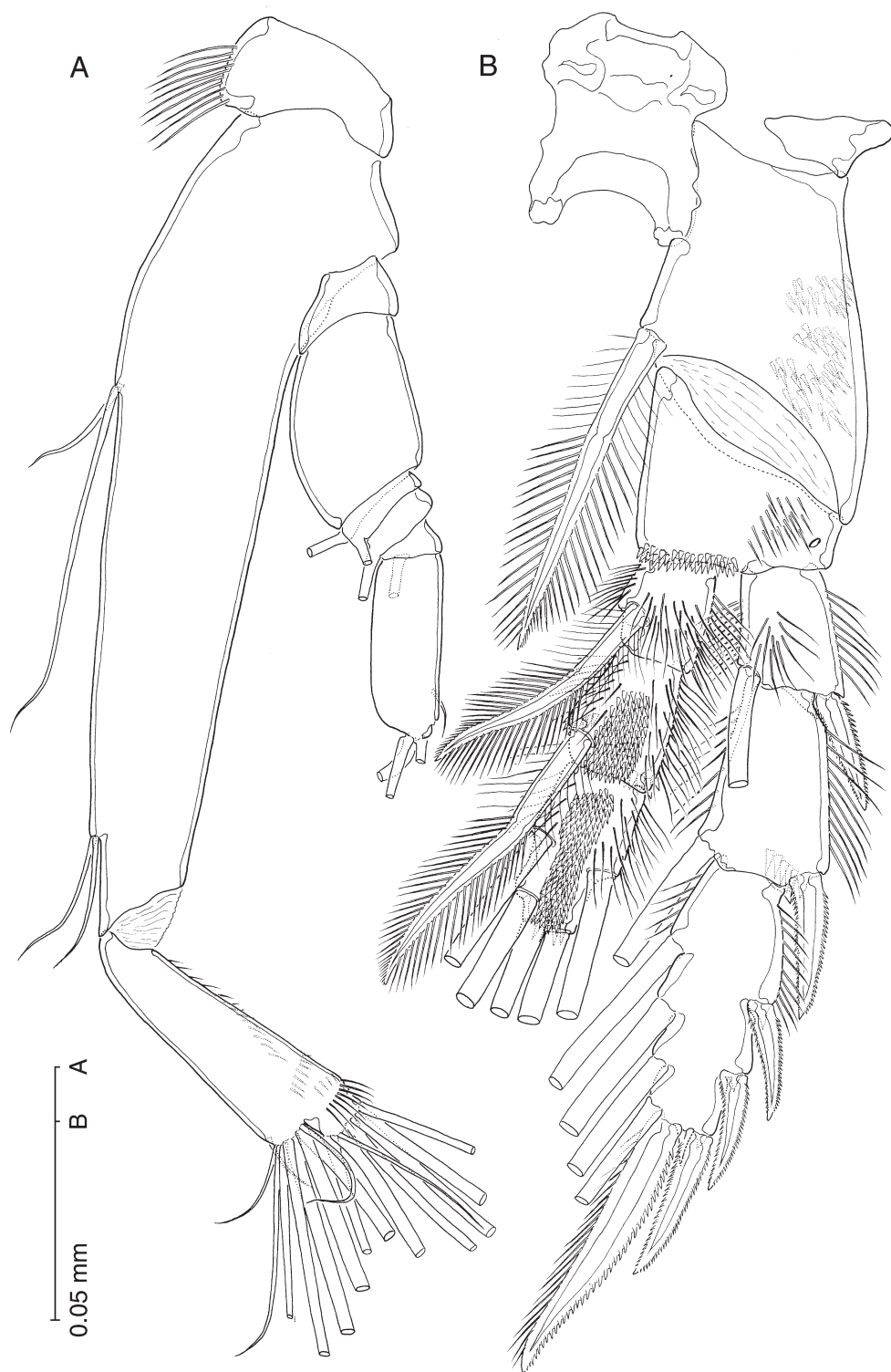


Fig. 4. *Thompsonopia mediterranea* gen. et sp. nov., adult ♀. A, antenna; B, fourth leg, posterior.



setae + ae. Two sensillae on dorsal surface of first segment; one sensilla on second segment.

Antenna (Fig. 4A) biramous. Coxa unarmed, with patch of long spinules along inner margin. Basis completely fused to first endopod segment forming elongate allobasis; two groups of two setae positioned along inner margin. Free endopod segment elongate, bilobed; inner lobe (corresponding to ancestral endopod segment II) with nine setae; outer lobe (corresponding to ancestral segments III-IV) with seven distal setae; several combs of long spinules as figured. Exopod 6-segmented; segment 2 representing ancestral segments II-IV, plus partially incorporated segment V; segment 6 representing partially incorporated ancestral segments IX (elongate, bearing reduced seta) and X (bearing three setae); exopod segmentation and setal formula: 0, (0 + 1), 1, 1, 1, (1 + 3). Segmental homology deducted after comparison with segmental pattern and armature of *Stygocyclopia philippensis* sp. nov., described below (Fig. 12A).

Mandible with short, heavily built coxal gnathobase; cutting blade with major group of four triangular teeth, plus complex array of serrate teeth and spines dorsally (Fig. 5A). Mandibular palp (Fig. 5B) with basis expanded, bearing two long plus one reduced setae on inner margin plus patch of spinules proximally. Endopod aligned with main axis of basis, shorter than exopod, 2-segmented; first segment with single seta plus patch of tiny spinules; second with 11 distal setae (two of them reduced), and comb of long spinules. Exopod apparently 4-segmented, but close analysis revealing partial fusion between proximal segment, somewhat spirally configured, and second and third segments, resulting in actual 2-segmented condition; setal formula (1 + 1 + 1), 3; distal segment derived from ancestral segments IV and V.

Maxillule (Fig. 6A) with praecoxal arthritis carrying nine stout marginal spines plus four more slender spines sub-marginally. Coxal epipodite with seven long and two reduced setae. Coxal endite discrete, with two setae distally; row of spinules along inner margin. Proximal basal endite elongate, with five distal setae. Distal endite incorporated into basis, with five setae and row of marginal spinules. Endopod fully incorporated into basis, forming lobe armed with 11 long distal setae. Exopod discrete, also incorporated to basis, with row of eight long marginal setae.

Maxilla (Fig. 5C) comprising syncoxa, allobasis, and unsegmented endopod. Proximal syncoxal endite with five long marginal setae plus short, hyaline spiniform process; remaining syncoxal endites each with three setae, one of them shorter, plus sub-marginal row of spinules; soft process of uncertain homology between proximal and second endite. Basal endite carrying two

stout spines plus two more slender elements distally; tiny seta remnant of incorporated endopodal segment close to insertion of free endopod. Free endopod short, bearing seven unequal setae.

Maxilliped (Fig. 6B) powerfully developed, 8-segmented, reflexed distally. Syncoxa with nine setae in four groups along medial margin: 1, 2, 3, 3; distal portion of medial margin produced into powerful lobe with microtuberculate integument and patch of short setules proximally. Basis slender, with three long setae along medial margin and sub-marginal row of spinules. Endopod 6-segmented; first segment somewhat reduced; setal formula: 2, 4, 4, 3, 3 + 1, 4; transverse row of coarse spinules on distal margin of segments 3 and 4; two rows of spinules on fifth.

Swimming legs (Figs 2C; 4B; 7) each retaining praecoxa and displaying 3-segmented exopod; endopod of first leg 1-segmented, that of second leg 2-segmented; those of third and fourth 3-segmented. Legs 1 and 4 somewhat reduced. Spine and seta formula as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	I-0	I-0; I-1; I,1,3	0,2,3
Leg 2	0-I	0-0	I-1; I-1; III,I,4	0-1; 1,2,2
Leg 3	0-I	0-0	I-1; I-1; III,I,4	0-1; 0-1; 1,2,2
Leg 4	0-I	0-0	I-1; I-1; III,I,4	0-I; 0-I; 1,2,2

Inner margin of first exopod segment of leg 1 swollen (Fig. 2C). Legs richly ornamented with denticles, spinules and setules, especially on posterior surfaces of segments except for coxa of leg 4, which lacks any ornamentation posteriorly.

Fifth legs (Fig. 8C) symmetrical, uniramous, very reduced. Legs 3-segmented, with two proximal segments unarmed, first fused to intercoxal sclerite. Distal segment about 1.7 times as long as wide, bearing two coarse, unequal bipinnate spines distally, innermost largest and incorporated basally to segment; additional coarse bipinnate spine sub-distally on outer margin.

Adult male. Body similar to female except for segmentation and armature of antennules and armature of fourth legs, morphology of fifth legs, and 5-segmented condition of urosome. Genital somite slightly asymmetrical, with single, left gonopore opening posterolaterally on ventral side. Right antennule 20-segmented (Fig. 3B); armature of segments as follows: segment 1 (ancestral segment I), 1 seta + aesthetasc; segment 2 (segments II-IV), 5 + 3 ae; segment 3 (V), 2 + ae; segment 4 (VI), 2 setae; segment 5 (VII), 2 + 2 ae; segment 6 (VIII), 1 seta; segment 7 (IX), 2 setae; segment 8 (X-XIV), 6 + 2 ae; segment 9 (XV), 1 seta; segment 10 (XVI), 1 + ae; segments 11 to 14 (XVII to XX), 1 seta each; segment 15 (XXI), 1 + ae; segment 16 (XXII-XXIII), with



Fig. 5. *Thompsonopia mediterranea* gen. et sp. nov., adult ♀. A, mandibular coxal gnathobase; B, mandibular palp; C, maxilla.

