A new genus and species of deep-sea cyclopoid (Crustacea, Copepoda, Cyclopinidae) from the Mid-Atlantic Ridge (Azores Triple Junction, Lucky Strike)

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ABSTRACT

Heptnerina confusa n. gen., n. sp. (Copepoda, Cyclopoida, Cyclopinidae) was gathered during *in situ* colonization experiments at the Mid-Atlantic Ridge (37°N), at a depth of 1698 m. The new genus is close to the heterogeneous genus *Cyclopina* Claus, 1863 and differs from the type species *Cyclopina gracilis* Claus, 1863 in the antenna, which has two exopodal setae, and in other details. The affinities of the new genus with the cyclopinids *Troglocyclopina balearica* Jaume & Boxshall, 1997 and *Cyclopina esilis* Brian, 1938 are also discussed. The detailed description reveals several primitive characters, such as the separate praecoxa and coxa of the maxilliped. One of four setae of one-segmented exopod of maxillule is shorter and armed with setules on tip. The presence of setae on the paragnaths is a new discovery for Cyclopinidae. The small internal segment of leg 5 is considered to represent the endopod and is interpreted as a reversal in the Cyclopoida.

KEY WORDS
Crustacea,
Copepoda,
Cyclopinidae,
Heptnerina confusa n. gen., n. sp.,
deep-sea hydrothermal vents,
Atlantic Ocean,
new genus,
new species.

RÉSUMÉ

Un nouveau genre et une nouvelle espèce de cyclopoïde des eaux profondes (Crustacea, Copepoda, Cyclopinidae) de la ride Médio-Atlantique (Azores Triple Junction, Lucky Strike).

Heptnerina confusa n. gen., n. sp. (Copepoda, Cyclopoida, Cyclopinidae) a été collecté au niveau de la ride Médio-Atlantique (37°N) à une profondeur de 1698 m lors d'expériences de colonisation *in situ*. Le nouveau genre est proche du genre hétérogène *Cyclopina* Claus, 1863 et diffère de l'espèce type *Cyclopina gracilis* Claus, 1863, principalement par l'exopodite de la P5 mâle muni de deux soies internes et par l'antenne portant deux soies exopodales. Ses affinités avec *Troglocyclopina balearica* Jaume & Boxshall, 1997 (Cyclopinidae) et *Cyclopina esilis* Brian, 1938 sont aussi discutées. La description détaillée révèle la présence de caractères primitifs, tels que les précoxa et coxa séparés sur le maxillipède. La structure de P5 montrant un petit segment, considéré comme un endopodite, est unique chez les Cyclopoida et pourrait être interprétée comme une réversion. La présence de spinules sur les paragnathes est aussi une nouvelle découverte pour les Cyclopinidae.

INTRODUCTION

Copepods are the most species-rich and abundant invertebrates recorded from deep-sea hydrothermal vents and seeps (Desbruyères & Segonzac 1997; Tsurumi & Tunnicliffe 2001; Gebruk 2002). At present, the list of these copepods, all reported from the Pacific and Atlantic oceans, includes 81 species (37 genera, 20 families, six orders); but only a few studies of their biology, functional morphology, and evolution have been conducted (Humes & Segonzac 1998; Heptner & Ivanenko 2002; Tsurumi *et al.* 2003). The largest and most widespread family of deep-sea hydrothermal vent copepods (and invertebrates) is the siphonostomatoid family Dirivultidae Humes & Dojiri, 1980 (52 species, 13 genera) known only from hydrothermal systems (Ivanenko & Ferrari 2003).

Copepods of the family Cyclopinidae Sars, 1913 are known from shallow marine and brackish waters and are found in anchihaline caves and in the hyperbenthos of the deep-sea (Jaume & Boxshall 1996a, b, 1997; Martínez Arbizu 1997a, 2000b). However, only one cyclopinid (*Barathricola rimensis* Humes, 1999) has been described from the hydrothermal vents (Humes 1999).

This paper describes *Heptnerina confusa* n. gen., n. sp., as the first record of cyclopinids in the Mid-Atlantic Ridge. The copepods of a new genus and species were found among many undescribed copepods of the orders Calanoida, Cyclopoida, Harpacticoida, Poecilostomatoida, Misophrioida and Siphonostomatoida in trays with artificial substratum left on the sea floor during *in situ* colonization experiments (Azores Triple Junction, Lucky Strike). The copepods collected by this method represent epibenthic and sedimentary forms and are rarely collected in the deep-sea by other methods.

MATERIAL AND METHODS

The copepods were collected together with other invertebrates on an artificial substratum consisting of small glass globules lacking (in this case) organic supply. The specially designed trays (SMAC) with the substratum, protected from larger carnivorous animals, were placed by the submersible *Nautile* at the base of the active

chimney "Eiffel Tower" covered by a layer of *Bathymodiolus azoricus* (Bivalvia, Mytilidae) at temperatures ranging from 5 to 10-13°C and left for 322 days (M. Segonzac pers. comm.).

The specimens were cleared in lactic acid, stained by addition of a solution of chlorazol black E, and examined with bright-field or differential interference optics. All measurements and dissections were made in lactic acid. Drawings were made with a camera lucida on a Leica DMLB compound microscope.

SYSTEMATICS

Order CYCLOPOIDA Burmeister, 1934
Family CYCLOPINIDAE Sars, 1913

Genus *Heptnerina* n. gen.

TYPE SPECIES. — *Heptnerina confusa* n. sp.

ETYMOLOGY. — The new generic name derives from the family name of the marine biologist Mikhail V. Heptner (1940-2002), collaborator and teacher of the first author.

DIAGNOSIS. — First pedigerous somite free, concealed laterally beneath posterior outgrowth of cephalosome. Paragnath armed with four setae. Caudal ramus with seven setae, seta I short. Antennule of female 10-segmented, with subdivided third, fourth and fifth segments; antennule of male 17-segmented. Antenna with two long exopodal setae. Mandibular palp with two-segmented endopod and four-segmented exopod; distal segment with two setae, one shorter and with setules on tip. Maxillule with exopod bearing four setae, one shorter and with setules on tip. Maxilla with praecoxa and coxa separated by arthrodial membrane posteriorly. Maxilliped composed of seven segments: praecoxa with two endites armed with one and three setae; coxa and basis each with one endite armed with two strong setae; four-segmented endopod with setal formula 0, 0, 1, 4. Legs 1-4 with three-segmented rami; spine and seta formula as for type species. Endopod of leg 4 with three particularly robust setae (two setae on second segment and proximal seta of third segment). Fifth leg with intercoxal plate, and with protopod armed with external seta. Exopod of female leg 5 one-segmented, bearing two spines and one seta; exopod of male leg 5 one-segmented with two additional internal setae. Short segment-like endopodal structure of leg 5 in female present or absent. Sixth leg with three setae in both sexes.

Heptnerina confusa n. sp.
(Figs 1-8)

TYPE MATERIAL. — Holotype ♀ (MNHN-Cp2155). Paratypes: allotype ♂ (MNHN-Cp2156); 6 ♀ ♀, 5 ♂ ♂, 2 copepodids of stage 5, 4 copepodids of stage 4 (MNHN-Cp2157). The description is based mainly on the holotype female and allotype male. The type material is mounted on slides in glycerol and sealed with Eukitt (O. Kindler GmbH & Co., Freiburg, Germany) and deposited in the Muséum national d'Histoire naturelle, Paris.

TYPE LOCALITY. — Atlantic Ocean, Mid-Atlantic Ridge, Azores Triple Junction, Lucky Strike, cruise PICO, vessel *Nadir*, submersible *Nautile*, dive 1270, sample number SMAC A-1, 37°17.29'N, 32°16.45'W, 1698 m, 7.VII.1998.

