

PLEOMOTHRA FRAGILIS N. SP. (REMIPEDIA) FROM THE BAHAMAS,
WITH REMARKS ON MORPHOLOGIC REDUCTIONS AND POSTNAUPLIAR DEVELOPMENT

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A B S T R A C T

We describe a new species of remipede crustacean from an anchialine cave system in the Exuma Cays, Bahamas. *Pleomothra fragilis* n. sp. is the second species assigned to the genus *Pleomothra* Yager, 1989. It is a relatively small species that occurs in sympatry with other remipedes, copepods, ostracods and amphipods. *Pleomothra fragilis* can easily be distinguished from *Pleomothra apletocheles* by the shape of its head shield, relatively long caudal rami, differently shaped, smaller maxillules, and a completely reduced lacinia mobilis on the left mandible. The reduction of the left lacinia and the sixth maxillular segment represent unique features that are only found in *Pleomothra*. At present, interpretations of these reductions are purely speculative since developmental data of remipedes are largely lacking. However, our recent collection of five larvae included a postnauplius that could be identified as belonging to the genus *Pleomothra*. The postnauplius exhibits transitional morphologic features that facilitate to evaluate autapomorphies in *Pleomothra*.

KEY WORDS: anchialine caves, Godzillidae, lacinia mobilis, maxillules, nauplius, *Pleomothra*, Remipedia

INTRODUCTION

The description of *Pleomothra fragilis* brings the number of taxa within the remipede order Nectiopoda to a total of 19 species assigned to three families. Micropacteridae Koenemann et al., 2007b accommodates the monotypic genus *Micropacter*. Speleonectidae Yager, 1981 comprise the four genera *Speleonectes* Yager, 1981, *Cryptocorynetes* Yager, 1987, *Lasionectes* Yager et al., 1986, and *Kaloketos* Koenemann et al., 2004. Wollermann et al. (2007) described a second species of the genus *Cryptocorynetes* based on recently collected specimens. For a period of 20 years, the third family, Godzilliidae, was composed of three monotypic genera, *Godzillius* Schram et al., 1986, *Godzilliognomus* Yager, 1989, and *Pleomothra* Yager, 1989. The new species described herein, *Pleomothra fragilis*, is the second species assigned to the genus *Pleomothra*. It exhibits several distinct autapomorphies of the genus, in particular, a head shield with posterolateral projections, and massive, modified maxillules.

The description of the new species is based on specimens collected from Oven Rock Cave, an anchialine cave system on Great Guana Cay in the Exuma Cays (Bahamas). *Pleomothra fragilis* can easily be distinguished from *Pleomothra apletocheles* by the shape of its elongated head shield, a completely reduced lacinia mobilis on the left mandible, and relatively weakly developed pleurotergites in the anterior trunk. The detailed comparison of the two species of *Pleomothra* sheds new light on the reduction and modification of morphologic structures that are unique for this genus. However, correct interpretations of these reductions crucially depend on our knowledge of the development of *Pleomothra*. During a recent diving expedition, we were able to collect five nauplii that represented early developmental stages of Remipedia. The largest specimen, a 3.7 mm postnauplius, could be identified as belonging to *Pleomothra*. Based on these discoveries, we can now begin

to reconstruct the post-embryonic development of Remipedia. Moreover, the postnauplius provides first insights into the development of morphologic autapomorphies in *Pleomothra*.

Definitions and Terminology

In the following description, we adopt the modified terminology for setal structures proposed by Wollermann et al. (2007), which are based on qualitative definitions by Watling (1989). Thus, in this paper, we refer to any articulated (socketed) cuticular extension of variable shape or size as a ‘seta’, whereas a ‘spine’ is a non-articulated cuticular process or extension.

The terms ‘brachium’ and ‘lacertus’ were introduced by Koenemann et al. (2007b) to refer to the segments proximal and distal to the elbows in the three pairs of postmandibular cephalic appendages. However, the maxillule of *Pleomothra* exhibits a unique combination of modifications compared to all other remipedes, including a secondarily derived joint between segments three and four. In this particular case, the terms ‘brachium’ and ‘lacertus’ are irrelevant. For more convenient morphologic comparisons, we will therefore refer to the massive section distal to the elongate third maxillular segment as ‘subchelate unit’.

SYSTEMATICS

Pleomothra fragilis, n. sp.

(Figs. 1-4)

Type Locality.—Bahamas, Exuma Cays, Great Guana Cay, Oven Rock Cave (23°58.890'N; 76°19.576'W).

Material Examined.—Holotype (14 mm, 25 trunk segments) collected by T. Iliffe, 13 September 1996, type locality (National Museum of Natural History, Smithsonian Institution, USNM 1101656). 1 paratype (11 mm, 22 trunk segments) collected by B. Kakuk, February 1998, type