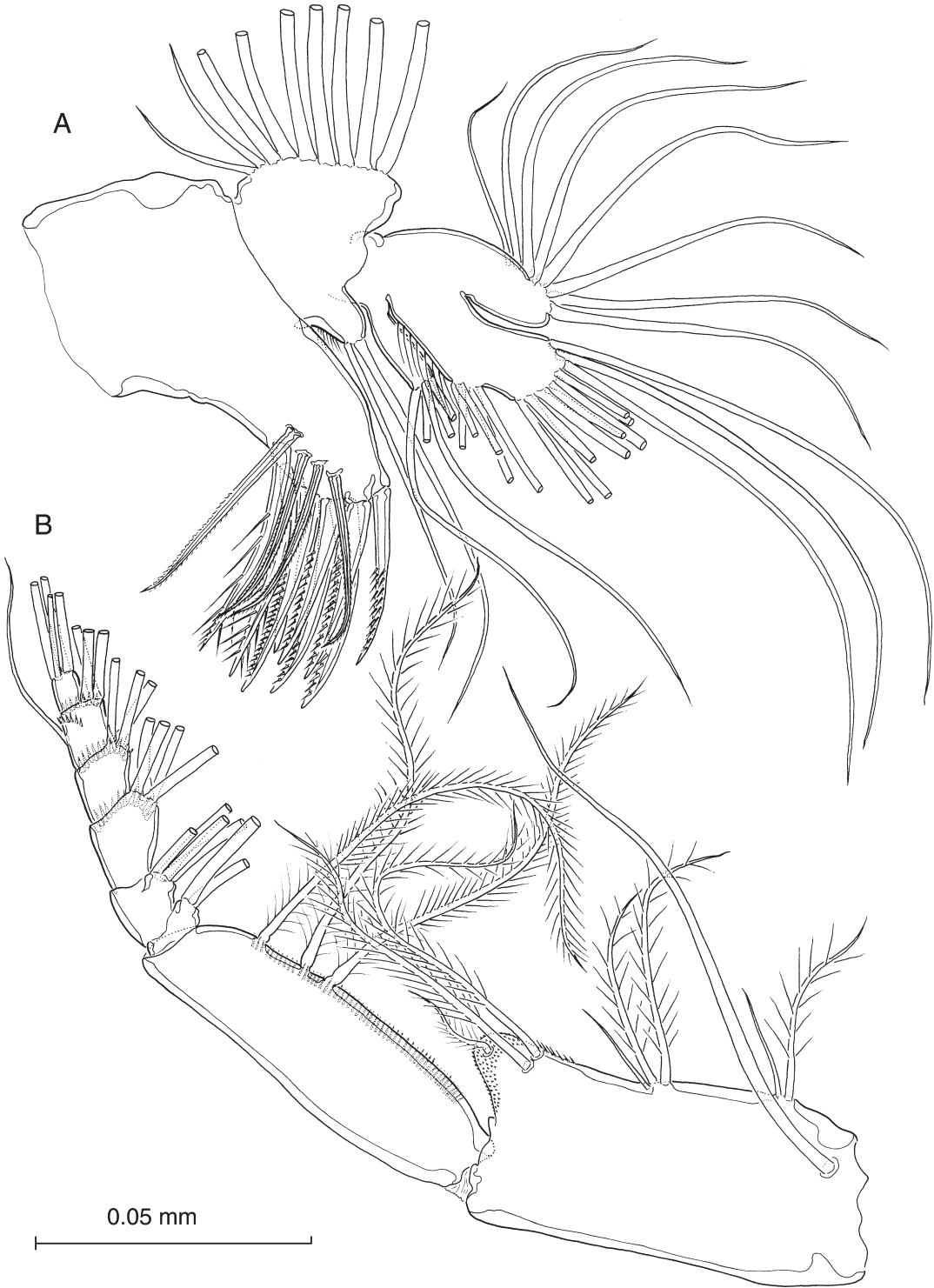


Fig. 6. *Thompsonopia mediterranea* gen. et sp. nov., adult ♀. A, maxillule; B, maxilliped, lateral.

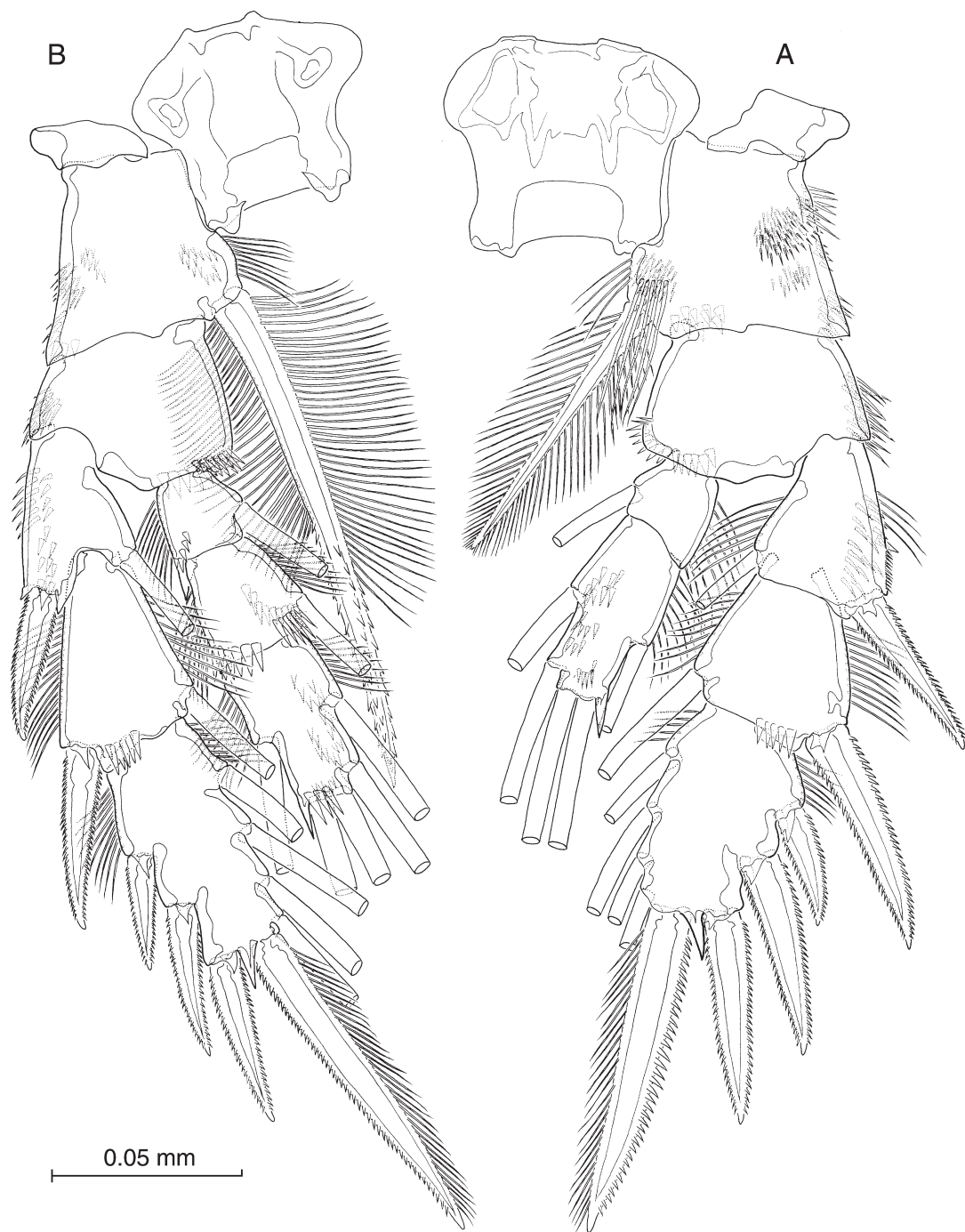


Fig. 7. *Thompsonopia mediterranea* gen. et sp. nov., adult ♀. A, second leg, anterior; B, third leg, anterior.

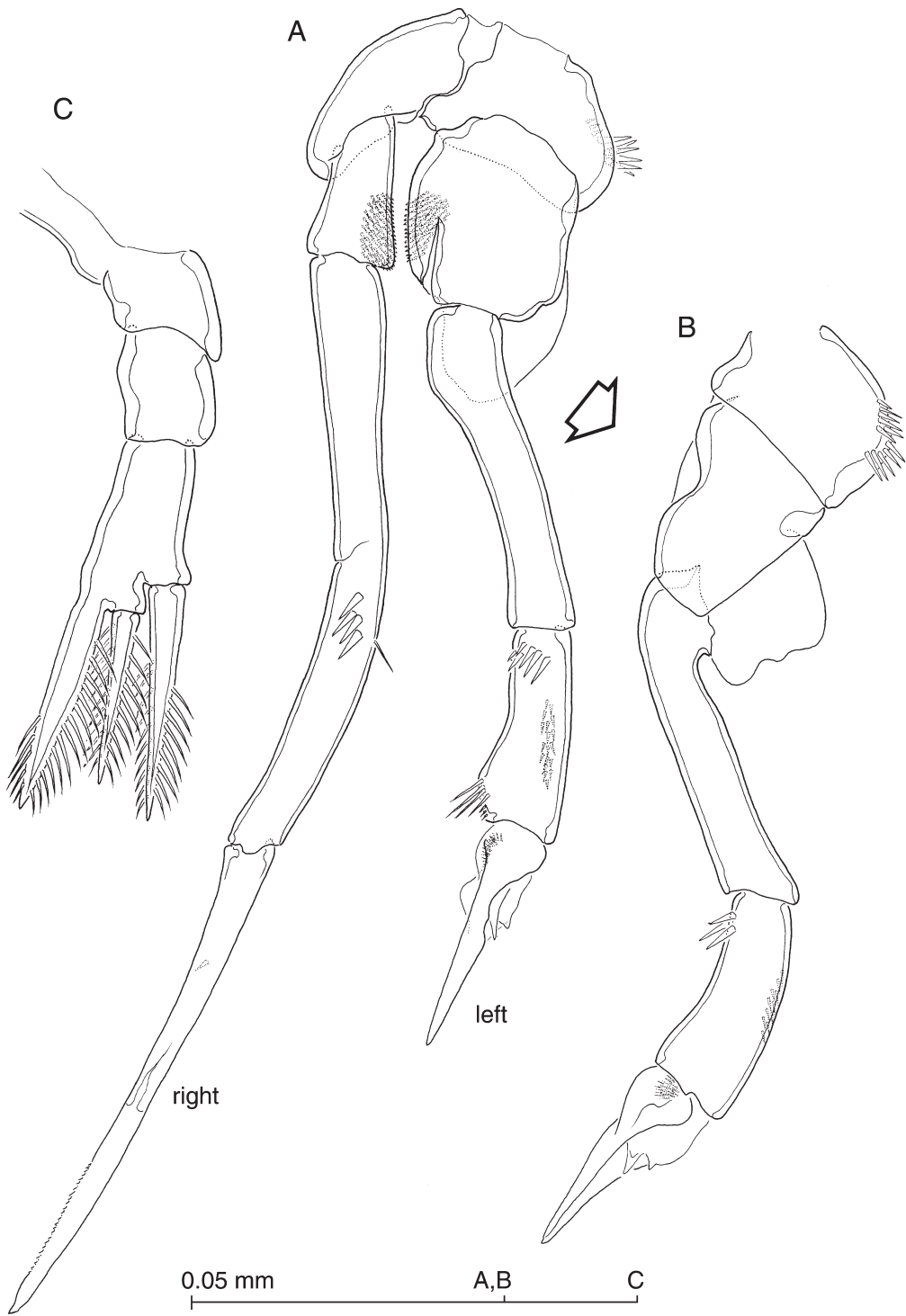


Fig. 8. *Thompsonopia mediterranea* gen. et sp. nov. A, adult ♂ fifth legs, anterior; B, detail of ♂ left leg, lateral; C, adult ♀ right fifth leg, posterior.



