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A new genus of monstrilloid copepods (Crustacea) with anteriorly pointing ovigerous spines and related adaptations for subthoracic brooding

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***Maemonstrilla* gen. nov.**, known exclusively from females, is proposed for *Monstrilla longipes* A. Scott, 1909, *M. turgida* A. Scott, 1909, and five new species from coral reef plankton in the Ryukyu Islands, Japan: ***Maemonstrilla hyottoko* sp. nov.** (type species), ***M. polka* sp. nov.**, ***M. spinicoxa* sp. nov.**, ***M. simplex* sp. nov.** and ***M. okame* sp. nov.** A syntype of *M. turgida* was examined, but the holotype of *M. longipes* is lost; the latter species, being similar to several of the new species, is regarded as unidentifiable, and the identity of specimens assigned to it by several authors is put in doubt. Until now, all known female monstrilloids have had posteriorly trailing ovigerous spines, but in ***Maemonstrilla* gen. nov.** these spines point anteriorly and hold the egg mass between the legs beneath the thorax. This is the first known instance of subthoracic brooding in a planktonic copepod; its functional significance is discussed, and brooding habits of non-planktonic copepods are briefly reviewed. The intercoxal sclerites of legs 1–4 in ***Maemonstrilla* gen. nov.** are very wide, making room for the eggs. In all species except ***M. turgida* comb. nov.**, the inner seta of the proximal segment of each leg ramus is either absent or reduced to a nub; this may lessen interference of the egg mass with leg movement. All species have a uniramous leg 5 with two setae, except ***M. turgida* comb. nov.** (biramous with setae on both rami); ***M. turgida* comb. nov.** is evidently the sister-group of its congeners, each sister-group in the genus being defined by additional autapomorphies. Scanning electron micrographs of all the Ryukyuan species except ***M. simplex* sp. nov.** are provided; these constitute a preliminary survey of monstrilloid integumental organs and cuticular ornamentation. Among the unusual features are two lobes at the base of the coxa in legs 1–4 of ***M. polka* sp. nov.** and ***M. spinicoxa* sp. nov.** and two pairs of posterodorsal spine-like scales on the first and second free pedigers of ***M. turgida* comb. nov.** Newly hatched nauplii of ***M. okame* sp. nov.**, examined by scanning electron microscopy, are generally similar to those of *Monstrilla hamatapex* Grygier & Ohtsuka, 1995, but with a different mandibular structure in which the distal hook and seta clearly represent the endopod, not enditic armament of the basis. © 2008 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2008, **152**, 459–506.

ADDITIONAL KEYWORDS: Copepoda – coral reef plankton – cuticular ornamentation – egg brooding – *Maemonstrilla* – Monstrilloida – nauplius larva – Ryukyu Islands – scanning electron microscopy – taxonomy.

INTRODUCTION

The copepod order Monstrilloida Sars, 1901 (*q.v.*) comprises about 120 nominal species in the single family Monstrillidae Dana, 1849 (*q.v.*); their literature was reviewed in detail by Grygier (1995a), following which Eduardo Suárez-Morales and colleagues have issued a large body of new taxonomic work (e.g. Suárez-Morales & Vásquez-Yeomans, 1996; Suárez-Morales & Riccardi, 1997; Suárez-Morales, 2000, 2001a, b; Suárez-Morales & Dias, 2000, 2001a; Suárez-Morales & Ivanenko, 2004; Suárez-Morales & Gasca, 2004; Suárez-Morales, Bello-Smith & Palma, 2006). Monstrillids have non-feeding, free-swimming adults that lack appendages between the antennules and swimming legs. Their endoparasitic larvae are

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*Corresponding author. E-mail: grygier@lbm.go.jp known from an increasingly diverse assortment of polychaetes, molluscs and other invertebrates (Huys *et al*., 2007), although the details of many recent finds remain to be published.

The relationship of the Monstrillidae to other taxa within the Copepoda, especially the morphologically and ontogenetically similar family Thaumatopsyllidae Sars, 1913 (see Ho *et al*., 2003; Boxshall & Halsey, 2004) as well as the order Siphonostomatoida Thorell, 1859, has been the matter of much recent discussion. Even the validity of the order Monstrilloida is in question. Huys *et al*. (2007) provide an entry to this literature while providing evidence for a placement of the Monstrillidae within the Siphonostomatoida as the sister group to the caligiform families of that order. Be that as it may, the present paper is concerned only with the genus-level taxonomy of monstrillids. The validity of almost all the nominal genera universally assigned to the Monstrillidae has been disputed or doubtful, although the status of some has been clarified recently. The eight genera, and the current status of each, are listed here.

1. *Thaumatoessa* Krøyer in Gaimard, [1842] (see Krøyer, [1842]): invalid, placed on the Official Index of Rejected and Invalid Generic Names in Zoology; suppressed in favour of *Monstrilla* Dana, 1849 for purposes of the Principle of Priority by ICZN Opinion 1869 (International Commission on Zoological Nomenclature, 1997; see also Grygier, 1994a, 1995b).
2. *Monstrilla* Dana, 1849 (*q.v.*): valid, placed on the Official List of Generic Names in Zoology; subjective junior synonym of *Thaumatoessa*, but conserved for purposes of the Principle of Priority by ICZN Opinion 1869 (International Commission on Zoological Nomenclature, 1997; see also Grygier, 1994a, 1995b). The genus concept needs to be clarified by designation and detailed description of a neotype for the type species, *M. viridis* Dana, 1849.
3. *Thaumaleus* Krøyer, 1849 (*q.v.*): available but invalid, placed on the Official List of Generic Names in Zoology; objective junior synonym of *Thaumatoessa* and subjective junior synonym of *Monstrilla*; conserved for purposes of the Principle of Priority with respect to *Thaumatoessa* by ICZN Opinion 1869 (International Commission on Zoological Nomenclature, 1997; see also Grygier, 1994a, 1995b).
4. *Cymbasoma* Thompson, 1888 (*q.v.*): valid (see Grygier, 1994a).
5. *Haemocera* Malaquin, 1896 (*q.v.*): status uncertain. Variously treated as valid or as junior subjective synonym of *Monstrilla* or *Thaumaleus* (i.e. *Cymbasoma*), depending on each author's view of the validity and, if valid, the generic assignment, of the type species, *H. danae* (Claparède, 1863) (*q.v.*).
6. *Thaumatohessia* Giard, 1900 (*q.v.*): validity in doubt.
7. *Monstrillopsis* Sars, 1921 (*q.v.*): valid (see Suárez-Morales & Ivanenko, 2004; Suárez-Morales *et al*., 2006).
8. *Strilloma* Isaac, 1974 (see Isaac, 1974a): invalid; junior subjective synonym of *Monstrilla* (see Suárez-Morales & Gasca, 2004).