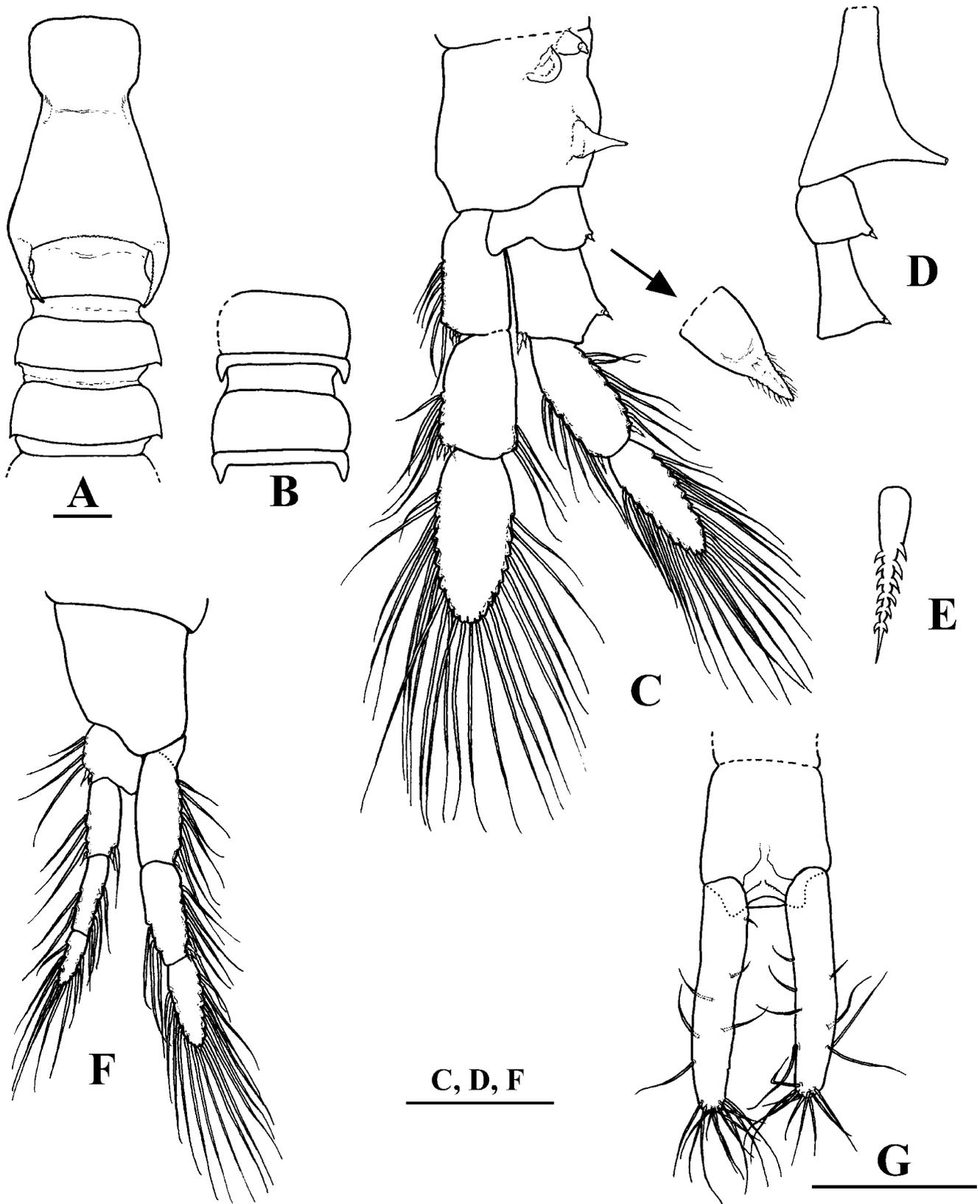


Fig. 1. *Pleomothra fragilis* n. sp., 18.5 mm paratype. A, dorsal view of head shield and anterior trunk segments; scale bar = 0.5 mm; B, ventral view of trunk segments 9 and 10, with sternites and sternal bars; C, 14th trunk appendage, with arrow pointing at enlarged plumose seta; D, lateral view of 14th trunk limb showing protopod and proximal 2 segments of endopod; E, short, stout, serrate seta (from trunk appendage); F, 25th trunk appendage; G, anal segment and caudal rami; scale bar = 0.5 mm. Scale bar C, D, F = 0.5 mm.