intersegmental articulation partially expressed), 2 setae; segments 17 to 19 (XXIV to XXVI), 2 setae each; segment 20 (XXVII-XXVIII), 5 + ae. One short sensilla on dorsal surface of each of first three segments.

Left antennule as for the right except for the complete failure to express, instead of partial, of the articulation between segments XXII and XXIII.

Swimming leg 4 as in female except for absence of inner coxal spine. Setal condition of armature elements on two proximal endopod segments unconfirmed.

Fifth legs (Fig. 8A, B) uniramous, asymmetrical, elongate. Coxae of both legs fused, although retaining transverse suture line; patch of stout spinules posterolaterally on left coxa. Right leg longest, with short and slender basis bearing patch of tiny spinules posteromedially; segments 3 and 4 partially fused, about same length, with patch of four stout, plus one more slender spinule; fifth segment longest, spiniform, with lateral margin serrate distally; tiny spinule on posterior surface of segment. Left leg with basis expanded posteriorly into rounded lobe and bearing patch of tiny spinules posteromedially. Third segment longest, reflexed proximally (see Fig. 8B); fourth expanded mediodistally, with three clusters of spinules; fifth segment tapering, with ridges and short digitiform process as figured; spinulose posteromedial lobe implanted proximally on segment.

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

Remarks. This new genus is erected to embrace the two previously known species of *Pseudocyclopia* exhibiting 20-segmented antennules, plus the new taxon described above. A common pattern of antennular segments resulting in compound segments II-IV and X-XIV is displayed in these taxa, as opposite to the condition exhibited in *Pseudocyclopia* of a single compound segment I-IX. In addition, the segmentation pattern is sexually dimorphic proximally in *Thompsonopia* gen. nov.: the males have the articulation between segments I and II completely expressed, whereas the females have segment I completely incorporated into the compound segment II-IV. The duplication of aesthetascs in the male antennule (segment VII) of *Thompsonopia* contrasts also with the condition exhibited in *Pseudocyclopia*, where none of antennular segments carries a quadrithek.

The condition of the sexual dimorphism affecting the fourth legs' armature differs also in both genera: the inner coxal spine is lacking in the males of both genera, but the setae on the two proximal segments of the endopod are transformed into stout spines in the female of *Thompsonopia* only; in *Pseudocyclopia* both sexes display unmodified setae in homologous positions. It has been suggested elsewhere that these spines could

be involved in scraping away empty spermatophores attached to the genital double-somite (Ohtsuka 1992).

The form of the rostrum is also different in both genera, being completely incorporated into the cephalosome in *Pseudocyclopia* but movable in *Thompsonopia*.

The new species can be easily distinguished from its two congeners by the morphology of the fifth legs of both sexes. Differences from *T. muranoi* from the Japanese Pacific coast include the condition of the outer distal spine on the terminal segment of the female fifth legs, which is completely articulated to segment (whereas it is incorporated basally into the segment in *T. muranoi*). In addition, the right male fifth leg displays the articulation between the third and fourth segments only partially expressed in *T. mediterranea*, with both segments elongate and uniformly slender. The condition is different in *T. muranoi*, where both segments are completely fused and are considerably shorter than their *T. mediterranea* counterparts; additionally, segment 3 is expanded proximally, whereas segment 4 is expanded distally.

Thompsonopia mediterranea differs from *T. stephoides* from the North Sea and the coasts of Mauritania in the absence of the spiniform processes on the inner margin of the two proximal segments of the female fifth legs. The right male fifth leg of the latter taxon has segments 3 and 4 completely fused, and segment 5 extremely elongate and bent; the right leg segment 4 is more elongate and constricted halfway compared to that of *T. mediterranea*.

The sexual dimorphism involving the expression of the articulation between segment I and compound segment II-IV in the males of the new genus deserves a comment here. Whereas this state is manifested in the new species and also in the population of *T. stephoides* described by Andronov (1986) from the coast of Mauritania, both Thompson (1895) and Sars (1901-1903) described the male antennules of *T. stephoides* as being similar to the female, except they did not figure them. Nevertheless, examination of material of this species from other Norwegian localities has demonstrated that the articulation is fully expressed in the males. The same is also possibly true for the males of *T. muranoi* since Ohtsuka (1992) did not figure the male antennules.

Genus *Pseudocyclopia* T. Scott, 1892 (emend.) (Fig. 9)

Material examined. Three new, not formally described, sympatric species collected off Lyroddane, Norway, with an Ockelmann epibenthic sledge (see Ockelmann 1964), 27-10 m depth. Species labelled sp. 1, sp. 2, and sp. 3 accordingly to their possession of 18, 17, and 16-

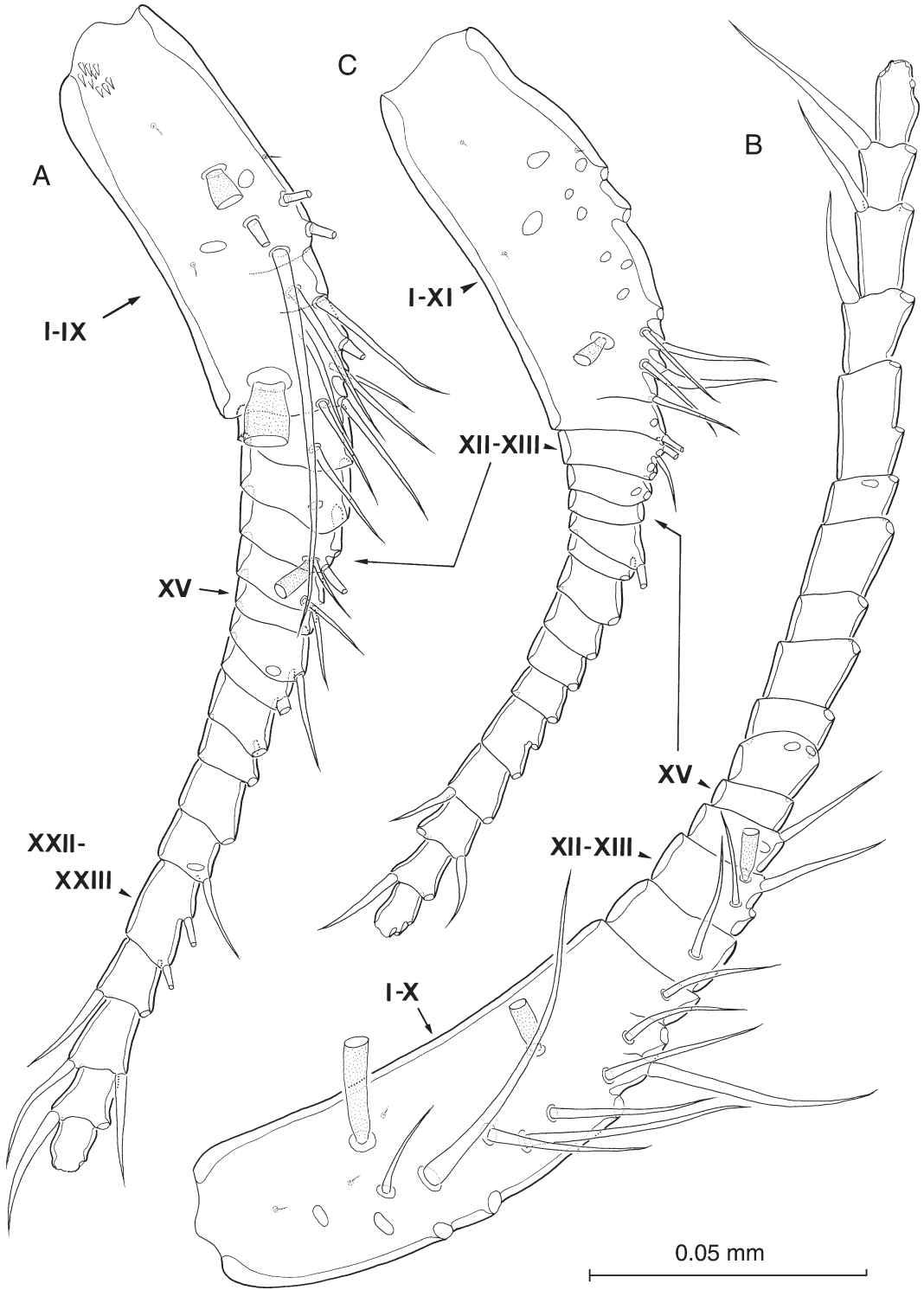


Fig. 9. *Pseudocyclopia* spp., adult ♂ antennules, medial. A, sp. 1; B, sp. 2; C, sp. 3.



segmented antennules in ♀♀, and 17, 16, and 15-segmented antennules in ♂♂, respectively. Material fairly damaged. Collected by A. Fosshagen, 7 April 1970.