With the exclusion of *Strilloma*, which had been listed as valid by Boxshall & Halsey (2004), only three monstrillid genera can now be considered as clearly valid, *Monstrilla*, *Cymbasoma* and *Monstrillopsis*. The current concepts of even these genera are based on very few characters (e.g. keys in Isaac, 1975; Boxshall & Halsey, 2004). Females have been classified primarily on the basis of having three, four or five urosomal segments (somite of fifth legs through telson), and secondarily on the position of the oral papilla along the cephalothorax and whether or not the eyes are well developed. Males have been classified principally on the basis of having four or five urosomal segments (defined as above), secondarily on eye development, and, with many exceptions and qualifications, on the presence or absence and setation of the fifth legs. Before the revision by Davis (1949), the number of furcal setae had also been used in generic diagnoses, and this practice has recently been revived (Suárez-Morales *et al*., 2006). Huys & Boxshall (1991) reported somewhat genus-specific apical structures on the antennules of males. It should be obvious that primary reliance on a potentially convergent reduction character like ursomal segment number results in the possibility that a greater or lesser number of segments characterizes paraphyletic or polyphyletic nominal taxa, respectively. Furthermore, incomplete division of urosomal segments is common among monstrillids, which raises the question of how to count them unambiguously.

In the present paper we propose a new genus of Monstrillidae that includes two previously known species originally collected by the Siboga Expedition (A. Scott, 1909) and five new species. This work thus adds to the list of recently redescribed Siboga monstrillids (see Suárez-Morales, 2001a, b). Unlike the other genera, our new one is defined by a detailed set of synapomorphies. The most important diagnostic features are connected with subthoracic egg brooding, a behaviour first observed here among planktonic copepods. Outlines of these findings were previously reported in a published meeting abstract (Grygier & Ohtsuka, 1996) and at two international meetings in 1998 and 2002.

MATERIAL AND METHODS

COLLECTION

Plankton was collected at six locations in the Ryukyu Islands, Japan. The major site was off the pier of the Sesoko Station, Tropical Biosphere Research Center, University of the Ryukyus, on Sesoko Island (26°38.2′N, 127°51.8′E), where sampling was performed occasionally in 1988, 1989, 1992, 1996 and 2003, usually shortly after dark, using a conical plankton net of 20 cm in mouth diameter and NXX13 nylon mesh (about 95-μm mesh openings). Surface sampling was done by repeatedly casting the net on the end of a rope while vertical tows were made from 1 to 2 m depth through a cloud of plankton attracted by a flashlight (most effective on moonless nights). The second site was the entrance channel to Kabira Bay, north-west Ishigaki Island (24°27.7′N, 124°8.7′E), 9 March 1993, 20:00 h; a flashlight sample was taken from a moored boat with the same kind of net. The third site was off Kabira, Ishigaki Island (geographical coordinates unknown), 14 April 1996, 20:00 h, using a light-trap for larval fish placed at 18 m depth. The fourth site was off a groin on a sandy beach on the central south coast of Ishigaki Island (24°20′N, 124°11′E), 30 April 1994, 21:30–22:00 h; a flashlight sample was taken with a conical plankton net of 30 cm mouth diameter and NXX13 mesh. The fifth site was Hirara port on Miyako Island (approx. 24°48.5′N, 125°17.5′E), 5 May 1993, and the sixth was Shirahama, Iriomote Island (24°21.6′N, 123°44.9′E); in both places a plankton net was used but other details are unknown. All plankton samples were fixed in 5% or stronger seawater formalin. The monstrillids were sorted later under a dissecting microscope and stored in seawater formalin through all examinations. Most were transferred to 70% ethanol upon being deposited in museums.

PREPARATION

Colour photographs of some specimens from Ishigaki Island were taken with an Olympus SZH photomicroscope within a few days of preservation. For light microscopy, specimens were examined as whole mounts in glycerine in a depression slide, using a Nikon Optiphot microscope equipped with both differential interference contrast and phase contrast optics, and a drawing tube; pores and pit setae were sought using normal optics with an open diaphragm. To avoid collapsing the often hollow cephalothorax of the copepods, a small amount of glycerine was added to a drop of seawater formalin containing the specimen as an intermediate step. Dissected legs were mounted on glass slides in glycerine jelly for microscopical examination.

For scanning electron microscopy (SEM), adult specimens were dehydrated through a graded ethanol series, infiltrated with isoamyl acetate, critical-point dried from liquid CO_2, mounted on brass stubs, and photographed with a JEOL JSM-T20 scanning electron microscope at an acceleration voltage of 20 kV. Nauplius larvae of *Maemonstrilla okame* were obtained by removing the egg masses from living females and leaving them to hatch in seawater in 8-mL glass vials for a couple of days; a few drops of concentrated formalin were then added. Several attempts were made to prepare such nauplii for SEM following the protocol of Grygier & Ohtsuka (1995). Most attempts failed due to incomplete dehydration or loss of all specimens, but one trial resulted in preparations of rather low quality, which, nonetheless, yielded some usable micrographs.