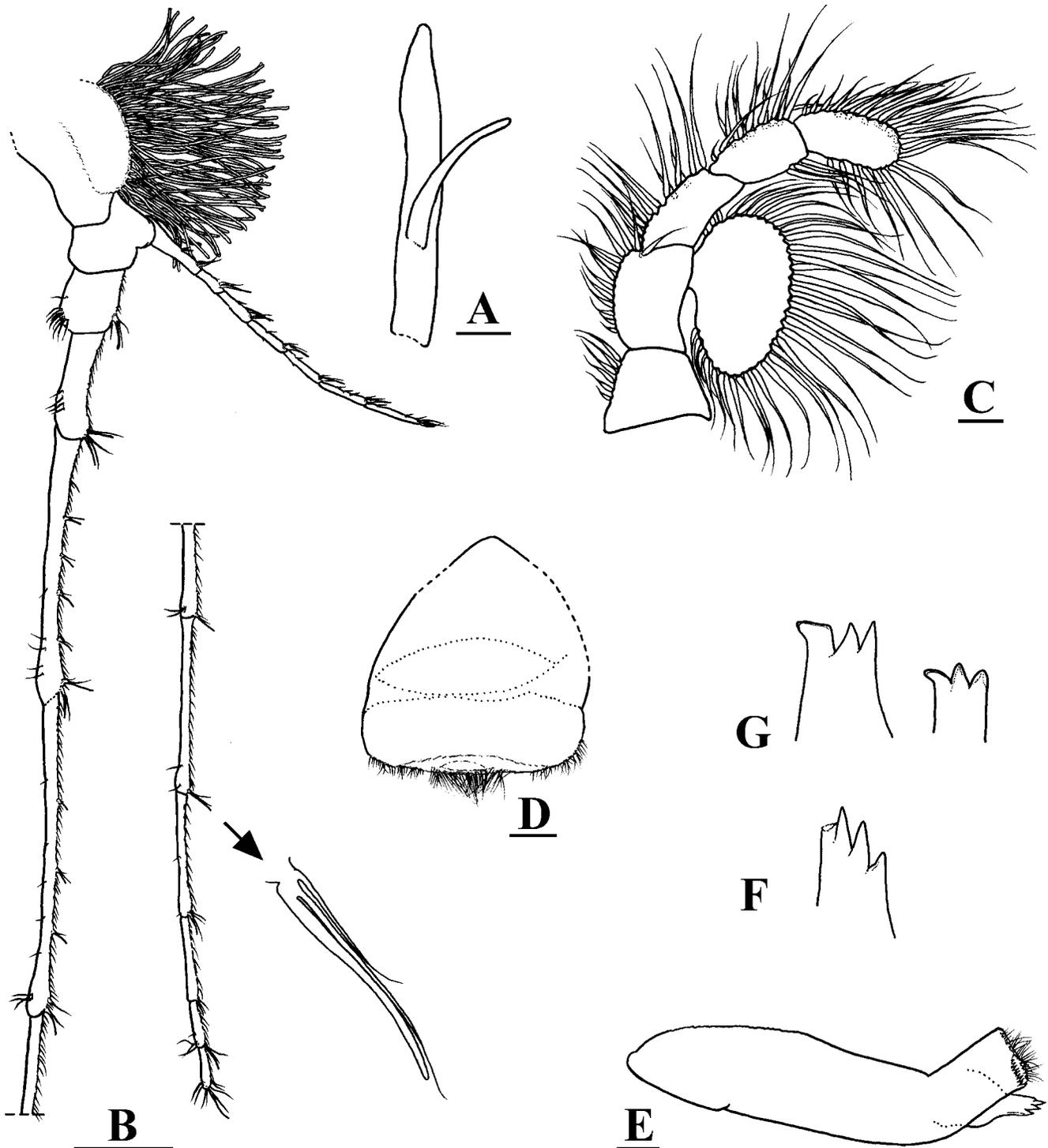
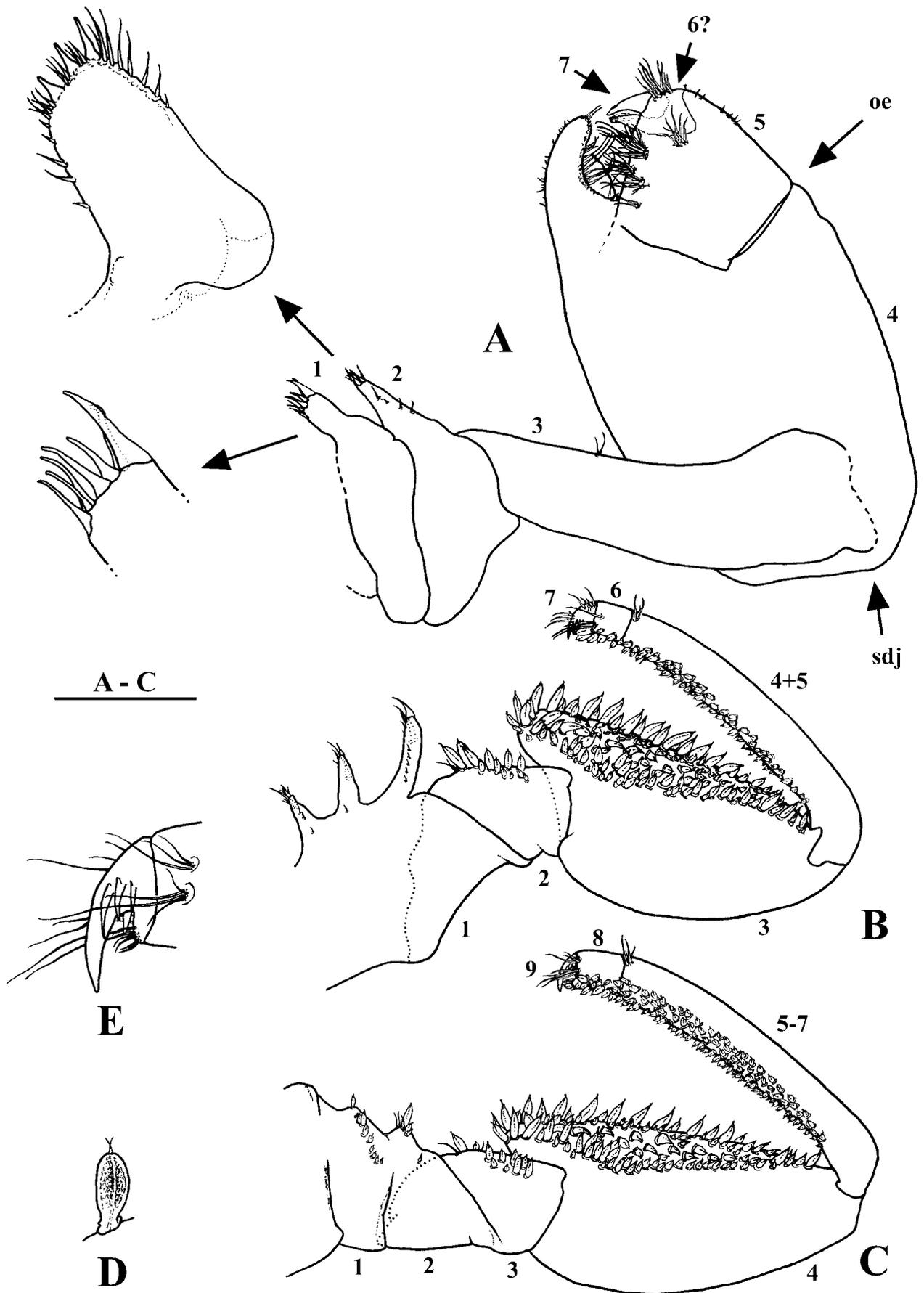