ETYMOLOGY. — From the Latin *confusus*, referring to the difficulty in interpreting the morphological features of the new species.

DESCRIPTION
Holotype female
Body cyclopiform (Fig. 1A, B). Total length, excluding caudal setae: 0.82 mm, greatest width 0.32 mm. First pedigerous somite free, concealed laterally by extension of cephalosome. Tergites of second to fourth pedigerous somites sclerotized laterally and pointed posteriorly. Urosome five-segmented. Genital and first abdominal somites fused to form genital double somite (Fig. 1C, D). Genital field with single medioventral copulatory pore, connecting internally into a wide copulatory tube leading to the seminal receptacle organized into two arms, each extending to dorsolateral gonopore associated with leg 6; accessory rounded structure of unknown function (possibly glandular), present on each side, proximal to seminal receptacle (Fig. 1D, E). Terminal margin of anal somite with ventral row of small spinules. Caudal rami (Fig. 2A) parallel, three times longer than wide, ventral side subdistally lined by row of flattened spinules; bearing seven setae. Accessory lateral seta (seta I) short, difficult to see; inner terminal seta 1.47 times longer than caudal ramus and longer than dorsal and distal outer setae; median inner terminal seta long, 5.3 times longer than caudal ramus and 1.7 times longer than median
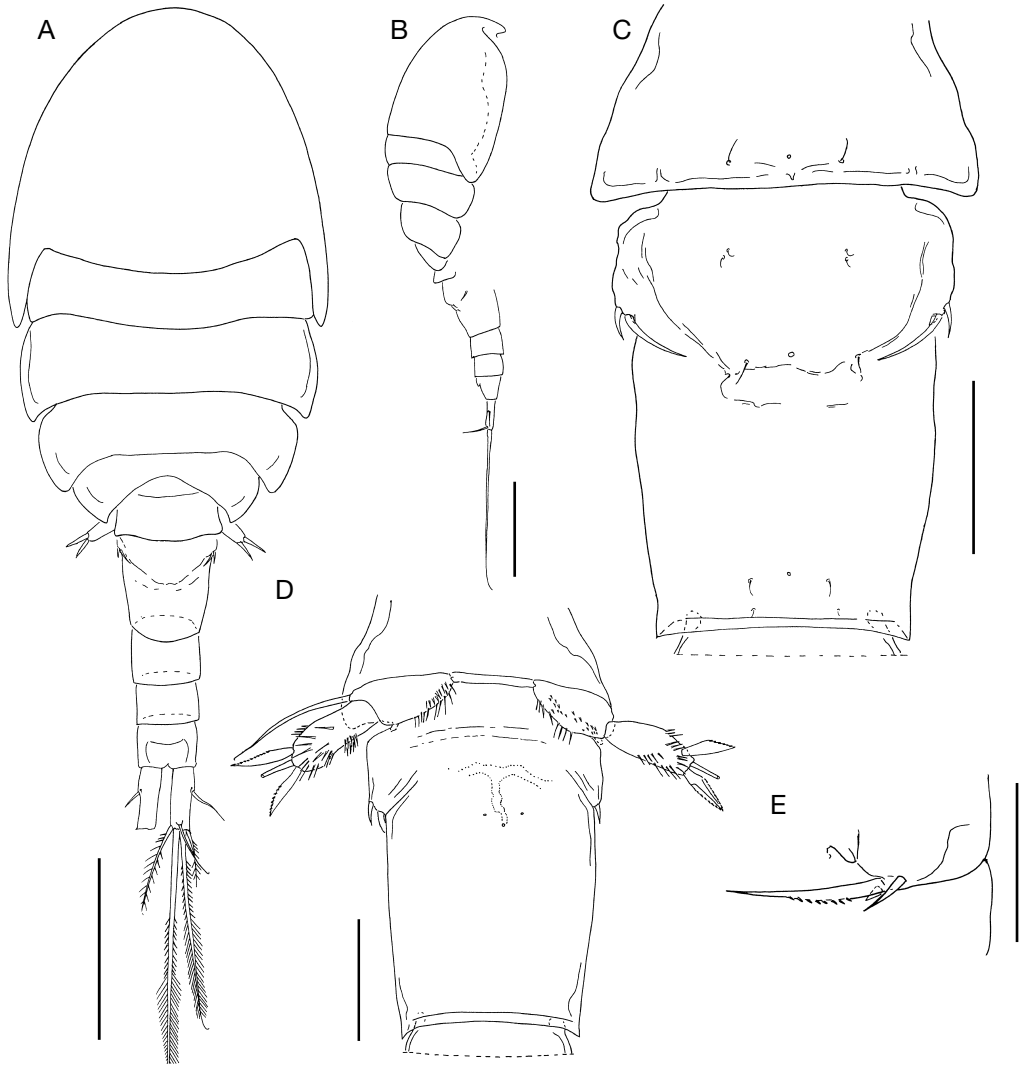
Fig. 1. — *Heptnerina confusa* n. gen., n. sp., ♀ holotype; **A**, habitus, dorsal; **B**, habitus, lateral; **C**, genital double somite, dorsal; **D**, genital double somite, ventral; **E**, gonoporal area and P6, lateral. Scale bars: A, B, 0.2 mm; C-E, 0.05 mm.

external seta. Median caudal setae with heteronomous setation.

Egg sacs not observed.

Rostrum (Fig. 2B) weakly developed.

Labrum with anterior outgrowth and patches of setules as shown on Figure 2B.

Paragnath (Fig. 2C, D) lobate with four spinulate setae, normally covered ventrally by gnathobase of mandible.

Antennule (Fig. 2E-G) 10-segmented; third, fourth and fifth segments subdivided, expressing partially, intersegmental articulations on their medial margin. Setation formula as follows: 3, 5, 8, 4, 6+s, 6+a, 3+a, 2, 2+a, 8+a (s: spine, a: aesthetasc), corresponding to ancestral segments: I-II, III-V, VI-IX, X-XI, XII-XIV, XV-XX, XXI-XXIII, XXIV, XXV, XXVI-XXVIII respectively. First segment ornamented with setules.
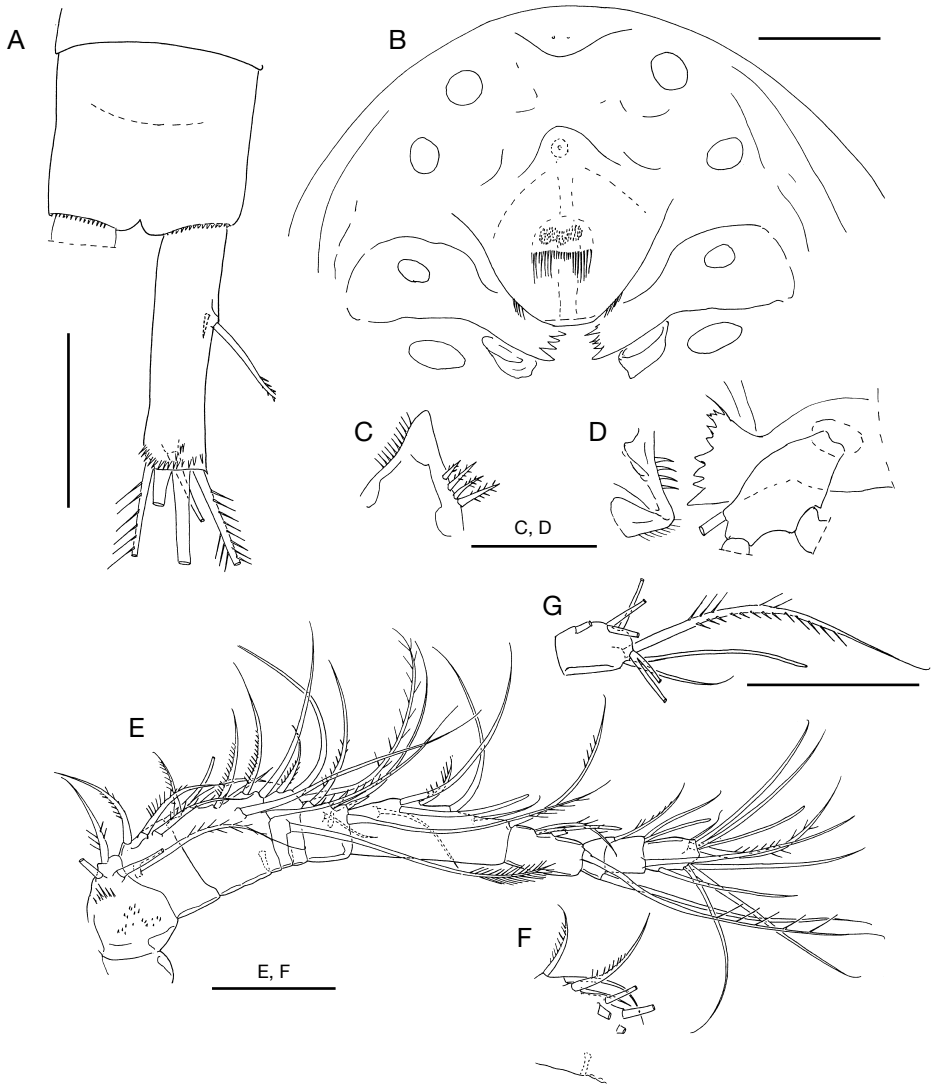
FIG. 2. — *Heptnerina confusa* n. gen., n. sp., ♀ holotype; **A**, caudal ramus, ventral; **B**, rostral and oral area showing labrum and mandibles; **C**, paragnath; **D**, paragnath and mandible (part); **E**, antennule; **F**, setation of third segment of antennule; **G**, distal segment of antennule. Scale bars: 0.05 mm.