Diagnosis. *Pseudocyclopiidae*. Rostrum completely incorporated into cephalosome, pointed, with two tiny terminal filaments. Female antennules with compound segments I-IX and XII-XIII resulting in 18-segmented condition, although most species with segment X, or segments X and XI, additionally incorporated into compound segment, resulting in 17 or 16-segmented condition. Male antennules symmetrical, with segmentation pattern identical to female except for additional compound segment XXII-XXIII, resulting in corresponding 17, 16 or 15-segmented conditions (Fig. 9A-C, respectively). Segment XV naked in both sexes. No duplication of aesthetascs on any segment of male antennules. First antennary endopod segment fully incorporated into basis. Maxillary endopod unsegmented. First leg without outer basal spine; endopod with five setae. First exopod segment of leg 3 frequently with accessory spine sub-marginally on posterior surface of segment, near to distal end of outer margin. Fourth legs of both sexes differing only in presence of inner basal spine in female and absence in male. Female fifth legs 3-segmented, uniramous, each ending in three points. Male fifth legs asymmetrical, uniramous, one leg with basis swollen laterally, other longer, filiform. Female genital double-somite symmetrical.

Type species. *P. crassicornis* T. Scott, 1892 (see Ohtsuka 1992).

Other species in the genus. *P. caudata* T. Scott, 1894; *P. giesbrechti* Wolfenden, 1902; *P. insignis* Andronov, 1986.

Remarks. *Pseudocyclopia minor* T. Scott, 1892 from the Firth of Forth, Scotland, does not fit into the diagnosis of the genus as presented. Even though it apparently exhibits a 17-segmented antennule, with a segmentation pattern similar to that of *Pseudocyclopia*, its other characters are very peculiar. For example, one of the male fifth legs (Scott (1892) did not state precisely which one) is biramous, the proximal compound segment of the antennule possesses a hook-like process, and the first legs display both an outer basal spine and only four setae on the endopod. The biramous condition of the male fifth leg is especially notable since all other pseudocyclopiids have uniramous legs. Unfortunately, Scott's (1892) description does not permit any refinement of the diagnosis, and he did not mention if the material was deposited at any museum. *P. minor* is treated here as species *incertae sedis* within the *Pseudocyclopiidae*.

Genus *Stygocyclopia* Jaume & Boxshall, 1995 (emend.)

Diagnosis. *Pseudocyclopiidae*. Rostrum fused to cephalosome, with two apical filaments. Antennules symmetrical in both sexes, 23-segmented in females, 22-segmented in males; compound segments I-IV and X-XI present in both sexes, XXII-XXIII in males; segment XII naked. Male antennules with quadritheke on segments III, V, VII and IX. First antennary endopod free, not incorporated into basis. Maxillary endopod 2-segmented. Endopod of first leg with five setae. First exopod segment of third leg without accessory spine. Fourth legs of both sexes similar, with or without inner coxal spine. Male fifth legs slender, uniramous, asymmetrical, each ending in two points; left longer than right, 5-segmented, not swollen proximally; right 3 or 4-segmented. Female fifth legs 3-segmented, uniramous, each ending in three points. Female genital double-somite symmetrical.

Stygocyclopia philippensis sp. nov.
(Figs 10-16)

Material examined. Calingoob Cave (Stn 85-067), located near village of Tangnan, 9°37'N, 123°47'E (Panglao Island, Philippines). Plankton net towed in 0.5 to 6 m water depths of the anchialine pool. Holotype: adult ♀ 0.57 mm [BMNH reg. no. 1998.2639]. Paratypes: 2 adult ♂♂, 2 adult ♀♀ and 5 copepodids [BMNH reg. nos. 1998.2640-2648]; one of adult ♀ paratypes partially dissected on two slides and mounted in lactophenol sealed with nail varnish. Collected by T. Iliffe, 6 April 1985.

Adult female. Eyes absent. Body (Fig. 10A, B) colourless, robust, 0.57 to 0.61 mm long, laterally compressed. Prosome about three times longer than urosome. Rostrum (Fig. 10C) short and tapering, directed ventrally, with pair of long and slender distal filaments. First pedigerous somite incorporated into cephalosome conforming cephalothorax. Dorsal fold of cuticular membrane, resembling posterior projection of cephalothorax, covering anterior dorsal half of second pedigerous somite. Second and third pedigerous somites with rounded lateral margins bearing row of sub-marginal setules along anterior half; margins of third somite with long and robust sensilla implanted sub-marginally in posterior half. Fourth and fifth pedigerous somites fused, symmetrical.

Urosome (Fig. 10D, E) 4-segmented. Surface of somites covered with both lamellar and ordinary long spinules; spinules easily lost when manipulation or examination, making it impossible to describe distribu-

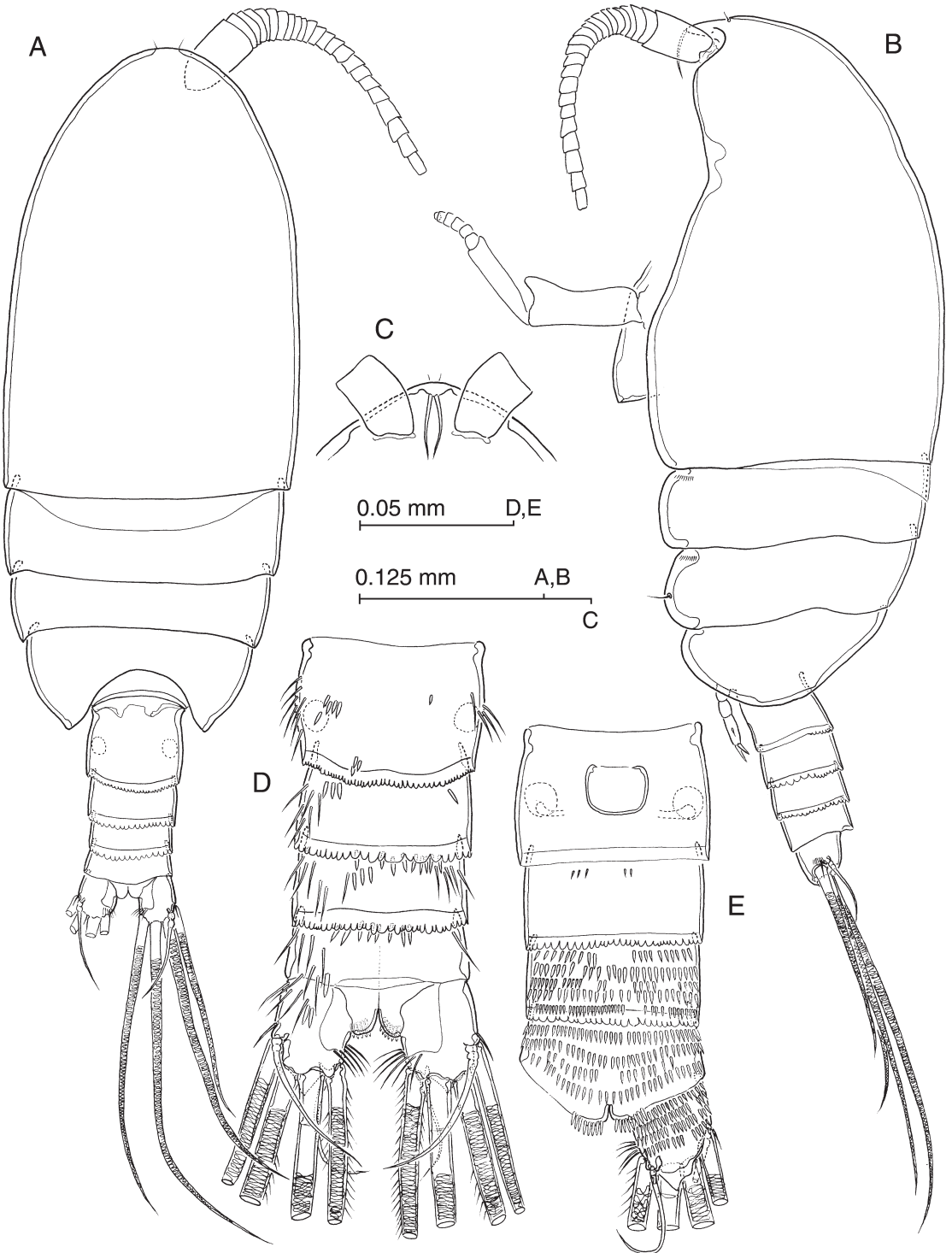


Fig. 10. *Stygocyclopia philippensis* sp. nov., adult ♀. A, habitus, dorsal; B, lateral; C, rostrum, ventral; D, urosome, dorsal; E, same, ventral.



tion pattern precisely. Genital double-somite symmetrical, with faint, lobate hyaline frill around dorsal rear margin; smooth hyaline frill around ventral rear margin. Ovoid seminal receptacle on each side of somite, communicating to single gonopore opening ventrally; operculum quadrangular. Anal somite with smooth operculum. Caudal rami symmetrical, short, about as long as wide, armed with seven setae and with transverse row of long setules midway along medial margin; setae III to VI implanted distally, I, II and VII subdistally; setae III to VI thick, with internal tissue finely corrugated; seta I very much reduced. Rear margin of rami with broad, triangular projections ventrally.

Antennules (Fig. 11B) short, symmetrical, 23-segmented, directed ventrally, not reaching distal end of cephalothorax. First segment largest, representing ancestral segments I to IV. Other compound segments, X-XI and XXVII-XXVIII. Armature elements as follows: segment 1, 6 setae + aesthetasc; segment 2 (corresponding to ancestral segment V), 2 setae; segment 3 (VI), 2 setae; segment 4 (VII), 2 + ae; segment 5 (VIII), 1 seta; segment 6 (IX), 2 setae; segment 7 (X-XI), 3 + ae; segment 8 (XII), naked; segment 9 (XIII), 1 seta; segment 10 (XIV), 2 setae; segment 11 (XV), 1 seta; segment 12 (XVI), 1 + ae; segments 13 to 16 (XVII to XX), 1 seta each; segment 17 (XXI), 1 + ae; segments 18 and 19 (XXII and XXIII), 1 seta each; segments 20 to 22 (XXIV to XXVI), 2 setae each; segment 23 (XXVII-XXVIII), 6 + ae. Two sensillae on dorsal surface of first segment; one sensilla on second segment.