DEFINITIONS AND DESCRIPTIVE CONVENTIONS

The antennular setation is described according to the nomenclature proposed by Grygier & Ohtsuka (1995: fig. 6). The ‘hyaline bodies’ noted as being absent in *Maemonstrilla* are a pair of clear, uncoloured, lens-like objects found between the external body cuticle and the lateral cups of the naupliar eye in some as yet undescribed monstrillids (our unpubl. data). So-called ‘scars’ behind the bases of the antennules presumably mark the sites of the larval absorptive processes. The oral papilla is the conical structure with an apical pore, found near the anterior end of the ventral side of the cephalothorax. The rear of the cephalothorax (corresponding to the incorporated second thoracomere or first pediger) and the succeeding four somites each bear from one to five pairs of pit setae *sensu* Grygier & Ohtsuka (1995), i.e. hair-like sensilla each arising from a round, shallow pit. No special distinction is made between spines and setae on legs 1–4 (the swimming legs) because the so-called spines are a kind of seta (spiniform seta herein) and the outer apical seta of the third exopodal segment is homologous to a ‘spine’ in the legs of other copepods (Huys & Boxshall, 1991). We refer to the long, egg-bearing structures that arise from the genital somite as ovigerous spines. There are fewer urosomal segments in monstrilloids than in ordinary copepods and it is unclear which segments are fused or undeveloped. We have thus adopted the following terminology for this part of the body: fourth free pediger, anterior and posterior parts of genital compound somite, penultimate segment, and telson (for the so-called ‘anal somite’) (Fig. 1B). The drawings exhibit some simplifications compared with those of Huys & Boxshall (1991). Unless stated otherwise, all the long, strap-like setae (series II–V) in the antennules have two rows of fairly widely spaced setules, all the longer,

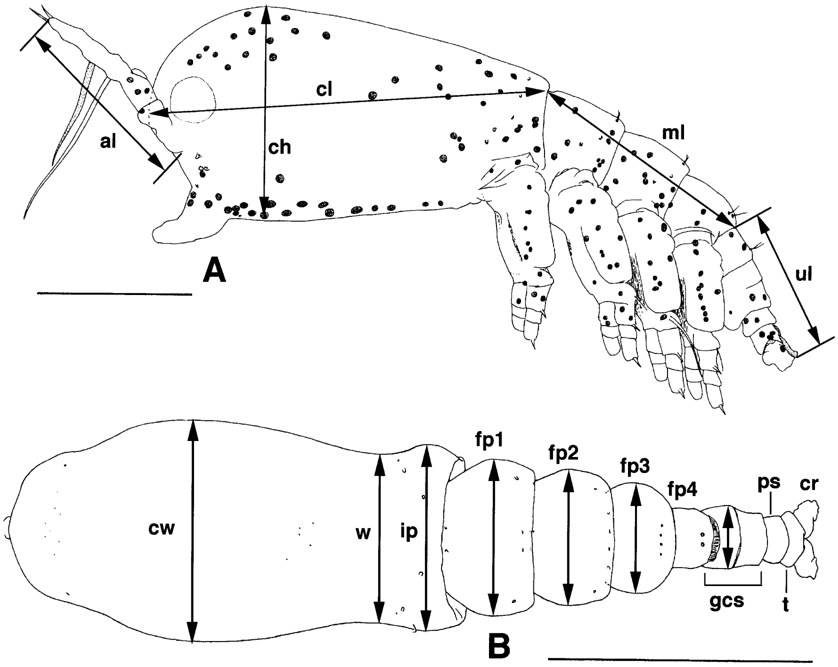


Figure 1. Body form of females of representative species of ***Maemonstrilla* gen. nov.**, with explanation of segmental terminology and measurements taken. A, ***Maemonstrilla polka* sp. nov.**, south coast of Ishigaki Island, 30.iv.1994, lateral view (paratype, SO lab; same specimen as Fig. 7A), with red dots. B, ***Maemonstrilla turgida*** (A. Scott, 1909) **comb. nov.**, Sesoko Island, 31.viii.1989, dorsal view (KMNH IvR 700 225). Abbreviations: al, antennal length; ch, cephalothorax height; cl, cephalothorax length; cr, caudal ramus; cw, cephalothorax width; fp1–4, free pedigers 1–4 (i.e. thoracomeres 3–6); gcs, genital compound somite; ip, incorporated pediger (i.e. thoracomere 2); ml, metasome length; ps, penultimate somite; t, telson; ul, urosome length; w, waist. Scale bars = 0.5 mm.

non-spiniform setae of legs 1–5 are biserially plumose except for the outer apical exopodal setae of legs 1–4 (uniserially plumose on the inner side) and all the furcal setae (except sometimes the short dorsal one) are biserially plumose. The bulbous cephalothorax made length measurements difficult in dorsal view. Usually the following convention was adopted, in lateral view (Fig. 1A): cephalothorax length (straight-line distance from anterior end of body to dorsal boundary between cephalothorax and first free pediger), metasome length (distance thence to dorsal boundary between third and fouth free pedigers) and urosome length (distance thence to tips of caudal rami).

Deposition of types

Holotypes of all new species, and most paratypes and other specimens used in the preparation of the included drawings, have been deposited in the Kitakyushu Museum of Natural History and Human History, Kitakyushu city, Japan (KMNH). All other paratypes and voucher specimens, except for specimens mounted on SEM stubs, have been deposited in the following institutions: Lake Biwa Museum, Shiga Prefecture, Japan (LBM); National Museum of Natural History, Smithsonian Institution (USNM); Institute for Systematics and Population Biology (Zoölogisch Museum), University of Amsterdam (ZMA); and The Natural History Museum, London (NHM). Although the descriptions of new species presented here are largely based on SEM observations, and the specimens involved must therefore be counted among the paratypes of the respective species, we regard SEM preparations as intrinsically ephemeral (and probably already useless for re-observation). All SEM stubs are therefore retained for now in the second author's laboratory at Hiroshima University, Japan (SO lab). Negatives of SEM photos are held by the first author at the Lake Biwa Museum.