Antenna (Fig. 3A, B) consisting of four segments: basis with one inner seta and two external setae representing exopod; endopod three-segmented with setal formula 1, 5, 7. Basis with basal patch of spinules on frontal surface; first endopodal segment with lateral outer distal prominence bearing group of tiny spinules, and with inner margin with two rows of small spinules, one in each half of segment; last endopodal segment with outer spiny prominence distally as on first endopodal segment, a proximal row of spinules on same margin, and terminal patch of spinules on lateral surface.

Mandible (Fig. 3C, D) with toothed gnathobase; palp biramous; basis with one inner seta and two
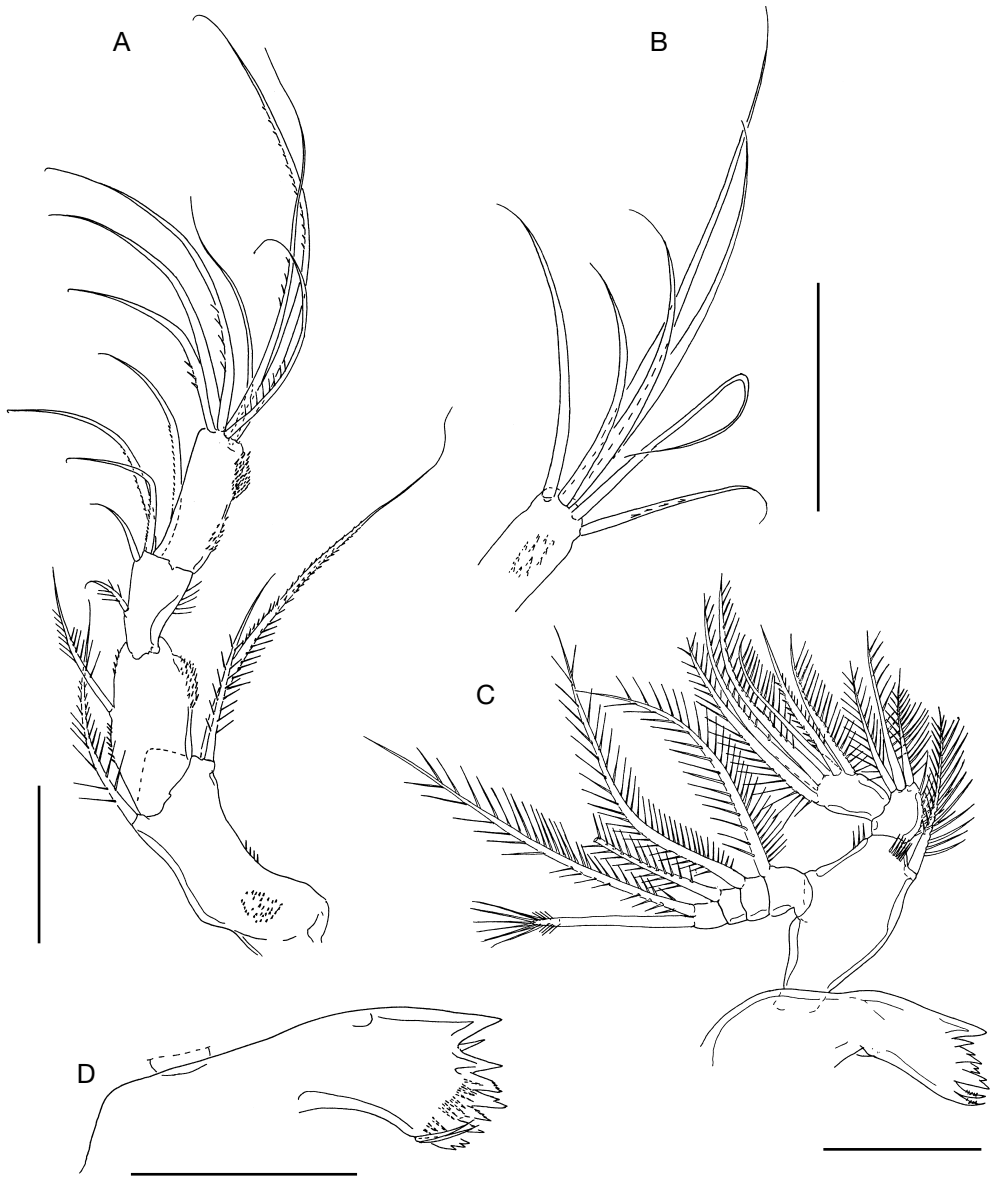
Fig. 3. — *Heptnerina confusa* n. gen., n. sp., ♀ holotype; **A**, antenna; **B**, distal segment of antenna; **C**, palp of mandible; **D**, gnathobase of mandible. Scale bars: 0.05 mm.

rows of setules; endopod two-segmented, setal formula 3, 6; exopod four-segmented, setal formula 1, 1, 1, 2; one seta on distal segment with patch of setules on tip.