Antenna (Fig. 12A) biramous. Coxa with distal seta and patch of coarse spinules along inner margin. Basis with two distal setae on inner margin. Endopod longer than exopod, 2-segmented, with proximal segment completely separate from basis, elongate, bearing two unequal setae at two-thirds of distance along inner margin and short row of tiny spinules proximally; distal segment short, bilobed; inner lobe (representing ancestral segment II) with 9 setae; outer lobe (ancestral segments III and IV) with 7 distal setae and two combs of spinules. Exopod 7-segmented; segment 2 representing ancestral segments II-IV; segment 7 representing segments IX-X, with intersegmental articulation partially expressed; setal formula: 1, 3, 1, 1, 1, 1, 1 (1 + 3).

Mandible coxal gnathobase (not figured) heavily constructed, short, with cutting blade bearing sharp denticles. Mandibular palp (Fig. 12B) with basis expanded, bearing three setae and two patches of spinules. Endopod shorter than exopod, 2-segmented, first segment bearing one seta; second with 11 distal setae, three of them reduced, and comb of spinules. Exopod apparently 4-segmented, but close analysis revealing only partial expression of articulation between proximal segment - rather spirally configured - and second segment,

resulting in actual 3-segmented condition; setal formula (1 + 1), 1, 3; distal segment derived from ancestral segments IV and V.

Maxillule (Fig. 12C) with segmentation not clearly defined; praecoxal arthrite with ten stout spines plus four setae; coxal epipodite with six long and one reduced setae; coxal endite with two setae on tip; proximal basal endite discrete, with four distal setae; distal endite incorporated into segment, bearing five marginal setae and row of sub-marginal spinules; endopod fully incorporated into basis forming lobe with 12 long, distal setae; exopod discrete, with row of seven long and one reduced marginal setae.

Maxilla (Fig. 12D, E) comprising syncoxa, basis, and 2-segmented endopod. Proximal syncoxal endite with five long and one short marginal setae; remaining syncoxal endites each armed with three setae, one of them shorter, and sub-marginal row of spinules; soft process of uncertain homology between praecoxal endites. Basal endite with four setae distally, one of them very thick and denticulated. Endopod short, about half length of basal endite, 2-segmented, with setal formula: 4, 3.

Maxilliped (Fig. 13A) powerfully developed, 8-segmented, reflexed distally. Syncoxa with nine setae distributed in four groups along medial margin: 1, 2, 3, 3; distal portion of medial margin produced into powerful lobe; lobe integument with two microtuberculate patches and row of short setules. Basis about as long as syncoxa, slender, with three long setae along medial margin and sub-marginal row of coarse spinules. Endopod 6-segmented; small first endopodal segment defined medially but not apparent laterally; setal formula: 2, 4, 4, 3, 3 + 1, 4; transverse row of coarse spinules on distal margins of third and fourth segments; row of slender spinules along distal margin of fifth.

Swimming legs (Figs 13B; 14; 15) increasing progressively in size from 1 to 4, each with 3-segmented exopod; praecoxa present on each leg. Endopod of first leg 1-segmented, that of second leg 2-segmented; those of third and fourth legs 3-segmented. Spine and seta formula as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	0-0	I-0; I-1; I,1,3	0,2,3
Leg 2	0-1	0-0	I-1; I-1; III,1,4	0-1; 1,2,2
Leg 3	0-1	0-0	I-1; I-1; III,1,4	0-1; 0-1; 1,2,2
Leg 4	0-0	0-0	I-1; I-1; III,1,4	0-1; 0-1; 1,2,2

Endopod of leg 1 (Fig. 13B) with cluster of coarse spinules about midway of lateral margin, plus three groups of slender spinules; medial margin of first exopod segment swollen. Inner spine on coxae of legs 2 and 3 (Fig. 14A, B) stout and straight; that of leg 3

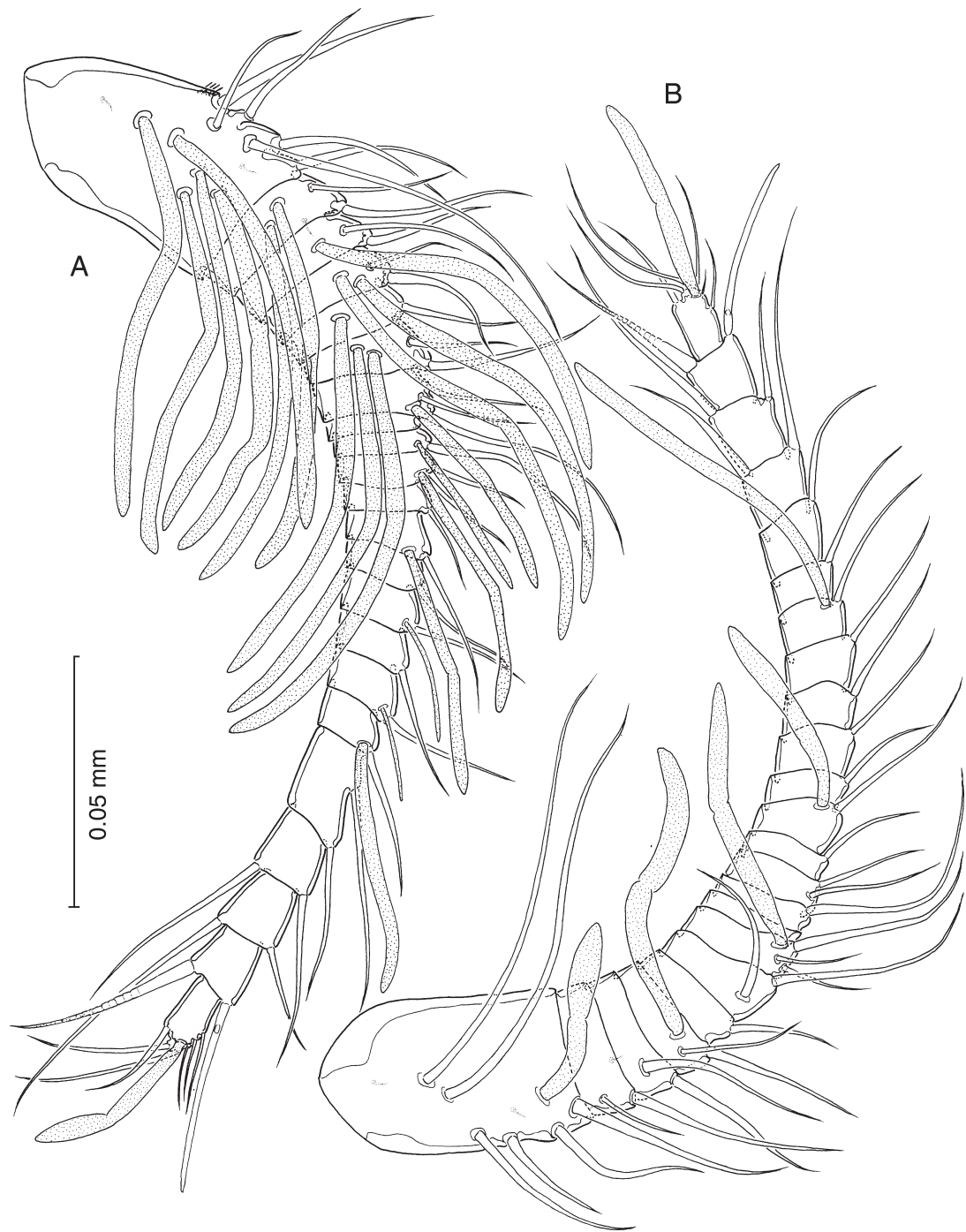


Fig. 11. *Stygocyclopia philippensis* sp. nov. A, adult ♂ antennule, ventral; B, adult ♀ antennule, ventral.