TAXONOMY

ORDER MONSTRILLOIDA SARS, 1901

FAMILY MONSTRILLIDAE DANA, 1849

GENUS *MAEMONSTRILLA* GEN. NOV.

Diagnosis for females: Ovigerous spines pointing forward between thoracopods. Legs 1–4 widely separated across midline; intercoxal sclerites of legs 1–4 low and approximately as wide as legs themselves. Cephalothorax bulbous, constituting about half of body length, with often very prominent oral papilla in anterior third of length and 2–4 (usually 3) small scars clustered behind base of each antennule. Naupliar eye well developed; hyaline bodies absent in front of the widely separated lateral cups. Dorsum of metasomal pedigers and all urosomal segments except telson occupied by extensive, more or less rectangular patches of denticles or spinules. Antennules with branched outer distal b-setae. Single pore on anterior face of third segment of each ramus in legs 1–4. Leg 5 either a long, narrow rod with two distal setae and at most a tiny, unarmed endopodal lobe, or bilobed with three setae on exopodal lobe and one (or supposedly two in one instance) on endopodal lobe. Urosome four-segmented; genital compound somite usually with obvious dorsal suture, lacking dorsal pores. Caudal rami with six setae and ventral pore. Males unknown (or unrecognized).

Etymology: From Japanese *mae* (front), referring to the anteriorly pointing ovigerous spines, and *Monstrilla*, the type genus of the family.

Type species: Maemonstrilla hyottoko sp. nov.

Remarks: Two species groups can be recognized within this new genus, one containing a number of species that are generally similar to *M. hyottoko*, and the other consisting of *M. turgida* (A. Scott, 1909) alone.

MAEMONSTRILLA HYOTTOKO SPECIES GROUP

Diagnosis: Cephalothorax with reticulate pattern of cuticular ridges. Antennules, lateral sides of metasomal somites and urosomal segments, dorsum of telson, and caudal rami also so ornamented, except in *M. simplex* sp. nov. Dorsal surface of metasomal pedigers and first three urosomal segments, as well as outer face of thoracopods (coxa and exopod), densely denticulate or spinulose, except in *M. simplex.* No spine-like scales posteriorly near dorsal midline on first and second free pedigers. Outer basis seta of leg 3 at least as long as exopod. No inner seta on first exopodal segment of legs 1–4; inner seta of first endopodal segment of these legs absent or represented by socket-like or button-like structure. Leg 5 a long, thin rod with two distal setae, one apical and one slightly subapical; endopodal lobe absent (or reportedly tiny and unarmed in one instance). Posterior part of genital compound somite with ventral protrusion.

***MAEMONSTRILLA HYOTTOKO* SP. NOV.**

FIGURES 2–6, 29

Diagnosis: Reticular ridges of cephalothorax sporadically spinulose and with many short side branches; complex cuticular figures present within wide anterior and posterior reticular meshes, but not within narrow meshes in between. On antennule, 2v-setae prominent and straight, $2v_2$ and $2v_3$ being particularly long; $4v_1$ seta about half as long as 3-seta, and latter over three times longer than other 4-setae. Oral papilla prominent. Pair of tubular pores anterior to oral papilla, with four spines on lip of each tube. Dorsal posterior margins of genital compound somite and penultimate segment each bearing six clusters of 3–4 large denticles; denticles immediately preceding these bigger than those over rest of dorsal surface. Posteroventral part of genital compound somite produced into large spur.

Etymology: Noun in apposition, from the Japanese festival mask called ‘Hyottoko’, which has a conical, protruding mouth similar to the oral papilla in this species.

Material examined: Eleven females collected by M. J. Grygier at Sesoko Island (type locality): holotype (used for microscopic drawings; vial and slide KMNH IvR 700 202) and seven paratypes, 13.viii.1989 (co-occurring with *M. spinicoxa* and *M. turgida*, see below) [of paratypes, four intact (ZMA Co. 205908), three used for SEM (SO lab), but one of latter also used for microscopic drawings (slide of legs: KMNH IvR 700 203)]; one intact paratype, 14.ix.1988 (NHM Reg. No. 2006. 1911); one intact paratype, 2.x.1992 (USNM 1093747) (co-occurring with *M. turgida*, see below); one intact paratype, 22.v.1996 (LBM Reg. No. 1430000926). In addition, one intact paratype female collected by S. Ohtsuka (LBM Reg. No. 1430000927), south coast of Ishigaki Island, 30.iv.1994. Four nontype females tentatively assigned to this species, all intact: three collected by A. Murase off Kabira, Ishigaki Island (co-occurring with *M. spinicoxa* and *M. turgida*, see below), 14.iv.1996 (LBM Reg. No. 1430000928); one collected by S. Kubota (KMNH IvR 700 204), Hirara Port, Miyako Island, 5.v.1993.

Description: Cephalothorax distinctly bulbous anteriorly (Fig. 2A); incorporated first pediger widening again in dorsal view behind distinct ‘waist’ (as in Fig. 1B). Measurements taken from seven or (for some) eight specimens from Sesoko Island. Body length in lateral view (sum of lengths of cephalothorax, metasome and urosome as defined in Fig. 1A) 1.15–1.60 mm, with these body regions contributing 49.6–52.1, 28.1–31.2 and 19.2–20.7%, respectively.