Fig. 2. *Pleomothra fragilis* n. sp., 18.5 mm paratype. A, frontal filament; scale bar = 0.1 mm; B, antennule, with arrow pointing at enlarged compound aesthetasc; scale bar = 0.5 mm; C, antenna; D, labrum; scale bar = 0.1 mm; E, left mandible; scale bar = 0.1 mm; F, enlarged incisor process of left mandible; G, enlarged incisor process (left) and lacinia mobilis of right mandible.

Fig. 3. *Pleomothra fragilis* n. sp., 18.5 mm paratype. A, maxillule, with enlarged endites of segments 1 and 2; oe: arrow pointing at original elbow, sdj: arrow pointing at secondarily derived elbow; 6? = possible remnant of segment 6; B, maxilla; C, maxilliped; D, small foliaceous seta from brachium of maxilla and maxilliped; E, claw of maxilliped. Scale bar A-C = 0.5 mm. Single numbers indicate individual limb segments; "4+5" and "5-7" represent presumed fusions of several segments into single segments.



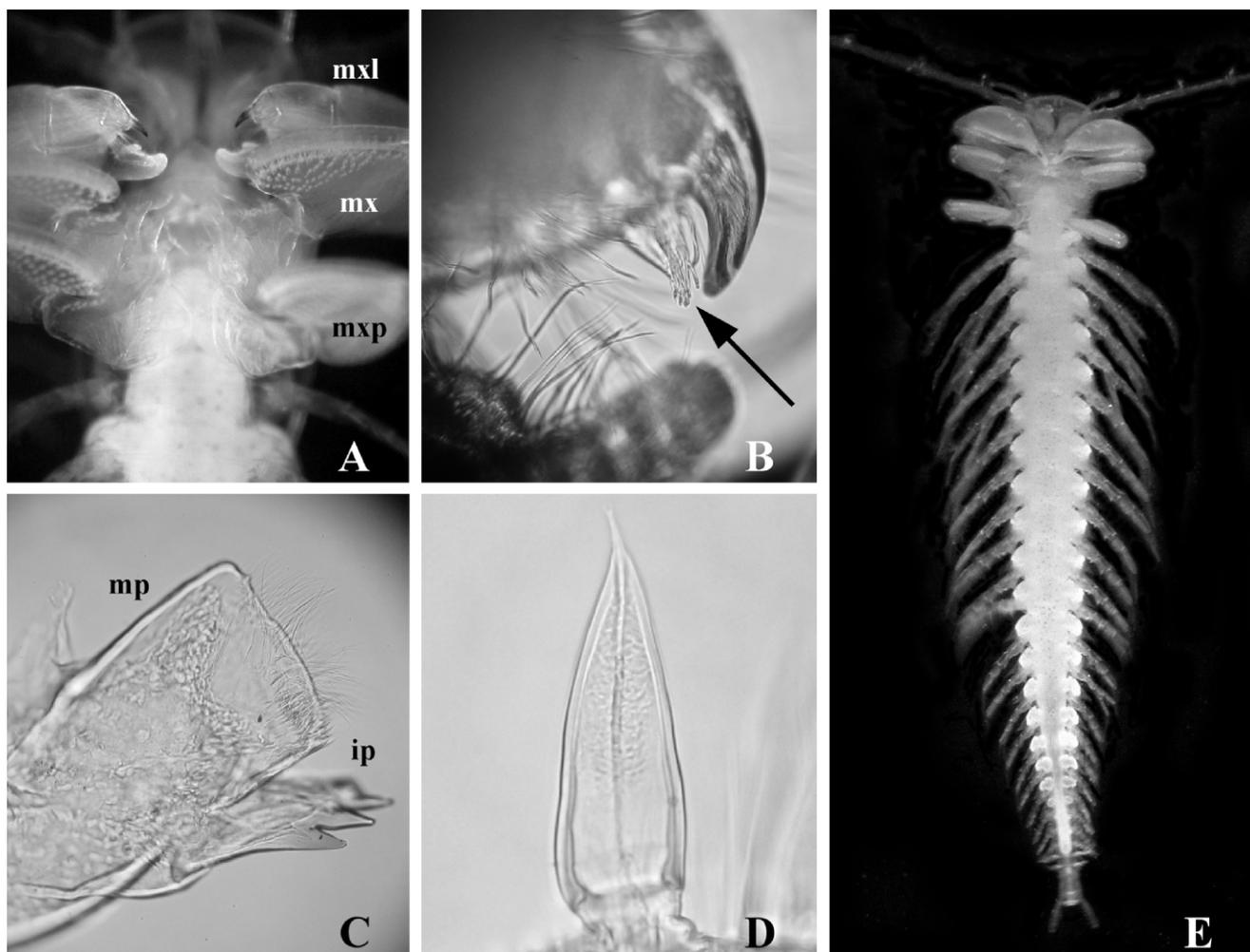


Fig. 4. *Pleomothra fragilis* n. sp. Light microscopy photographs of 18.5 mm paratype. A, ventral view of head and anterior trunk; mxl = maxillule, mx = maxilla, mxp = maxilliped; B, enlarged detail of distal end of maxillule; arrow points at slender process below claw (possible remnant of segment 6); C, detail of left mandible; mp = molar process, ip = incisor process; D, foliaceous seta from lacertus of maxilla and maxilliped; E, photograph of living specimen.

locality (collection J. Yager, BH 317); 1 paratype (18.5 mm, 26 trunk segments) collected by T. Iliffe, 22 August 2003, type locality (research collection S. Koenemann).

Etymology.—The epithet *fragilis* (Latin for ‘fragile’) refers to the slender habitus of this species.

Diagnosis.—Relatively small and slender species, body length of adult specimens ca. 11–18.5 mm, with up to 26 trunk segments. Head shield rather long, with quadrangular-shaped anterior part and trapezoidal posterior section, bearing long, thin posterolateral processes (Fig. 1A). First trunk segment not covered by head shield. Pleurotergites comparatively weakly developed. Maxillule relatively small, with long and narrow third segment, inner surface of terminal subchelate unit slightly concave (Fig. 3). Lacinia mobilis of left mandible completely reduced (Figs. 2E + F, 4C). Caudal rami 1.4 times longer than anal segment (Fig. 1G).

Description.—Based on holotype and 2 paratypes. Body slender, up to 18.5 mm long; adult trunk composed of 22–26 segments; pleurotergites comparatively weakly developed,

with pointed distolateral corners; first trunk segment slightly reduced, not covered by cephalic shield, tergites without pointed distolateral corners; sternal bars isomorphic, with distinct posterolateral corners (Fig. 1A, B). Female gonopores small; male gonopores large, cylindrical.

Cephalic shield 1.4 times longer than maximum width (measured from mid-anterior to mid-posterior margin), subdivided into quadrangular-shaped anterior part and subtrapezoidal posterior section; bearing rather long and thin posterolateral processes with serrate medial margins (Fig. 1A). Frontal filaments long, with slender medial processes (Fig. 2A).