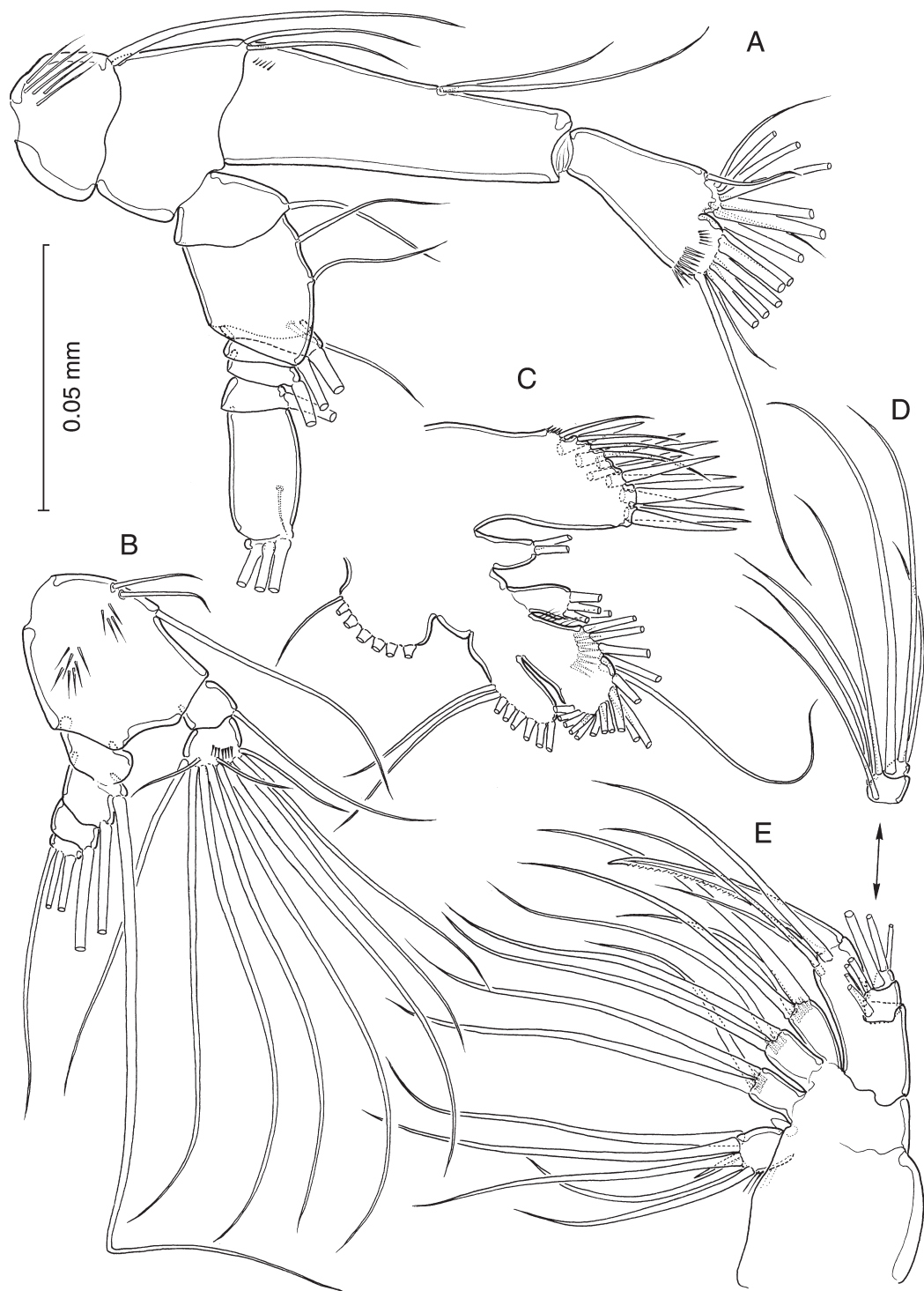


Fig. 12. *Stygocyclopia philippensis* sp. nov., adult ♀. A, antenna; B, mandibular palp; C, maxillule (ornamentation of spines on praecoxal arthrite omitted); D-E, maxilla.

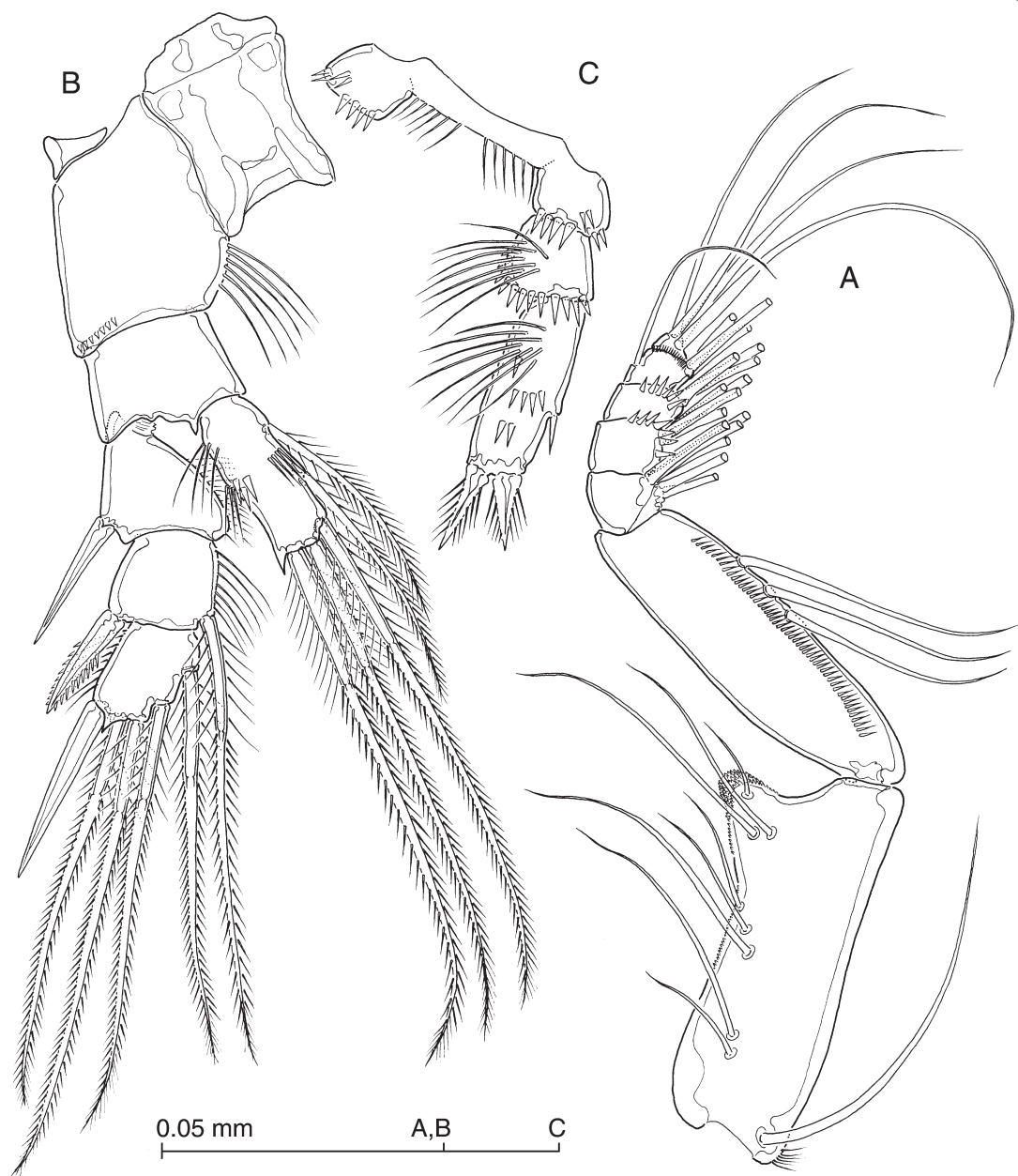


Fig. 13. *Stygocyclopia philippensis* sp. nov., adult ♀. A, maxilliped; B, first leg, anterior; C, fifth leg, posterior.

especially developed, but not extending beyond tip of endopod. Legs richly ornamented with denticles, spinules and setules, especially on posterior side of leg 4 (Fig. 15B).

Fifth legs (Fig. 13C) symmetrical, uniramous, reduced, 3-segmented, with proximal segment fused to

intercoxal sclerite; distal segment elongate, 2.4 times as long as wide, bearing two coarse, bipinnate spines distally plus one smooth, reduced spine at two thirds of distance along outer margin. All segments, plus intercoxal sclerite, richly ornamented with setules and spinules.

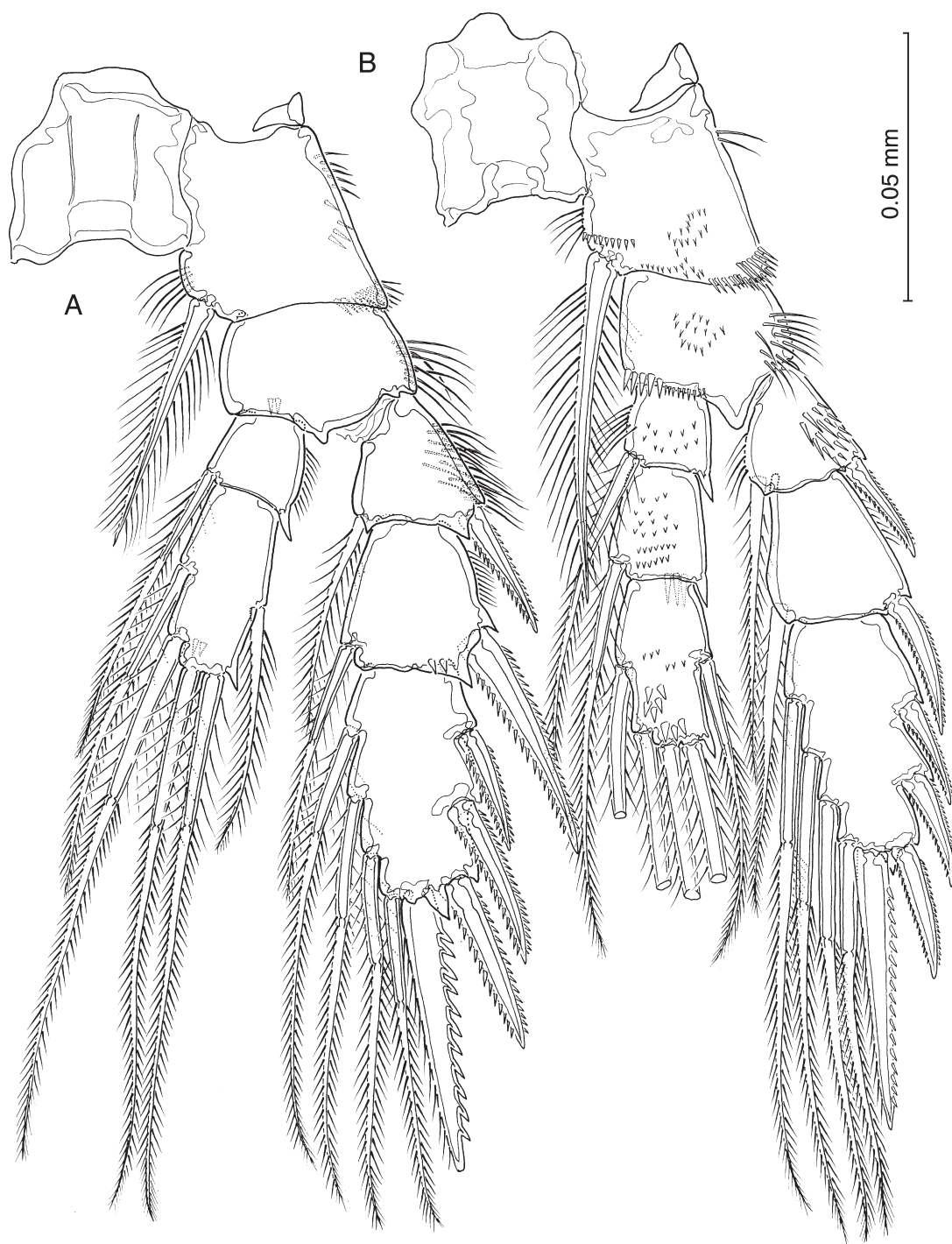


Fig. 14. *Stygocyclopia philippensis* sp. nov., adult ♀. A, second leg, anterior; B, third leg, anterior.