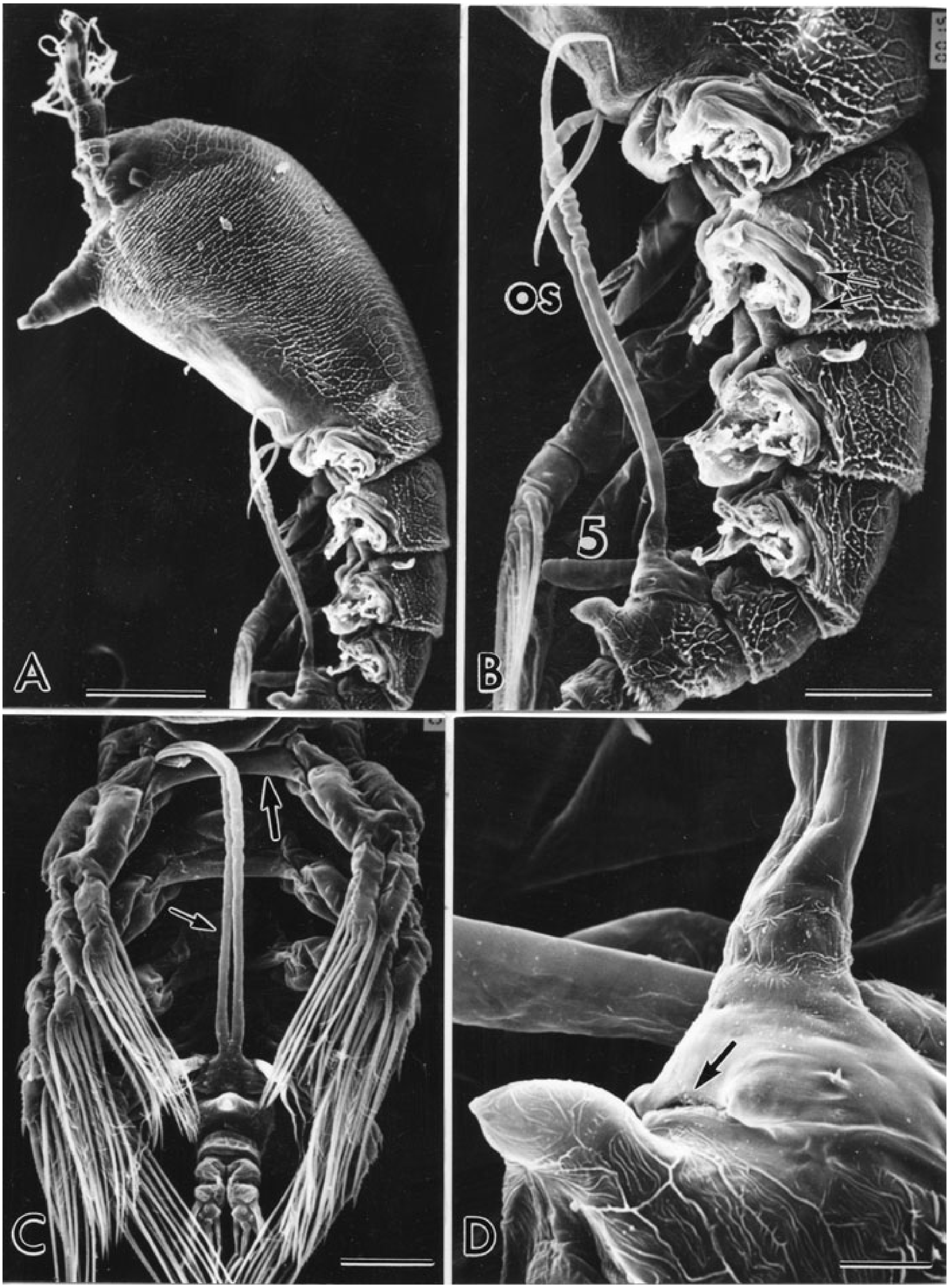


Figure 2. ***Maemonstrilla hyottoko*** **sp. nov.**, female paratypes (SO lab), Sesoko Island, 13.viii.1989, SEM. A, cephalothorax and metasome in lateral view, left legs removed. B, metasome and urosome of same specimen, lateral view, showing ovigerous spines (os) and leg 5 (numbered). C, metasome and urosome of different specimen, ventral view, showing ovigerous spines (small arrow), widely spaced legs 1–4, and low, wide intercoxal sclerites (e.g. large arrow). D, genital compound somite of specimen in A, ventrolateral view, showing base of ovigerous spines, copulatory opening (arrow), and spur-like posteroventral process. Scale bars = 200 μm in A; 100 μm in B, C; 20 μm in D.