Maxillule (Fig. 4A, B): praecoxal arthrite with 12 setae; coxal epipodite with two unequal setae, coxal endite with one seta; basis with two endites, proximal endite with three setae, distal endite with two setae; endopod one-segmented with seven setae; exopod one-segmented, with four setae; one seta shorter than others and ornamented with patch of spinules on tip.
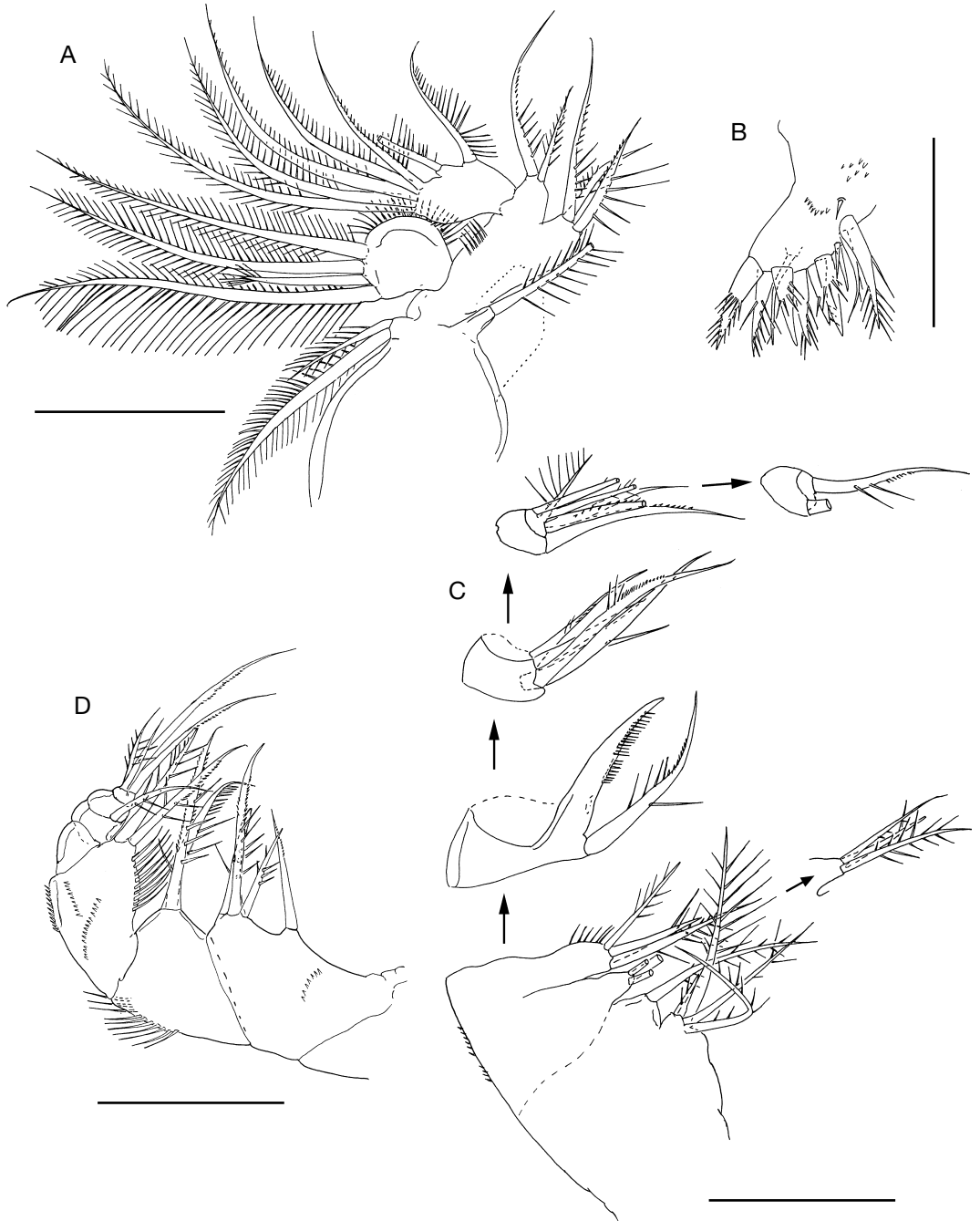
FIG. 4. — *Heptnerina confusa* n. gen., n. sp., ♀ holotype; **A**, maxillule; **B**, inner lobe of maxillule, ventral; **C**, maxilla; **D**, maxilliped. Scale bars: 0.05 mm.

TABLE 1. — Spine and setal formula of swimming legs in *Hepterina confusa* n. gen., n. sp., ♀.

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

Maxilla (Fig. 4C) with praecoxa separated from coxa by arthrodial membrane posteriorly only and with two endites, proximal with four setae, distal with one seta; coxa with two endites, each with three setae; basis produced into claw, with one seta; endopod three-segmented, first segment with four setae; second and third segments with total of six setae.

Maxilliped (Fig. 4E) with praecoxa and coxa separated by arthrodial membrane on both sides. Praecoxa with two endites armed with one and three setae; coxa and basis with two setae each; coxa with row of long setules along outer margin, basis with small distal row of spinules along outer and two others on surface of segment; row of long setules on internal margin; endopod four-segmented, setal formula 0, 0, 1, 4.

Swimming legs 1-4 biramous (Figs 5; 6A, B), with three-segmented rami; spine and setal formula: see Table 1.

Formula of spines of exopods: 4, 4, 4, 3. Formula of setae of exopods: 4, 5, 5, 5.

Leg 1 with one seta on second segment of endopod.

Leg 4 with setae on second endopodal segment and proximal inner seta on third (Fig. 6B) particularly strong.

Leg 5 (Fig. 6C) connected by narrow intercoxal plate; undivided protopod with outer seta and setules along inner margin; exopod one-segmented, armed distally with two spines and one long median seta; inner margin of protopod bearing short, stout, digitiform segment-like structure, with or without ornamenatation of spinules, interpreted as representing endopod.

Leg 6 (Fig. 1E) located laterally on genital double-somite, with three unequal setae, one

small; longest seta, located more posteriorly, strong, curved dorsally.

Allotype male
Differing from female as follows:
Body (Fig. 7A, B): total length, excluding caudal setae 0.65 mm, greatest width 0.23 mm. Urosome six-segmented; genital and first abdominal somites separate (Fig. 7 D). Caudal rami (Fig. 7A, E) with few spinules on each side of ventral distal margin. Rostrum and labrum with anterior outgrowth (shown in lateral view in Figure 7C).

Antennule (Fig. 8A, B) indistinctly 17-segmented, fifth, sixth, seventh segments incompletely divided. Setation formula as follows: 3, 5, 3, 2, 2, 2, 2, 1, 3, 2, 2, 2+a, 1, 2, 4, 2+a, 11+a; segmental homologies as: I-II, III-V, VI-VII, VIII, IX, X, XI, XII, XIII, XIV, XV, XVI, XVII, XVIII, XIX-XX, XXI-XXIII, XXIV-XXVIII.

Leg 1 (Fig. 8C): distal segments of right endopod fused partially.

Leg 5 (Fig. 7F): without endopod, one-segmented exopod with two internal setae, not present in female.

Leg 6 (Fig. 7D) with three setae, outermost longest, innermost very short, as small spine, median seta bearing a few (one on allotype) setules.

Variation: dissected paratypes (six females, four males, six copepodid stages)
From the six female paratypes, three have leg 5 of general shape (as in Figure 6D); in these specimens, the endopodal structure varies in size and proportion; the endopodal structure, when present, is not always symmetrical on right and left legs. In addition, it can be present on one side only. No muscle connected to the presumed endopod has been found within protopod. The three other paratypes have a leg 5 lacking the endopod-like structure (Fig. 8G, H).