Antennule (Fig. 2B): Peduncular pad expanded, bearing dense rows of aesthetascs. Dorsal ramus with 10 segments, reaching 39% of body length; all segments with a row of short setae along medial margin and clusters of double and triple compound aesthetascs on distomedial corners (see Koenemann et al., 2007b for definitions of flagellar and peduncular aesthetascs); segments 3 and 4 also with groups of double aesthetascs along medial margins. Ventral flagellum composed of 7 segments, short, reaching about 23% of length of dorsal ramus.

Antenna (Fig. 2C): Proximal segment of protopod with 6 setae, distal segment with 13 setae. Exopod ovate, and 1.6 times longer than adjacent distal segment of protopod, bearing 35 long marginal setae. Endopod bent in a semi-circular way; first (proximal) segment with a row of 10 setae and 2 separate setae on medial margin; second segment with 2 rows of setae (6 + 8); distal segment bearing setae along entire margin, with 2 rows on medial and apical margins. All setae plumose.

Labrum fleshy, apical margin bearing 3 fields of lateral and central setules (Fig. 2D).

Mandibles: Right incisor process equipped with 3 denticles (one of which stout, with a flattened apical surface), lacinia mobilis with 3 denticles (Fig. 2G). Left incisor process with 4 denticles (largest denticle with flattened apical surface); lacinia mobilis completely reduced (Figs. 2E, F, 4C). Molar processes prominent; distal surface bearing long setules and a few short, pointed spinose setae on medial rim (Figs. 2E, 4C).

Maxillule (Figs. 3A, 4A, B, D): Massive, composed of 6 segments. Segment 1 with well-developed endite, bearing 1 prominent seta and 6 smaller setae on apical margin. Segment 2 slightly wider than segment 1, with broad enditic plate, perpendicular to main limb axis, equipped with 3 robust apical setae, and a row of more slender setae on apical and subapical margins. Segment 3 very long and narrow. Secondarily derived joint between segments 3 and 4 (see discussion). Segment 4 massive, with bowed distal process forming a sub-chelate unit with segments 5 (6?) and 7 (claw); inner margin of distal process irregular, with prominent, rounded proximal lobe, and rows of longer setae accompanied by round fields of densely inserted short setae (abundance of fields increasing towards apex of process); outer margin of distal process with irregular row of short setae. Segment 5 relatively short, connected to segment 4 via a joint (original elbow), with several clusters of long setae on inner and (sub-) apical margins; inner margin of segment 5 with a long, slender, bowed subapical process, parallel to claw, terminating into 6-8 seta- or spine-like filaments (possible residual structure of segment 6). Subchelate terminal unit composed of segments 4-7, with flat or slightly concave inner surface. Claw small, with sub-terminal pore.