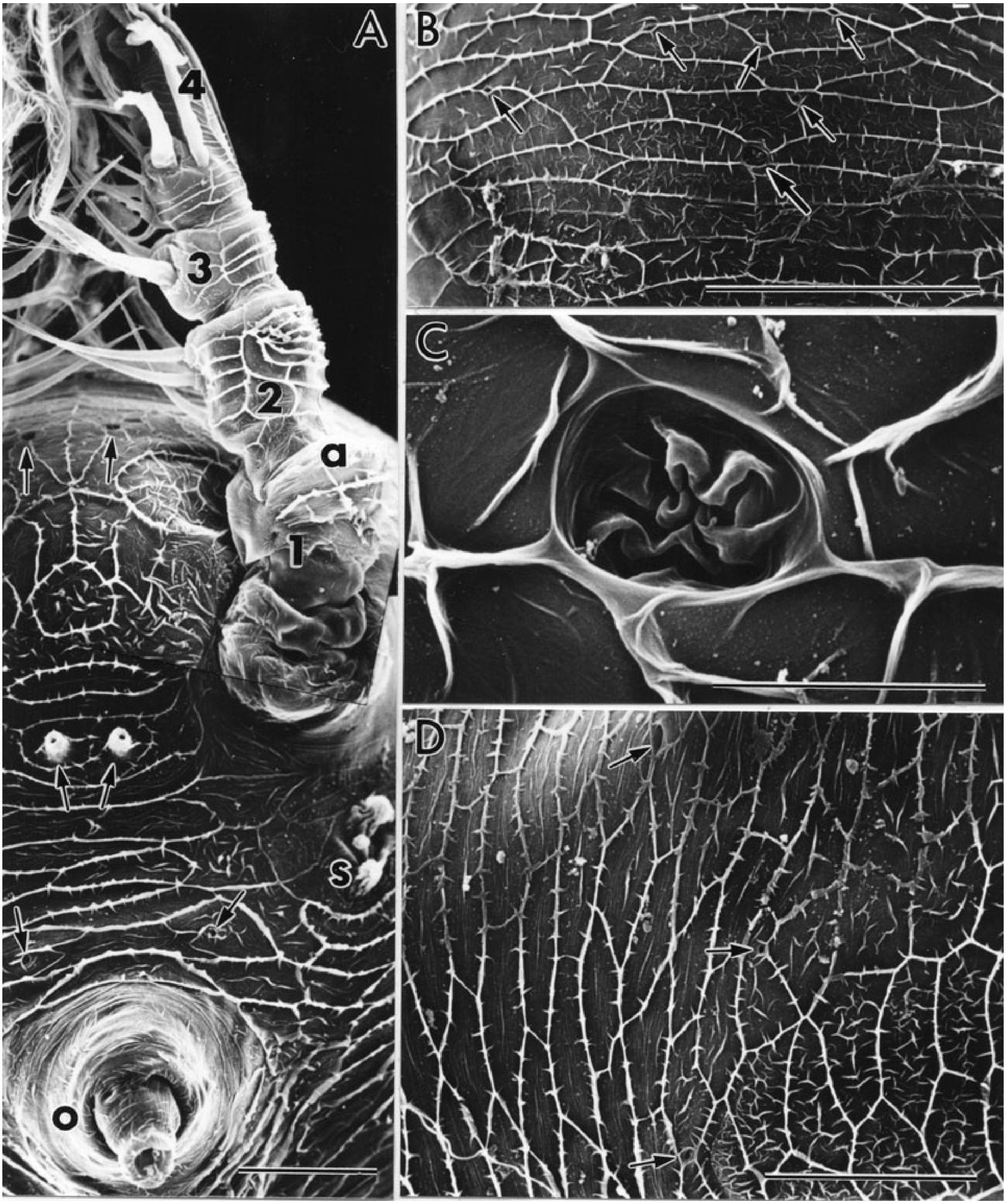


Figure 3. ***Maemonstrilla hyottoko* sp. nov.**, female paratypes (SO lab), Sesoko Island, 13.viii.1989, SEM. A, 'face' and left antennule (a), ventral view, showing oral papilla (o), scars (s), three pairs of pores (arrows), and segments of antennule (1–4). B, anterodorsal surface of cephalothorax (anterior at bottom), showing pores (small arrows) and pit-like organ (large arrow). C, detail of pit-like organ in B. D, pores (arrows) at border between narrow and wide reticular meshes in posterior half of cephalothorax, posterior to right. Scale bars = 50 μm in A, D; 100 μm in B; 10 μm in C.