In one adult male, leg 1 does not show any fusion of the distal endopodal segments, as it is the condition in the allotype. Leg 5 lacks the endopod, as in the allotype. Leg 5 of the three other paratype males lacks the endopodal structure, as in the allotype male.
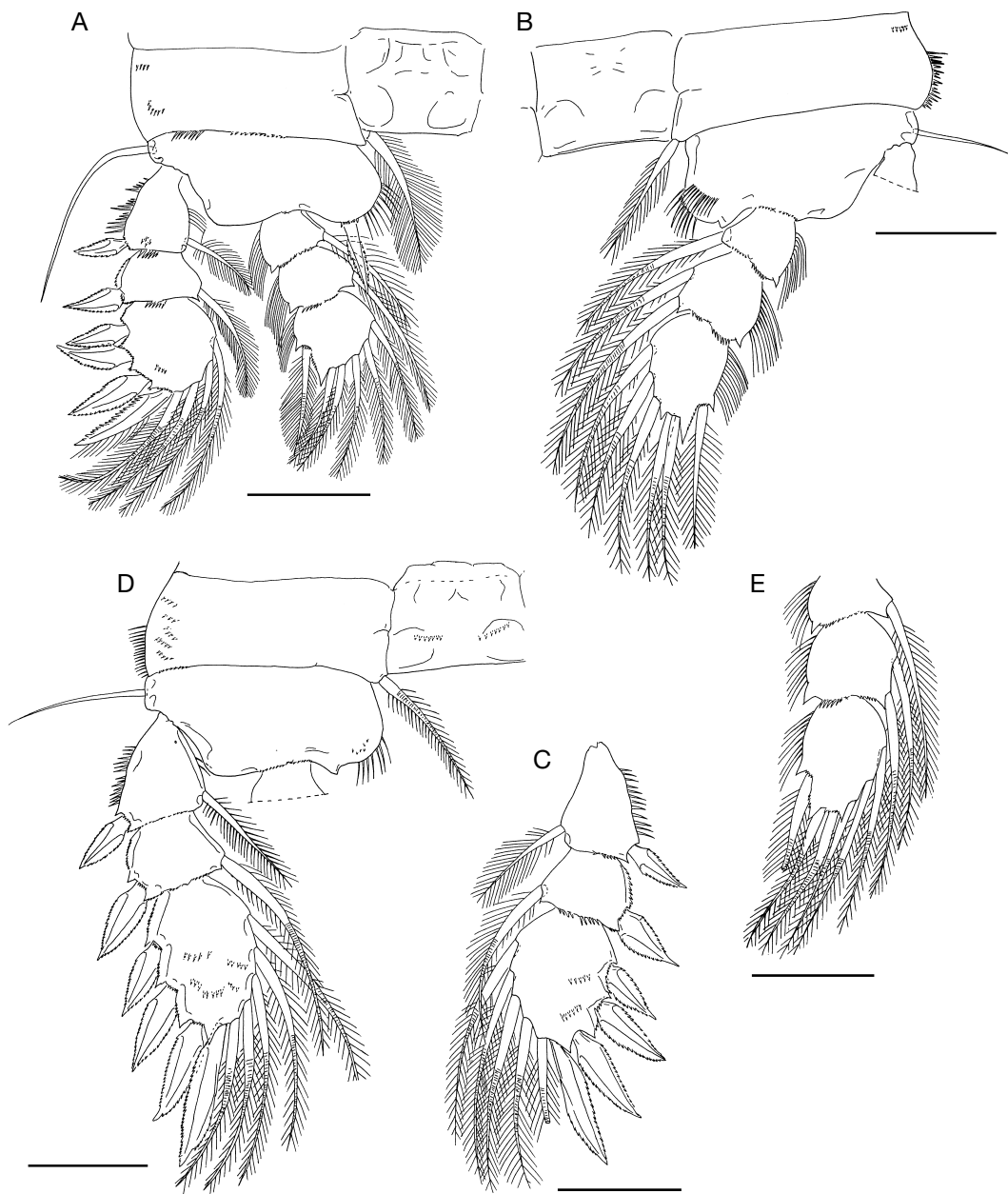
Fɪɢ. 5. — *Heptnerina confusa* n. gen., n. sp., ♀ holotype; **A**, leg 1, anterior; **B**, leg 2, anterior; **C**, exopod of leg 2, anterior; **D**, leg 3, anterior; **E**, endopod of leg 3, anterior. Scale bars: 0.05 mm.

Female copepodid stage V: leg 5 as in Figure 8E. Male copepodid stage V: leg 5 as in Figure 8D. Copepodid stage IV (four specimens): leg 5 as in Figure 8F.