Maxilla (Figs. 3B, D, E, 4A): Segment 1 with 3 long, thin endites, each with a strong, curved apical seta accompanied by several simple setae, and a single, robust subapical seta; endites 1 and 3 also bear rows of short setae on medial margins. Segment 2 without endite, bearing a field of about 10 foliaceous (leaf-like) stout setae (Figs. 3D, 4D). Segment 3 (= lacertus) robust, arrow-shaped, with field of densely inserted foliaceous setae on entire inner margin. Segments distal to elbow (= brachium) very narrow; segments 4 and 5 fused into single segment, segment 6 short; brachium with field of relatively short and distally rounded foliaceous setae along inner margin. Claw (segment 7) with 1 prominent denticle flanked by several smaller and shorter denticles, bearing several clusters of long simple setae; basal pad of claw rather flat, with short and long setae (Fig. 3E). All foliaceous setae appear in various sizes.

Maxilliped (Fig. 3C): Shape and size similar to that of maxilla. Segments 1-3 forming complex (interconnected)

articulation, with rows or fields of 3-11 foliaceous setae accompanied by several simple setae. Lacertus similar to that of maxilla, but slightly less expanded. Brachium generally similar to that of maxilla, fused into 3 segments (5-7 + 8 + claw); armature on inner margin denser than in maxilla. Claw (segment 9) similar to maxilla (Fig. 3E).

Trunk appendages (Fig. 1C-F): Limbs of anterior and mid-trunk largest, becoming gradually smaller and narrower towards posterior end of trunk and on first (anterior-most) trunk segment; last (posterior-most) trunk segment with incipient limb buds. Anterior and mid-trunk limbs: Protopod with prominent pointed process. Segment 1 of endopod bearing 1 short, stout, plumose seta on medial projection. Segment 2 with 1 short, stout, serrate seta on midmedial projection and 2 stout serrate setae on distolateral corner. Segment 3 with long plumose setae along both inner and outer margins, and a few stout serrate setae on distal corners. Segment 4 rather narrow, with marginal plumose setae. Exopod with 3 approximately equally long segments; segment 1 bearing a row of long plumose setae on lateral margin and several short, stout, serrate setae on distolateral corner. Segment 2 similar to segment 1, but with a few additional plumose setae on distomedial margin. Segment 3 bearing continuous row of long plumose setae. Limbs of posterior trunk (Fig. 1F) more slender than those of anterior and mid-trunk sections; projections and processes of protopod and endopod reduced.

Anal segment longer than wide (Fig. 1G). Caudal rami 1.4 times longer than anal segment, with marginal and apical setules.

DISCUSSION

Taxonomic Affinities

Pleomothra is distinguished from all other genera in the remipede order Nectiopoda by a number of prominent autapomorphic features. These include, in particular, massive, modified maxillules, and a head shield with posterolateral projections (see also discussion on "The lost maxillular segment" below). The new species described herein is assigned to *Pleomothra* because it exhibits all diagnostic characters of the genus.

Pleomothra fragilis n. sp. can be distinguished from the type species *P. apletocheles* by the shape of the head shield. In contrast to *P. apletocheles*, the head shield of *P. fragilis* appears longer and more slender; it does not cover the first trunk segment, and is equipped with very long and thin posterolateral processes (which are shorter and wider in *P. apletocheles*). The head shield in *P. fragilis* is also characterized by a distinct lateral contraction that divides the shield into a quadrangular-shaped anterior part and a sub-trapezoidal posterior section. Furthermore, the pleurotergites of the anterior trunk are much weaker developed in *P. fragilis* than in *P. apletocheles*.

Another unique diagnostic character is the absence of a lacinia mobilis on the left mandible in *P. fragilis*. In *P. apletocheles*, the left lacinia is reduced to a single spine-like denticle attached or fused to the molar process. In addition, the stout setae on the apical surface of the molar process are smaller and shorter in *P. fragilis* than in *P. apletocheles*.

Noticeable differences can also be found in the maxillules of both species. In *P. fragilis*, the third maxillary segment is much longer, and the subchelate unit, with a slightly concave inner surface, is smaller and less massive than that of *P. apletocheles*. Additional differences include the armature of maxilla and maxilliped: the foliaceous setae on the brachia in *P. fragilis* appear more pointed than the candeliform setae in *P. apletocheles*.

Moreover, the trunk appendages in *P. fragilis* do not show the tendency to become less setose towards the posterior end, as observed in several specimens of *P. apletocheles*, and the caudal rami are 1.4 longer than the anal segment (only slightly longer in *P. apletocheles*); the peduncular pad on the antennule is more expanded and bears denser rows of aesthetascs; and the antenna in *P. fragilis* exhibits a denser setation than in *P. apletocheles*.

Morphologic Particularities in the Light of Early Development

The Gnathobasic Character of the Mandible.—Recent discoveries of remipede larvae by Koenemann et al. (2007c) comprised four ortho- and metanauplii and a 3.7 mm postnauplius. Based on the posterolateral projections of its head shield, the postnauplius could be identified as belonging to the genus *Pleomothra* (Fig. 5). This unique character is only found in *Pleomothra*.