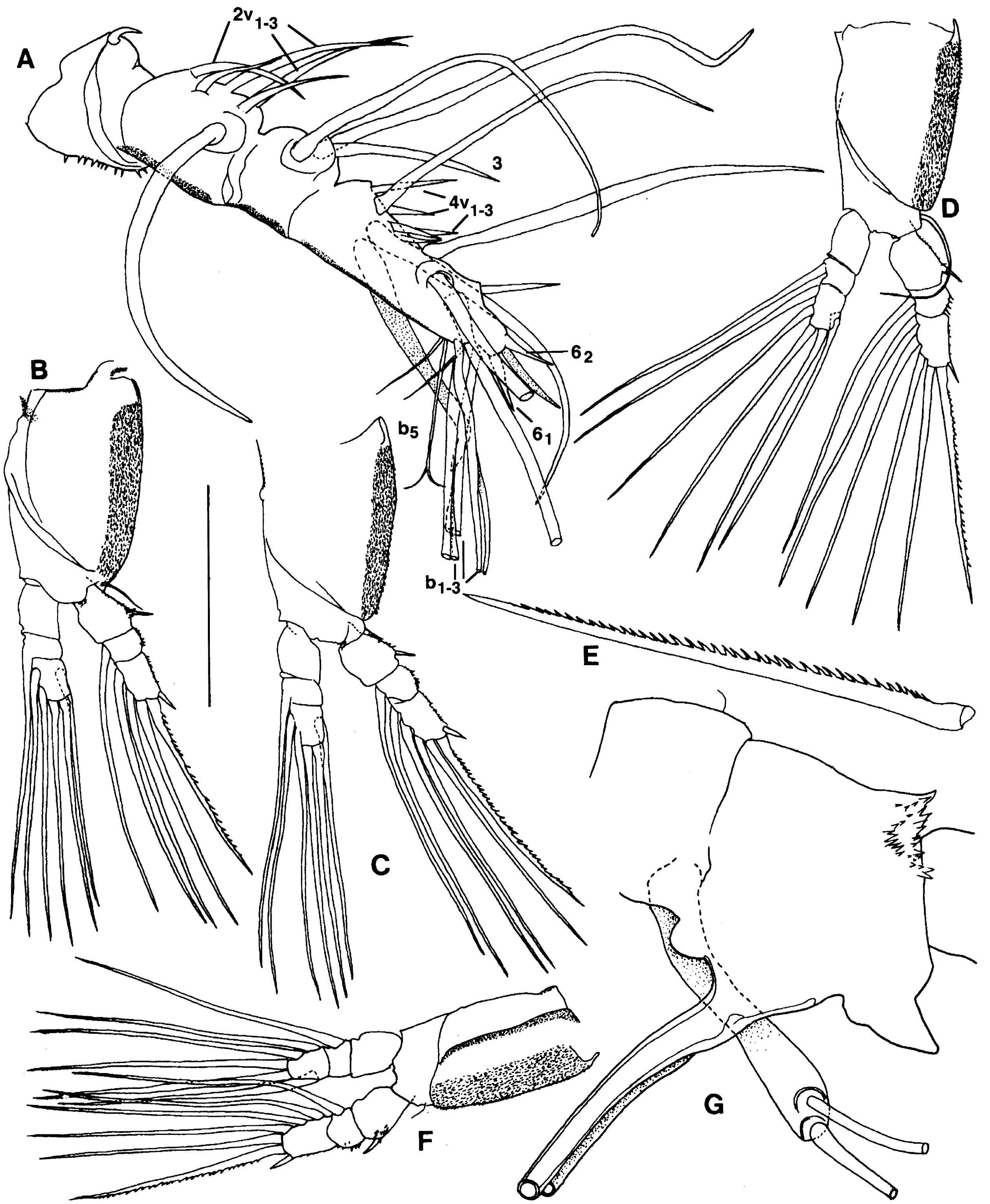


Figure 4. ***Maemonstrilla hyottoko*** **sp. nov.**, females, Sesoko Island, 13.viii.1989: A–D, F, G, holotype (KMNH IvR 700 202), E (same specimen as Fig. 2A; slide-mount of legs, KMNH IvR 700 203). A, right antennule, dorsal view, setules omitted, setal designations after Grygier & Ohtsuka (1995: fig. 6). B–D, right legs 1–3, respectively, posterior view, setules omitted. E, outer apical exopodal seta of left leg 3, setules along non-toothed side omitted (cf. Fig. 5C). F, right leg 4, posterior view, setules omitted. G, fourth free pediger and genital compound somite, lateral view, showing right leg 5, proximal parts of ovigerous spines, and posteroventral spur. Scale bar = 0.1 mm in A, E, G; 0.2 mm in B–D, F.

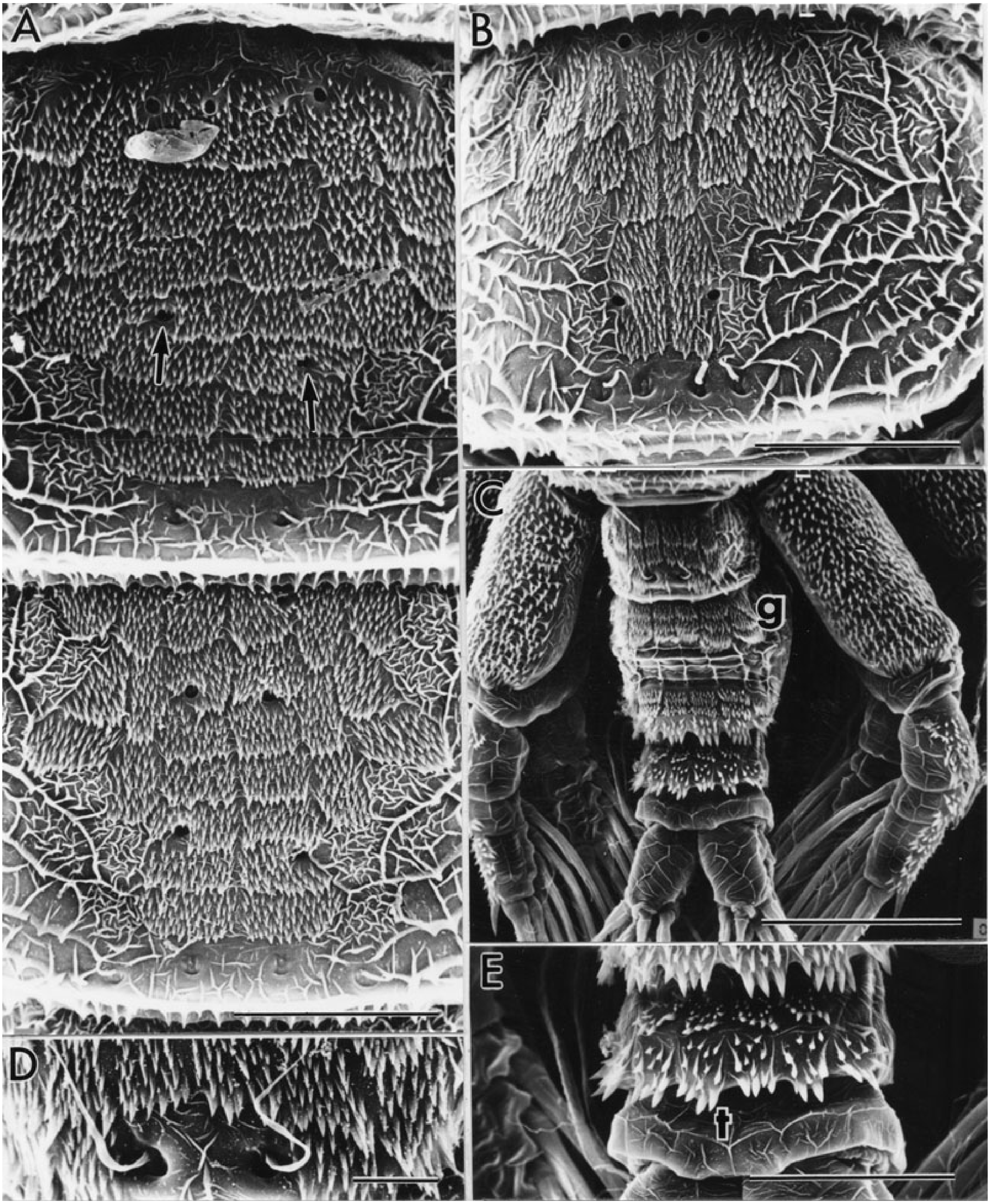


Figure 5. ***Maemonstrilla hyottoko*** **sp. nov.**, female paratype (SO lab), Sesoko Island, 13.viii.1989, SEM, anterior at top in all cases. A, dorsal surface of free pedigers 1 and 2; two obscured pores indicated by arrows. B, dorsal surface of free pediger 3. C, dorsal surface of urosome, including genital compound somite (g), and outer faces of legs 4. D, rear dorsal surface of free pediger 4, showing pit setae. E, dorsal surface of rear of urosome, including telson (t). Scale bars = 50 μm in A, B, E; 100 μm in C; 10 μm in D.