DISCUSSION

The diagnosis of the new genus conforms to the family Cyclopinidae. This family currently
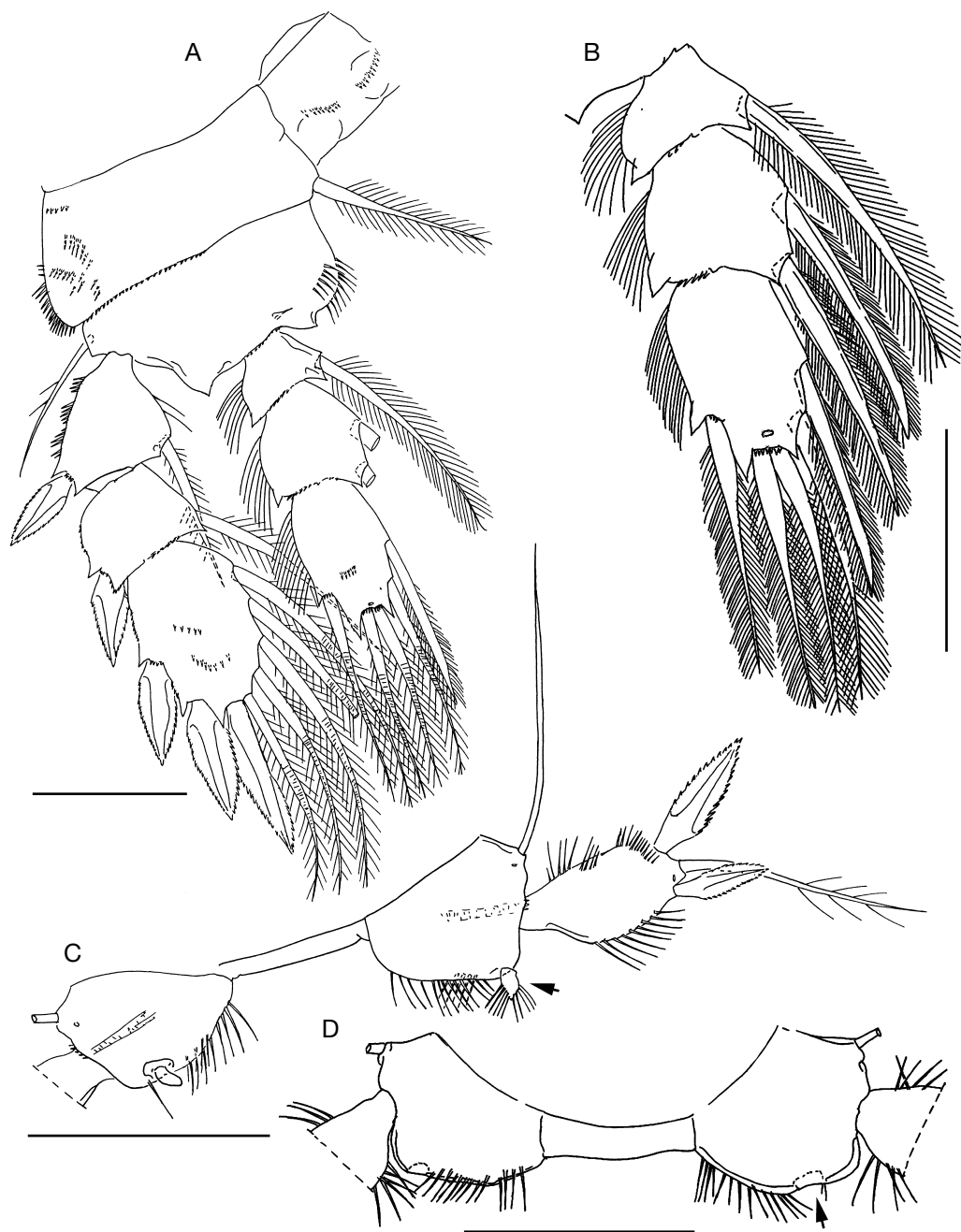
FIG. 6. — *Heptnerina confusa* n. gen., n. sp., ♀; **A**, holotype, leg 4; **B**, holotype, endopod of leg 4; **C**, holotype, leg 5 with endopod arrowed; **D**, paratype, leg 5. Scale bars: 0.05 mm.
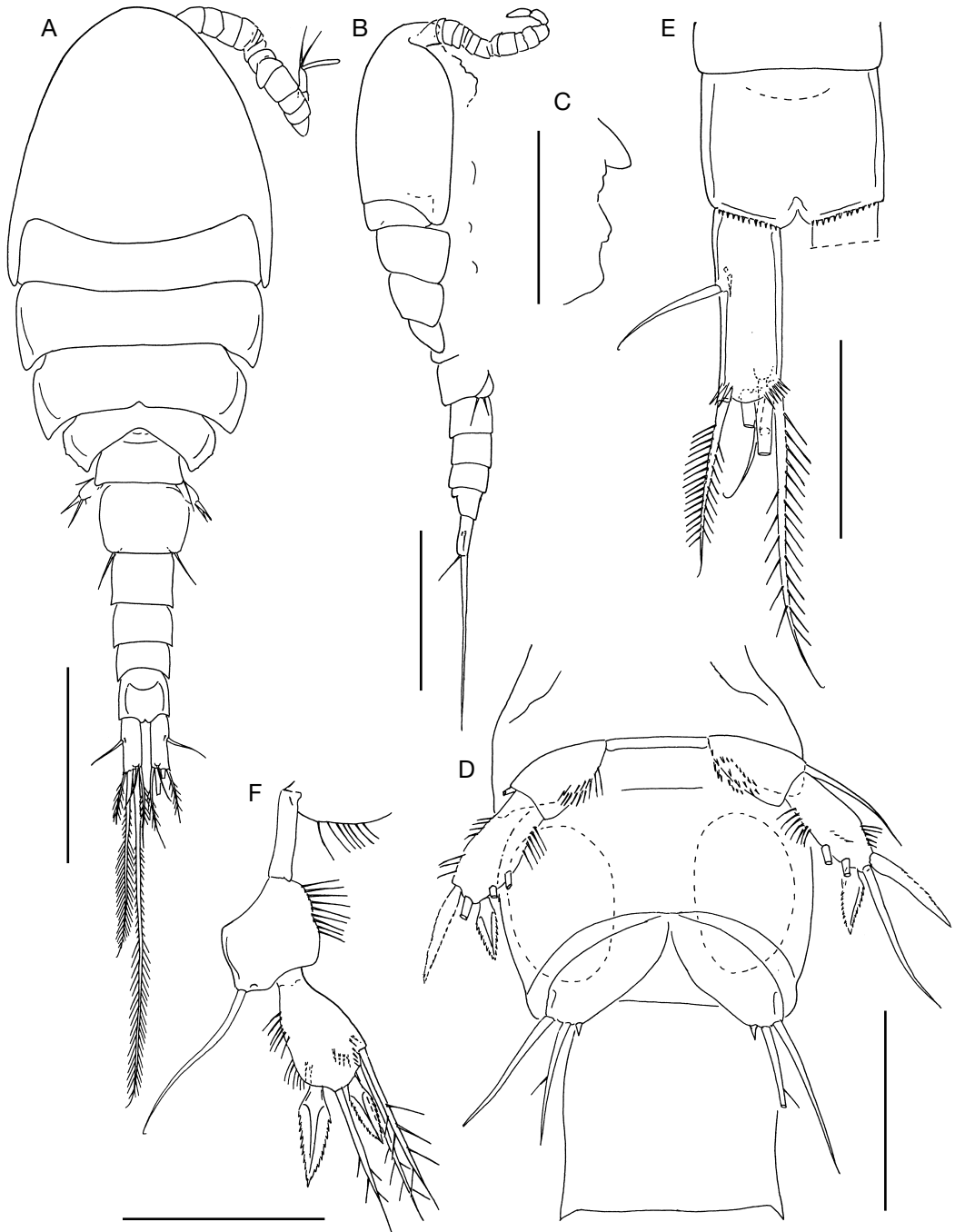
Fig. 7. — *Heptnerina confusa* n. gen., n. sp., ♂; **A**, habitus, dorsal; **B**, habitus, lateral; **C**, rostrum and labrum, lateral; **D**, leg 5 and genital somite, ventral; **E**, caudal ramus, ventral; **F**, leg 5. Scale bars: A, B, 0.2 mm; C, 0.1 mm; D-F, 0.05 mm.
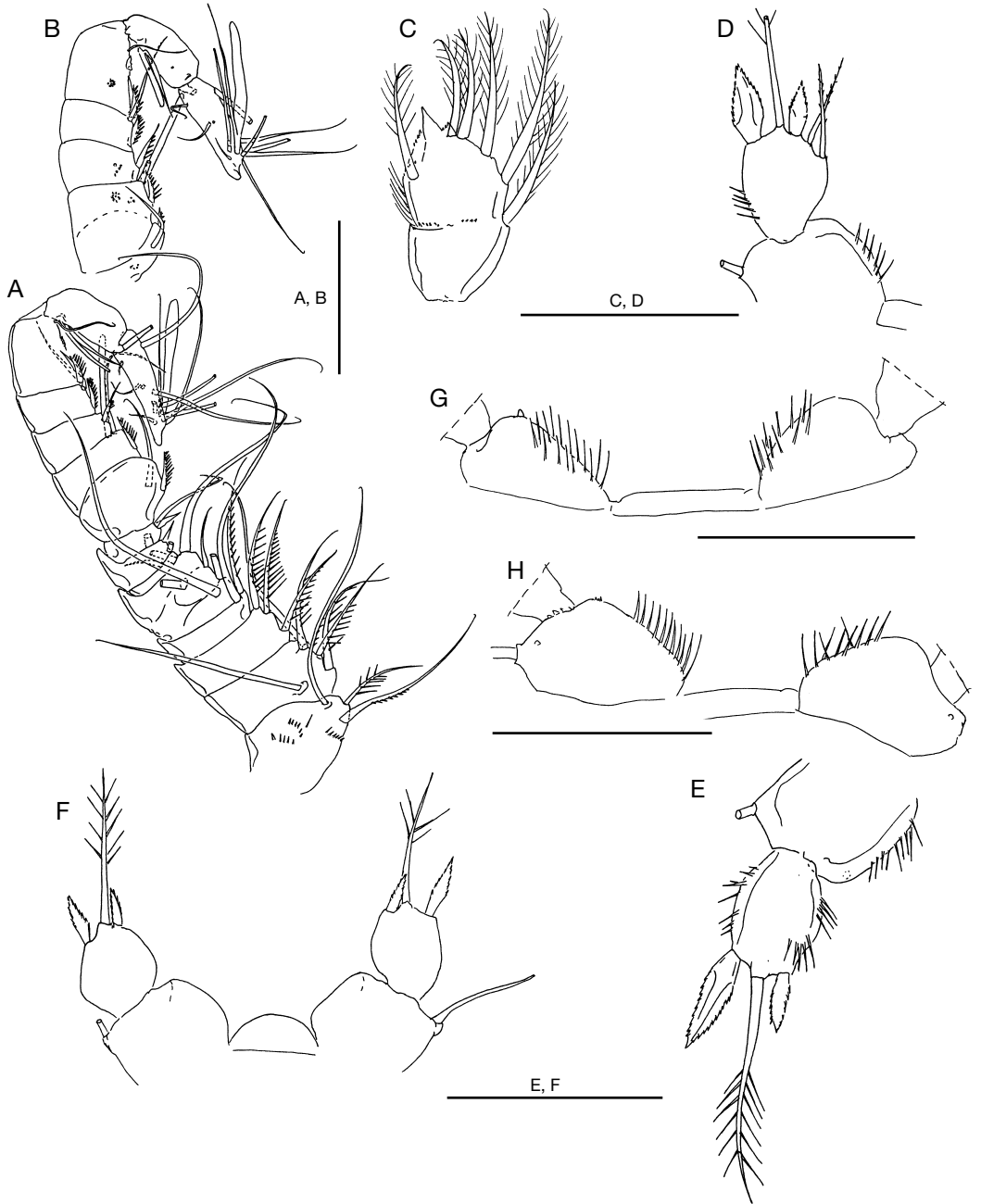
Fig. 8. — *Heptnerina confusa* n. gen., n. sp.; **A**, ♂ allotype, antennule; **B**, ♂ allotype, antennule, distal part; **C**, ♂ allotype, leg 1, distal segments of endopod, anterior; **D**, ♂ copepod V, leg 5; **E**, ♂ copepodid V, leg 5; **F**, copepodid IV, leg 5; **G-H**, ♀ paratypes, leg 5. Scale bars: 0.05 mm.