The postnauplius exhibits transitional developmental features between the earlier ortho-/metanaupliar stages and juvenile/adult morphology. The most conspicuous metamorphosis can be observed in the reduction of the long, biramous naupliar mandible to a compact, chewing and biting mandible in adult remipedes (see Koenemann et al. 2007c). In the postnauplius, the biramous telopodite is still present, but distinctly reduced, while the coxopodite has developed into a prominent, proximomedial endite. The reduced telopodite is inserted lateral to the developing proximomedial endite that is directed towards the stomatodaeum. This distinct positional separation suggests that the prospective gnathal parts (pars molaris, lacinia mobilis and incisor process) are likely to be derived from the proximomedial endite and not from the biramous telopodite. Hence, the developmental data generally accord with the gnathobasic character of the crustacean mandible (e.g., Scholtz et al., 1998).

The Lacinia ‘Immobilis’.—We were somewhat surprised to find that the lacinia mobilis on the left mandible in *P. fragilis* is entirely lacking. In all extant Remipedia, the laciniae are asymmetrical on left and right mandibles. The right lacinia mobilis is generally equipped with three prominent denticles, whereas the left lacinia has a straight to crescent-shaped apical margin with irregular serrations. Since the left lacinia is typically also slightly smaller than that on the right mandible, these asymmetrical features may point at a tendency towards a reduction of the left lacinia.

Our reexamination of specimens of *P. apletocheles* revealed a left lacinia that was greatly reduced to a single, finger-shaped denticle with a hardened apical cusp. This denticle appeared attached or partly fused to the molar (see also Yager, 1989; fig. 1c). A detailed comparative analysis

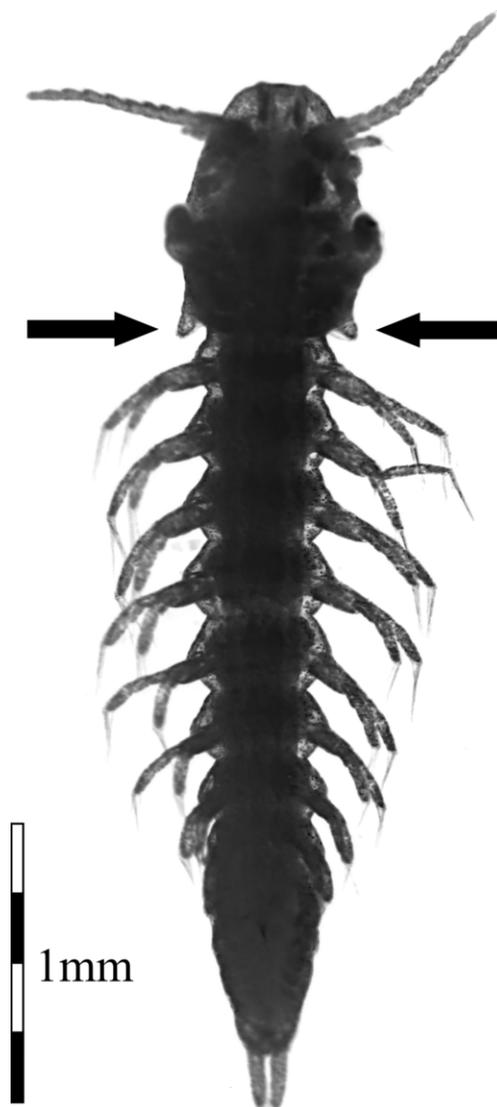


Fig. 5. Photograph of post-naupliar larval stage of *Pleomothra*. Arrows point at posterolateral projections of the cephalic shield.

of laciniae mobiles in various arthropods by Richter et al. (2002) suggested that these mandibular structures are not homologous between some higher crustacean taxa. Moreover, Richter et al. (2002) showed that the laciniae in Remipedia do not have articular condyles at their bases, and are, therefore, **not** moveable structures.

Based on the unique mandibular reductions in *Pleomothra*, we think that the lacinia in Remipedia is derived from the molar edge rather than from the pars incisivus. Lacinia and molar appear as fused units, well-separated from the incisor process. Of course, the ultimate clarification of these issues depends on unequivocal morphologic/developmental data. We now know that the development of the mandible into its adult form occurs in postnaupliar larvae of *Pleomothra* prior to the juvenile, feeding stage.

The Lost Maxillary Segment.—In all species of Remipedia, the maxillule is composed of seven segments (counting the claw as terminal segment). The sole exception is the six-