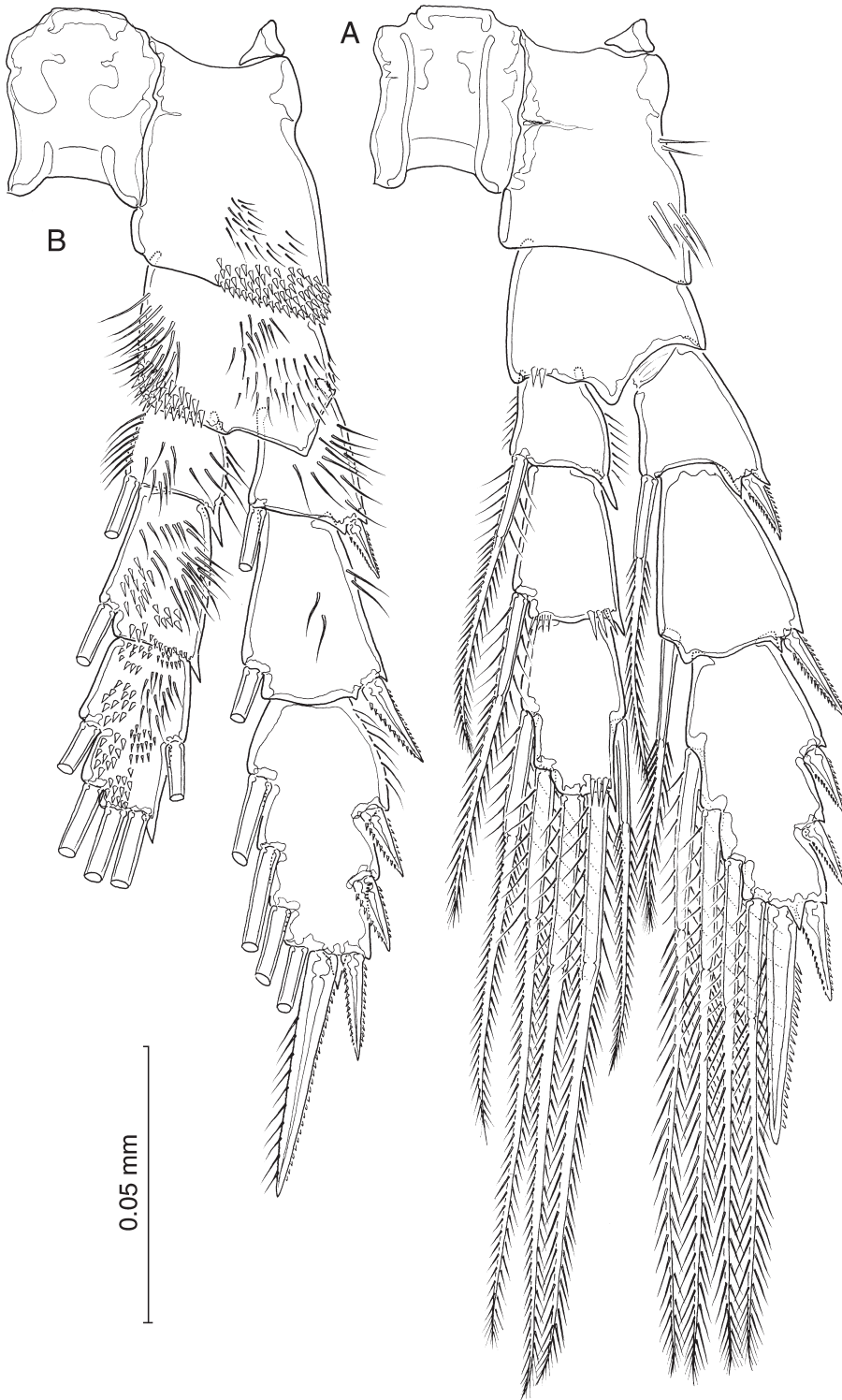


Fig. 15. *Stygocyclopia philippensis* sp. nov., adult ♀. A, fourth leg, anterior; B, same, posterior.

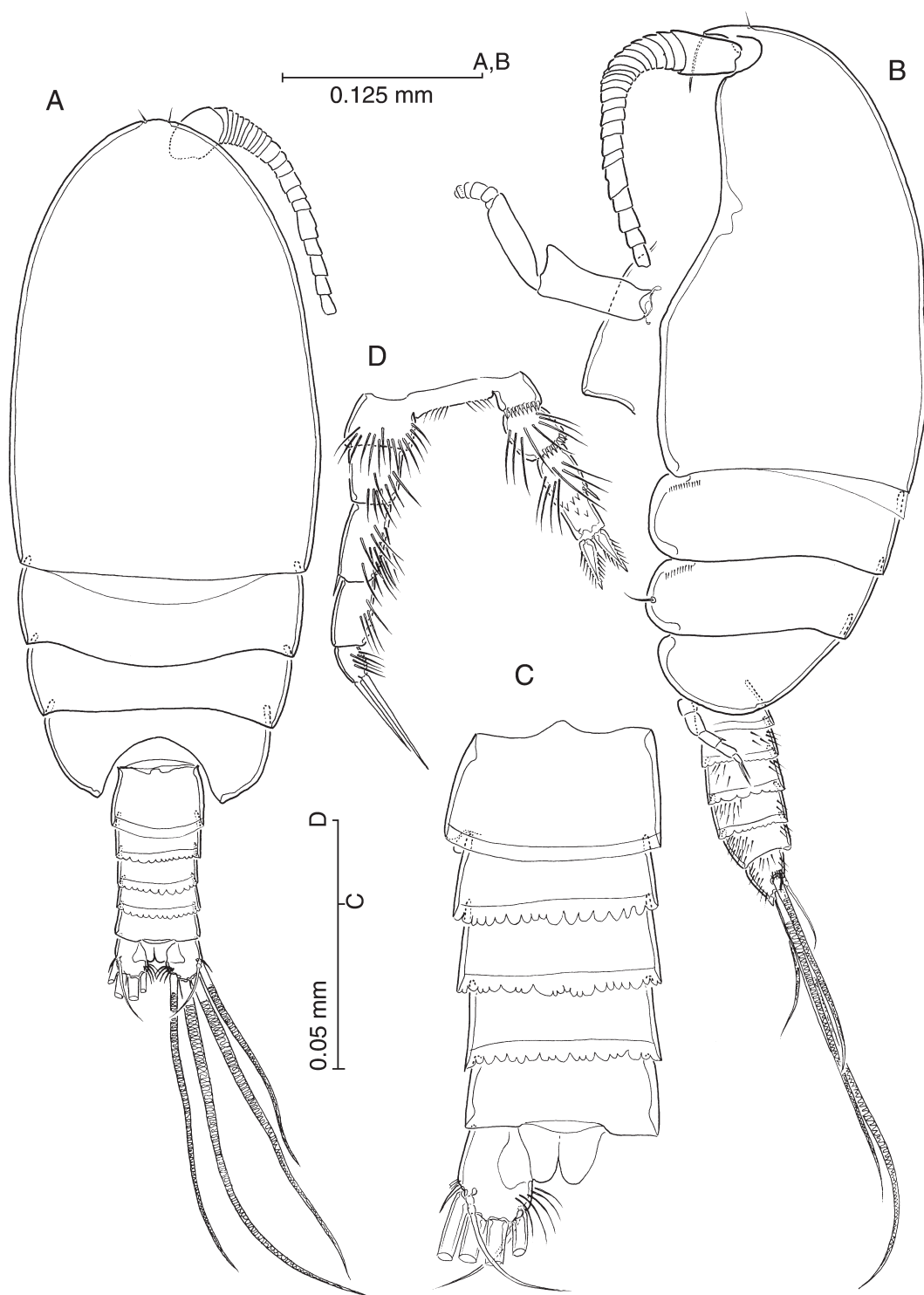


Fig. 16. *Stygocyclopia philippensis* sp. nov., adult ♂. A, habitus, dorsal; B, lateral; C, urosome, dorsal; D, fifth legs, posterior.



Adult male. Body (Fig. 16A, B) 0.52 to 0.55 mm long, similar to female except for antennules, urosome segmentation and fifth legs.

Urosome (Fig. 16C) 5-segmented, with genital somite asymmetrical, slightly produced and extended posteriorly on left side. Single gonopore opening ventrolaterally on left side close to posterior margin of somite.

Antennules (Fig. 11A) symmetrical, 22-segmented; segmentation pattern as in female, with additional compound segment involving ancestral segments XXII and XXIII. Armature as follows: segment 1 (corresponding to ancestral segments I to IV), 6 setae + 5 aesthetascs; segment 2 (V), 2 + 2 ae; segment 3 (VI), 2 + ae; segment 4 (VII), 2 + 2 ae; segment 5 (VIII), 1 + ae; segment 6 (IX), 2 + 2 ae; segment 7 (X-XI), 3 + ae; segment 8 (XII), naked; segment 9 (XIII), 1 + ae; segment 10 (XIV), 2 + ae; segment 11 (XV), 1 seta; segment 12 (XVI), 1 + ae; segment 13 (XVII), 1 seta; segment 14 (XVIII), 1 + ae; segment 15 (XIX), 1 seta; segments 16 and 17 (XX and XXI), 1 + ae each; segment 18 (XXII-XXIII), 2 setae; segments 19 to 21 (XXIV, XXV and XXVI), 2 setae each; segment 22 (XXVII-XXVIII), 6 + ae. Two sensillae on dorsal surface of first segment; one sensilla on second segment.

Fifth legs (Fig. 16D) asymmetrical, uniramous, slender. Left longer than right, 5-segmented, with proximal segment completely fused to intercoxal sclerite; segment 3 with tiny distal spine on outer margin; segment 5 with two long and slender distal spines, inner longest; both spines more than twice length of segment. Right leg exactly as in female. Both legs and intercoxal sclerite richly ornamented with setules and spinules.

Etymology. Species name derived from its type locality, the Philippines.