comprising 43 genera, is probably paraphyletic and a revision is needed to clarify its systematic status. The main characters distinguishing *Heptnerina* n. gen. from other genera of Cyclopinidae are the presence of endopodal-like structure of leg 5 in the female and the presence of setae on the paragnaths. These features have never been observed in the family before and are discussed below. The presence of a modified seta on the exopod of the maxillule is a derived state of the new genus, although precise information on the state of this character in other cyclopinids is necessary before detailed comparisons can be made. The fusion of the endopodal segments of leg 1, shown in the male allotype but not in the paratypes, is interpreted as a teratological feature or as part of the normal variability of the species, rather than attributed to sexual dimorphism. By contrast, the lack of the endopodal-like structure from leg 5 in all studied males appears to be a sexually dimorphic character. This interpretation is supported by the late appearance of this structure, at the moult from copepodid stage V to the adult.

Heptnerina n. gen. shows a number of plesiomorphic character states of Cyclopoida such as: two exopodal setae on the antenna, 12 setae on praecoxal arthrite and seven setae on the endopod of the maxillule, the presence of arthrodial membrane, at least posteriorly, separating praecoxa and coxa of both maxilla and maxilliped, the four-segmented endopod of the maxilliped, with one seta on third segment and four setae on the fourth, the presence of three setae on leg 6, and of seven setae on the caudal ramus (Jaume & Boxshall 1997; Martínez Arbizu 1997a).

The key to cyclopinine genera and the diagnosis of "cyclopinid-like" genera and families described recently (Jaume & Boxshall 1996a, b, 1997; Martínez Arbizu 1997a, b; Humes 1999; Martínez Arbizu 2000a, b) suggest an affinity between *Heptnerina* n. gen. and the common shallow water genus *Cyclopina* Claus, 1863. This genus is heterogeneous, composed of about 35 species, and is in need of revision (Martínez Arbizu pers. comm.). *Heptnerina* n. gen. shares with the type species *Cyclopina gracilis* Claus, 1863 the segmentation and the setation of the swimming legs. *H. confusa* n. gen., n. sp. differs from *C. gracilis* in having two exopodal setae on the antenna (rather than one seta in *C. gracilis*), by the male having two additional setae on the exopod of leg 5 (leg 5 of male of *C. gracilis* armed as in female, according to the text description of Sars [1913]).

H. confusa n. gen., n. sp. differs from *Cyclopina esilis* Brian, 1938, the only species of the genus redescribed in fine detail (Jaume & Boxshall 1996b), in the number of segments of the female antennule (10 in *H. confusa* n. gen., n. sp., 11 in *C. esilis*), in the exopod of the antenna, represented by two setae in the new species (instead of one in *C. esilis*), in the presence of modified seta on the exopod of the maxillule, and the presence of the caudal seta I (*sensu* Huys & Boxshall 1991). *H. confusa* n. gen., n. sp. shares with *C. esilis* the following features: four-segmented endopod of the maxilliped (three- in *C. gracilis*), one seta on the coxal endite of the maxillule, the setation of the mandible (but the brush-like tip of the distalmost seta of the exopod differs), and the segmentation and armature of the swimming legs.

H. confusa n. gen., n. sp. exhibits marked affinities with *Troglocyclopina balearica* Jaume & Boxshall, 1997. The species share subsequent characteristics: ten-segmented female antennule, two exopodal setae on the antenna, and the segmentation and setation of the swimming legs. The genera differ in the setation of the exopod of the mandible and in the endopod of the maxilliped (three-segmented in *T. balearica*), as well as in the exopod of maxillule (modified seta on exopod of maxillule in *H. confusa* n. gen., n. sp.).

The ventral cuticular fold on the female genital double segment appearing as connecting the legs 6, shown for *C. gracilis* by Huys & Boxshall (1991: figs 2.8.28 D, E) was not observed in *H. confusa* n. gen., n. sp. The internal genital area of the new taxon appears to be built on the same pattern as in *T. balearica*: a single copulatory pore opening mid-ventrally at the level of the first third of the somite, with a copulatory duct going to symmetric seminal ducts. The interpretation of Jaume & Boxshall (1996b) indicating the

presence of paired seminal receptacles has to be confirmed. The structures observed by these authors might correspond to glands without direct relationship to the genital system (see Defaye *et al.* 2003).

The articulation and setation of the maxilliped protopod (praecoxa with two endites armed with one and three setae, coxa and basis both with one endite armed with two setae) are consistent with the ground pattern of cyclopoid maxillipeds introduced by Ferrari & Ivanenko (2001: fig. 15). The alternative assumption: three endites derived from the coxa and one unarmed endite from the praecoxa fused with coxa, is not supported (Huys & Boxshall 1991: 297; Jaume & Boxshall 1996b).

In copepods, paragnaths are typically lobes often bearing setules arranged in rows or patches. The presence of (three) setae on the paragnath of *Archimisophria squamosa* Alvarez, 1985 (Misophrioida) was interpreted as a synapomorphy probably of the genus but not of the order (Huys & Boxshall 1991: 89, 344, 365). The presence of such setae is also suspected in a parasitic ascidicolid cyclopoid as reported by the same authors. Our discovery of setae on the paragnaths in a free-living cyclopoid demonstrates again the occurrence of such setae in the order Cyclopoida, and suggests that setae on the paragnath may have been overlooked in the family Cyclopinidae. The presence of setae on the paragnaths of *Halicyclops eberhardi* and *Metacyclops fiersi* (Cyclopidae), two new species recently described by De Laurentiis *et al.* (2001) from groundwaters in Western Australia supports this assumption.

The existence of setae on the paragnaths is difficult to interpret. One hypothesis is that the presence of the setae is a primitive state characterizing both cyclopoids and misophrioids. On the other hand, following the interpretation of Huys & Boxshall (1991), the occurrence of these setae in two distinct orders could be interpreted as novelties having evolved independently in two very primitive genera of two orders. The presence of setae on the paragnath suggests that the paragnath has derived from the proximal part of one

of the cephalic appendages (mandible, maxillule or maxilla) and not from a sternite (Walossek 1993: 115; Walossek 1999).