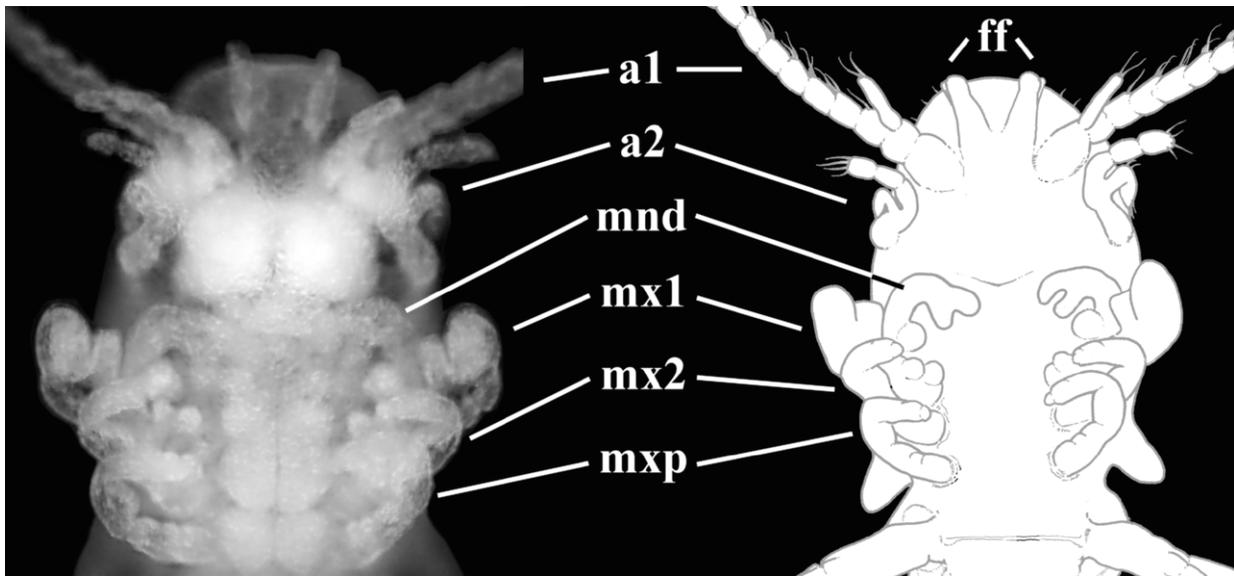


Fig. 6. Photograph (left) and drawing of post-naupliar larval stage of *Pleomothra* (modified from Koenemann et al., 2007c); ventral view of head. Abbreviations: ff = frontal filaments; a1 = antennule; a2 = antenna; mnd = mandible; mx1 = maxillule; mx2 = maxilla; mxp = maxilliped.

segmented, massive maxillule of *Pleomothra*, which exhibits several unique modifications. These include a second maxillulary joint between segments three and four (Fig. 3). How can we interpret this modification in the light of the transitional morphology of the postnauplius of *Pleomothra*?

Koenemann et al. (2007a), who compared individual maxillulary segments among remipede taxa, proposed that the sixth maxillulary segment, i.e., the segment proximal to the claw, is lost in *Pleomothra*. However, the morphology of the maxillules in the new species *P. fragilis* suggests that the sixth segment is not completely lost, but may be modified instead. The slender, bowed subapical process on the inner margin of segment five appears to correspond both with internal structures and fine surficial sutures that extend over the entire width of the limb, parallel to the claw (Figs. 3A, 4B). These structures may represent a modified remnant of the original sixth segment.

In the postnauplius, the three pairs of postmandibular limbs (maxillules, maxillae, and maxillipeds) already exhibit their characteristic prehensile forms. The elbows are developed, and some endites are beginning to emerge. For example, the first maxilla (maxillule) begins to resemble the massive adult maxillule of *Pleomothra*. However, articulations into individual segments are incipient or not yet detectable (Fig. 6).

If the sixth segment is indeed lost (as proposed by Koenemann et al., 2007a), or reduced and modified (as the morphology of the new species *P. fragilis* seems to imply), one would expect to see this kind of reduction or modification at some point of time during early development. However, in the postnauplius, the maxillule has taken its characteristic shape **before** individual segments have become distinguishable. A recapitulation of the speleonecid-type of maxillule followed by a transformation into the *Pleomothra*-type is not observable. In this case, it appears that the identification of reduced or modified maxillular

segments cannot be resolved by morphology but will depend on unraveling the control of developmental patterning genes.

Ecology and Biogeography

Oven Rock Cave on Great Guana Cay (Exuma Cays) contains one of the most diverse communities of anchialine stygobites known to date. In addition to the new species of *Pleomothra* described herein, the cave contains the remipede *Godzilliognomus* cf. *frondosus*; the epactericiscid copepods *Bofuriella vorata* Fosshagen, Boxshall & Iliffe, 2001; *Bomburiella gigas* Fosshagen, Boxshall & Iliffe, 2001; *Enantronoides bahamensis* Fosshagen, Boxshall & Iliffe, 2001; and *Oinella longiseta* Fosshagen, Boxshall & Iliffe, 2001; the halocyprid ostracods *Deeveya exleyi* Kornicker & Iliffe, 1998, *Danielopolina exuma* Kornicker & Iliffe, 1998, *Danielopolina kakuki* Kornicker & Iliffe, 2000, and *Spelaeoecia capax* Kornicker, 1990 (in Kornicker et al., 1990); the cirrolanid isopods *Bahalana exumina* Botosaneanu & Iliffe, 2002 and *Cirolana (Cirolana) troglaxuma* Botosaneanu & Iliffe, 1997; the pardaliscid amphipod *Spelaeonicippe provo* Stock & Vermeulen, 1982; the stenopodid shrimp *Macromaxillocaris bahamaensis* Alvarez, Iliffe & Villalobos, 2006; the hippolytid shrimp *Barbouria cubensis* (Von Martens, 1872), the thermosbaenacean *Tulumella* sp.; and the polynoid polychaete *Pelagomacellicephala*. A description and map of Oven Rock Cave is included in Kornicker & Iliffe (1998).

The new species *Pleomothra fragilis* is known from a single cave on the Great Bahama Bank, while *Pleomothra aplocheles* inhabits one cave each on Abaco and Grand Bahama, both islands on the Little Bahama Bank. These two shallow water banks are separated by the Providence Channel, a nearly 5 km deep, steep walled channel which is more than 225 km in length and 37 km wide at its widest point.

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