Remarks. This new Philippine taxon displays very similar segmentation and armature patterns of its appendages to those of *Stygocyclopia*. The similarities are sufficient to justify its accommodation in this genus. Apparent differences, such as the 23-segmented condition of the female antennule compared to only 22-segmented in *S. balearica*, the presence of nine setae on the inner lobe of the distal endopod segment of the antenna (only seven in *S. balearica*), the presence of seven setae on the coxal epipodite, and of 12 on the endopod of maxillule (6 and 11, respectively, in *S. balearica*), the presence of four setae on the proximal endopod segment and of six on the proximal syncoxal endite of maxilla (only 3 and 5, respectively, in *S. balearica*), and the armature of the second endopod segment of maxilliped (four setae rather than only three in *S. balearica*) are largely the result of inaccuracy in the original description of the latter taxon by Jaume &

Boxshall (1995). The segmentation of the mandibular exopod in *S. balearica* is reinterpreted here as 3-segmented as in *S. philippensis*, rather than 4-segmented.

Stygocyclopia philippensis can be readily distinguished from *S. balearica* by the structure of the fifth legs of both sexes, and by the absence in the former of the outer basal spine on leg 1 and the inner coxal spine on leg 4. The latter character state has proved to be sexually dimorphic in other pseudocyclopiids (see above).

The female fifth legs differ mainly in the reduction, loss of ornamentation, and more proximal positioning of the outer spine on the distal segment in *S. philippensis* compared to *S. balearica*.

The male fifth legs retain the same condition for the left leg in both taxa, although the two distal spines articulate with segment and are considerably longer in *S. philippensis* than in *S. balearica*. The right leg of *S. philippensis* is noteworthy in retaining the same appearance than the female fifth leg, whereas in *S. balearica* this leg is considerably modified: it is 4-segmented, with the two distal segments corresponding to the distal segment of *S. philippensis*, as can be deduced from the location of their armature elements; the latter on distal segment differ also in being non-articulated and smooth in *S. balearica*. These differences in the right leg could be indicative of a different generic status for the Philippine taxon, but we tentatively include it in *Stygocyclopia* pending the discovery of further new species that will help us to interpret the significance of these features.

Among other less conspicuous differences between them could be mentioned the absence in *S. philippensis* of the brush-like tips of the swimming legs setae displayed in *S. balearica*. Additionally, the first antennular segment of the female of *S. philippensis* lacks the two tiny setae present in *S. balearica*, thus resulting in an armature of only 6 setae + aesthetasc (compared with 8 + ae in *S. balearica*).

Stygocyclopia balearica Jaume & Boxshall, 1995

Paracyclopia gitana Carola & Razouls, 1996

Material examined. Lanzarote, Canary Islands. Jameos del Agua: adult ♂ and adult ♀ [BMNH reg. nos. 1998.2649-2650]. Collected by H. Wilkens, 2 March 1985. - Túnel de la Atlántida: gravel bottom in 8 m depth of entrance pool (Stn 5.92-024); Salinity: 37 psu. Adult ♂, adult ♀ and copepodid [BMNH reg. nos. 1998.2651-2653]. Water in 5-10 m depths in upper level (Stn 6.92-025). Adult ♂ [BMNH reg. no. 1998.2654]. Both samples collected by T. Iliffe, 25 July 1992. Upper level passages at 0-10 m depths (Stn 7.94-029);

Salinity: 35 psu. Two adult ♂♂ [BMNH reg. nos. 1998.2655-2656]. Collected by T. Iliffe, 4 June 1994. - Cueva de los Lagos: water column in 0-1 m depth (Stn 8, 94-034); Salinity: 35 psu. Adult ♀ [BMNH reg. no. 1998.2657]. Collected by T. Iliffe, 9 June 1994. - Well in salt-work ("salinas") on the east coast of Lanzarote: adult ♂ and adult ♀ [BMNH reg. nos. 1998.2658-2659]. Collected by H. Wilkens, 3 February 1986.

Comparative material examined. *Stygocyclopia balearica* Jaume & Boxshall, 1995. Mallorca, Balearic Islands. Holotype ♂ [MNCM. 253]; allotype ♀ [MNCM. 254]; 1 ♂ and 8 ♀♀ paratypes [MNCM. 255]; 4 ♀♀ [MNCM. 256]; 1 ♂ and 2 ♀♀ [BMNH reg. nos. 1995.18-20]; 1 ♂ [MNCM. 258]; 2 ♀♀ [MNCM. 259]; 10 ♂♂ and 7 ♀♀ [BMNH reg. nos. 1996. 1038-1047]; 2 ♀♀ [MNCM. 331]. - *Paracyclopia naessi* Fosshagen (in Fosshagen & Iliffe 1985). Devonshire Cave, Bermuda. Five adult ♀♀ and 1 ♂ copepodid [BMNH reg. nos. 1995.21-26].

This taxon has been collected in Lanzarote both in a lava tube flooded by the sea and in a well connected to the crevicular marine environment. Comparison with the type material has demonstrated that the Canarian material belongs to *S. balearica*. The comparative study has also revealed several character states which were incorrectly determined in the original description of the species by Jaume & Boxshall (1995). The number of segments of the female antennule was found to be variable: the failure to express of the articulation between ancestral segments XXII and XXIII is constant in males but not so in females. Only three (including the allotype and one paratype) out of 33 Balearic females examined for this character displayed failure to express this articulation, the remaining females displayed a 23-segmented condition. This is the condition displayed by all Canarian females examined. Another trait to be emended in both sexes from the original description concerns the nature of the armature element on the anteroventral margin of the penultimate segment of the antennule. This element was shown as an ordinary seta, but its appearance is intermediate between a seta and an aesthetasc, as represented for *S. philippensis* in Fig. 11.

The mandibular exopod, represented as 4-segmented with setal formula 1, 1, 1, 3 in the original description, is reinterpreted as 3-segmented with formula (1 + 1), 1, 3, exactly as for *S. philippensis* (Fig. 12B).

Other inaccuracies of the original description involve counts of setae on segments of the antenna, maxillule, maxilla and maxilliped; they have been consequently commented on and emended above (see remarks for *S. philippensis*).

Finally we want to comment on two integumental features: 1. The paired patches of tiny setules described as located on the lateral surfaces of the fifth pedigerous somite in the original description, are actually positioned on the inner surface at both sides of somite. 2. The urosomal somites are adorned with lamellar spinules, as in *S. philippensis*, although they are easily lost when manipulating individuals.

Remarks. *Paracyclopia gitana* Carola & Razouls, 1996, was described on the basis of two males collected in a littoral cave on Menorca, Balearic Islands (Carola & Razouls 1996). According to the figures presented by these authors, it exhibits several odd features unknown in the rest of pseudocyclopiids, although it is probable that the characters involved were not correctly resolved in the description. Thus, only five setae are present on the caudal rami (versus 6-7 setae in the remaining taxa), the maxillary endopod is 3-segmented (1 or 2-segmented in the other taxa), and the maxillipedal endopod is 4-segmented (5-segmented in other taxa). In addition, the first pedigerous somite is completely separate from the cephalosome in the individual figured, whereas this somite is incorporated into the cephalothorax in the moult from copepodid V to the adult in the rest of pseudocyclopiids (Jaume, pers. obs.). On the other hand, both *Paracyclopia* and *Stygocyclopia* display the antennular ancestral segment XII naked, whereas all antennular segments of the Menorcan taxon carry setae. These observations cast doubts on the correct assignation of the Menorcan taxon made by Carola & Razouls (1996).

The antennular ancestral segment I of the putative *Paracyclopia* from Menorca is completely incorporated to the compound segment II-IV (as it is in *Stygocyclopia*), whereas in *Paracyclopia naessi* both segments are separate. On the basis of the identical segmentation and armature of legs 1-5 (with the exception of the putative absence of the tiny outer basal seta of leg 1 in the Menorcan taxon), the identical relative lengths of spines on legs, and the incorporation of ancestral segment I to compound segment II-IV of the antennule, *Paracyclopia gitana* is considered here as a junior synonym of *Stygocyclopia balearica*. It should be mentioned that Menorca and Mallorca (the type locality of *S. balearica*) are separated by a narrow canal only 36 km wide and 80 m deep, and that both islands were merged in rather recent times (about 18 000 yr BP), during the last Quaternary glaciation.

Swimming habits. Observations carried out on specimens from Mallorcan caves have demonstrated that *Stygocyclopia* moves just above the bottom in the same way as described for *Thompsonopia* and *Paracyclopia*



(see Ohtsuka 1992 and Fosshagen & Iliffe 1985): swimming continuously by beating the antennae and with the ventral side of the body along the bottom.

Distribution. *Stygocyclopia balearica* was originally described from anchialine caves of the Balearics and has never been reported from either littoral or submarine caves (sensu Stock & al. 1986). This could be indicative of a very localised distribution, precluding consideration of its presence in the anchialine environment as only an opportunistic landward extension from a marine hyperbenthic habitat - an explanation that is probably appropriate for the presence of *Thompsonopia mediterranea* in littoral caves.

The discovery of *S. balearica* in anchialine environments of Lanzarote (Canary Islands) is amazing in light of this. The Canaries and the western Mediterranean islands share common, cave-dwelling marine genera exhibiting globally very localised, relictual distributions, but they are represented by vicariant species at each site. For example, the superornatiremid harpacticoid genus *Neoechinophora* Huys, the misophrioids *Expansophria* Boxshall & Iliffe, and *Speleophriopsis* Jaume & Boxshall, or the ridgewayiid calanoid *Exumella* Fosshagen (Jaume 1997; Jaume & Boxshall 1996a; Jaume, Fosshagen and Iliffe, pers. obs.). This could be interpreted as indicating that isolation and time have permitted differentiation of both clusters of taxa at the species level. If *S. balearica* dwells exclusively in the essentially discontinuous, anchialine environment, it is difficult to explain why the Balearic and Canarian populations have not differentiated. Jaume & Boxshall (1996b) confronted the same problem after the discovery of the monotypic anchialine cyclopinid *Muceddina multispinosa* in caves of Sardinia, the Balearics and

Lanzarote. They then postulated that the lack of morphological differentiation might indicate that this taxon is more widely distributed (and less isolated) than reported, or its morphology is highly conservative over evolutionary time. The latter could be the case also for *Stygocyclopia balearica*.

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