The position and shape of the articulated (separated from the basis by arthrodial membrane) structure on leg 5 in females of *H. confusa* n. gen., n. sp. suggest that it is the endopod. This endopodal structure has not been observed in all females of *H. confusa* n. gen., n. sp. and sometimes only a trace of its insertion could be observed (arrow, Fig. 6D). It can be considered either as a segment or as a modified seta. The second hypothesis is probably the right one as it bears spinules and presents more resemblance to a modified seta than to a segment. It varies in shape, occurs in females only, and lacks associated musculature in the protopod connected to it. Only misophrioids, among podoplean copepods, have an articulated endopod of leg 5. A number of harpacticoids and some siphonostomatoids have endopodal setae interpreted as remnants of the endopod after its fusion to the basis or its reduction. Whether it is interpreted as a segment or a seta, it represents the endopod, and it is the first time that an endopod of leg 5 has been shown in the Cyclopoida. The discovery of this endopod structure in the new taxon could be interpreted following two ways: either it represents the ancestral state of the Cyclopoida P5 or it illustrates the character reversal discussed by Huys & Boxshall (1991: 365, 366).

Reversals (atavisms) are found in few animals (Carroll 2000), and oligomerization, leading to reduction and fusion of repeated (serially homologues) structures, has been hypothesized for crustaceans as the main evolutionary mode (Dogiel 1954). The discovery of the endopod in *H. confusa* n. gen., n. sp. might argue that reappearance of modular units (such as segment, appendage, ramus) lost by the ancestor is possible and can be an additional way of copepod evolution. This suggestion is supported by the data showing that the loss of modular structures (such as appendages) as well as the modification of their shape can be achieved by little changes in HOX protein function, gene expression or HOX target genes (Levine 2002).

Three dirivultid species (*Aphotopontius atlanteus* Humes, 1996, *A. temperatus* Humes, 1997, *Stygiopontius rimivagus* Humes, 1997) and one harpacticoid copepod (*Bathylaophonte azorica* Lee & Huys, 1999) have been reported before from the hydrothermal vents of the Azores Triple Junction. The copepods described herein, gathered during *in situ* colonization experiments, could be attracted by the bacteria present in substratum due to the chemical conditions of the habitat (Gebruk 2002). The precise origin and the natural conditions of life of these animals remain unknown.

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REFERENCES

CARROLL S. B. 2000. — Endless forms: the evolution of gene regulation and morphological diversity. *Cell* 101: 577-580.

DEFAYE D., CUOC C. & BARTHÉLÉMY R.-M. 2003. — A new interpretation of the female genitalia in *Macrocyclops albidus* (Copepoda, Cyclopidae). *Acta zoologica* 84: 25-31.

DE LAURENTIIS P., PESCE G. L. & HUMPHREYS W. F. 2001. — Copepods from ground waters of Western Australia, VI. Cyclopidae (Crustacea: Copepoda) from the Yilgarn Region and the Swan Coastal Plain. *Records of the Western Australian Museum* Suppl. 64: 115-131.

DESBRUYÈRES D. & SEGONZAC M. 1997. — *Handbook of Deep-Sea Hydrothermal Vent Fauna.* IFREMER, Brest, 279 p.

DOGIEL V. A. 1954. — *Oligomerizaciya gomologichnyh organov kak odin iz glavnyh putei evolyucii zhivotnyh* [*Oligomerization of the Homologous Organs as One of the Main Ways of Evolution of Animals*]. Leningrad University Press, Leningrad, 368 p. (in Russian).

FERRARI F. D. & IVANENKO V. N. 2001. — Interpreting segment homologies of the maxilliped of cyclopoid copepods by comparing stage-specific changes during development. *Organisms, Diversity and Evolution* 1: 113-131.

GEBRUK A. (ed.) 2002. — [*Biology of Hydrothermal Systems*]. KMK, Moscow, 543 p. (in Russian).

HEPTNER M. V. & IVANENKO V. N. 2002. — Copepoda (Crustacea) of hydrothermal ecosystems of the World Ocean. *Arthropoda Selecta* 12 (2): 117-134.

HUMES A. G. 1999. — Copepoda (Cyclopinidae and Misophriidae) from a deep-sea hydrothermal site in the northeastern Pacific. *Journal of Natural History* 33: 961-978.

HUMES A. G. & SEGONZAC M. 1998. — Copepoda from deep-sea hydrothermal sites and cold seeps: description of a new species of *Aphotopontius* from the East Pacific Rise and general distribution. *Cahiers de Biologie marine* 39: 51-62.

HUYS R. & BOXSHALL G. A. 1991. — *Copepod Evolution.* The Ray Society n° 159, London, 468 p.

IVANENKO V. N. & FERRARI F. D. 2003. — A new genus and species of the family Dirivultidae (Copepoda, Siphonostomatoida) from a deep-sea hydrothermal vent at the Juan de Fuca Ridge (Pacific ocean) with comments of dirivultid distribution. *Arthropoda Selecta* 11 (3): 177-185 (dated 2002, published 2003).

JAUME D. & BOXSHALL G. A. 1996a. — Two new genera of cyclopinid copepods (Crustacea) from anchihaline caves on western Mediterranean and eastern Atlantic islands. *Zoological Journal of the Linnean Society* 117: 283-304.

JAUME D. & BOXSHALL G. A. 1996b. — Rare cyclopoid copepods (Crustacea) from Mediterranean littoral caves. *Bulletin of the Natural History Museum Zoology Series* 62 (2): 83-99.

JAUME D. & BOXSHALL G. A. 1997. — Two new genera of cyclopinid Copepods (Cyclopoida: Cyclopinidae) from anchihaline caves of the Canary and Balearic Islands, with a key to genera of the family. *Zoological Journal of the Linnean Society* 120: 79-101.

LEVINE M. 2002. — How insects lose their limbs. *Nature* 415: 848-849.

MARTÍNEZ ARBIZU P. 1997a. — *Cyclopicina sirenkoi* sp. n. (Copepoda: Cyclopinidae) from deep waters in the Laptev Sea (Arctic Ocean), with comments on the phylogenetic relationships of copepod orders. *Senckenbergiana Biologica* 77 (1): 89-99.

MARTÍNEZ ARBIZU P. 1997b. — A new genus of cyclopinid copepods (Crustacea), with a redescription of *Smirnovipina barentsiana* comb. nov. (Smirnov, 1931). *Sarsia* 82: 313-323.

Martínez Arbizu P. 2000a. — A new species of *Cyclopetta* from the Arctic Laptev Sea (Arctic Ocean), with recognition of Cyclopettidae fam. nov. a new monophylum of free-living Cyclopoida (Copepoda). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Biologie* 70: 91-101.

Martínez Arbizu P. 2000b. — Giselinidae fam. nov., a new monophyletic group of cyclopoid copepods (Copepoda, Crustacea) from the Atlantic deep sea. *Helgoland Marine Research* 54 (4): 190-212.

Sars G. O. 1913. — *Copepoda Cyclopoida*. Parts I and II. *Oithonidae. Cyclopinidae, Cyclopidae (part). An Account of the Crustacea of Norway* VI. Bergen Museum, Bergen, 31 p., 16 pls.

Tsurumi M. & Tunnicliffe V. 2001. — Characteristics of a hydrothermal vent assemblage on a volcanically active segment of Juan de Fuca Ridge, northeast Pacific. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 530-542.

Tsurumi M., Graaf R. C. de & Tunnicliffe V. 2003. — Distributional and biological aspects of copepods at hydrothermal vents on the Juan de Fuca Ridge, northeast Pacific Ocean. *Journal of the Marine Biological Association of the United Kingdom* 83 (3): 469-478.

Walossek D. 1993. — The Upper Cambrian *Rehbachiella kinnekullensis* Müller, 1983, and the phylogeny of Branchiopoda and Crustacea. *Fossils and Strata* 32: 1-202.

Walossek D. 1999. — On the Cambrian diversity of Crustacea, *in* Schram F. R. & Vaupel Klein J. C. von (eds), *Crustaceans and the Biodiversity Crisis*. Brill, Leiden 1: 3-27.