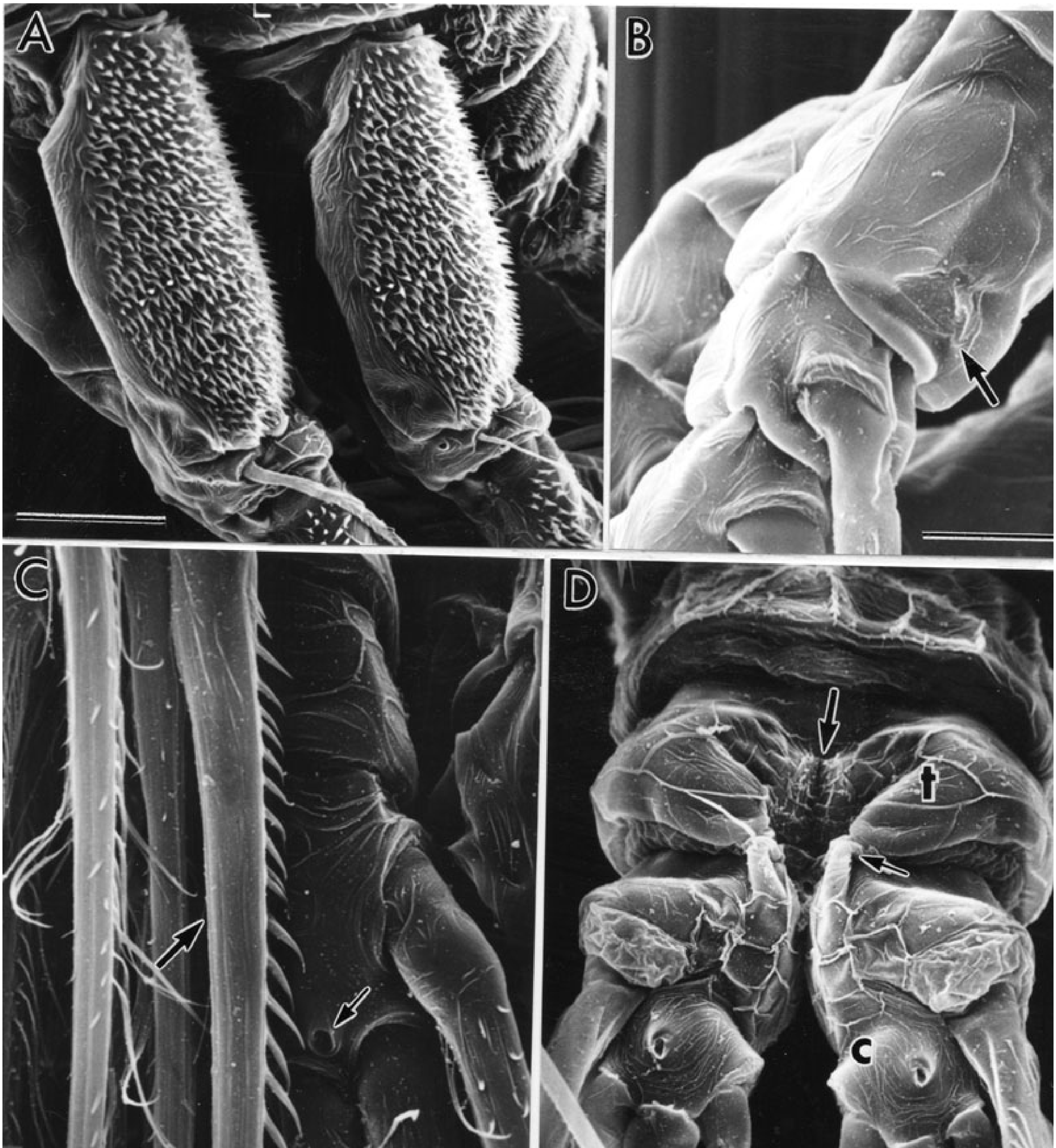


Figure 6. ***Maemonstrilla hyottoko* sp. nov.**, female paratypes (SO lab), Sesoko Island, 13.viii.1989, SEM. A, protopods of legs 3 and 4, outer view (anterior to left). B, endopod of a swimming leg, inner view showing site of absent seta on first segment (arrow). C, outer apical seta (large arrow) on third exopodal segment of leg 1 and pore (small arrow) on third endopodal segment of leg 2, anterior view. D, telson (t) and caudal rami (c), ventral view, showing anal opening (large arrow), and ventral pores and condylar articulations (small arrow) of rami. Scale bars = 50 μm in A; 20 μm in B, D; 10 μm in C.

Height and greatest width of cephalothorax 49.2–53.9 and 50.8–54.3% of cephalothorax length, respectively. Antennule length 40.1–46.1% of cephalothorax length. Width of incorporated first pediger 69.8–81.9% of greatest width; widths of succeeding three free pedigers and genital compound somite relative to that of incorporated pediger 81.1–89.5, 60.3–73.4, 53.4–56.3 and 32.2–37.5%, respectively. Ovigerous spines (seven pairs measured) 26.5–35.3% as long as body (as seen in dorsal view). Specimen from south coast of Ishigaki with wider first and second free pedigers (97.3 and 85.9% as wide as incorporated pediger, respectively) and slightly longer ovigerous spines (38.9% as long as body as seen in dorsal view). Non-type, tentatively included specimens from off Kabira and from Hirara port comprising two smaller specimens (body length as short as 1.07 mm) and ones exhibiting higher cephalothorax height/length ratios (57.9–64.5%).

Although mostly reticulate as mentioned in diagnosis, cephalothorax smooth in area posterodorsal to antennules and on posterior half of ventral side (except for band behind oral papilla) (Fig. 2A). Reticular meshes broad in posterior third and anterior sixth of cephalothorax, very narrow in intervening region; their borders and interiors as described in diagnosis.

Antennule clearly four-segmented, but proximal region of first segment consisting of complexly folded arthrodial membrane and sclerites for muscle attachment (Fig. 3A); reticular ridges becoming lower and simpler distally. All setal elements identified by Grygier & Ohtsuka (1995) present (Fig. 4A). Spiniform 2v-setae and 3-seta much longer than 4-setae; row of spinules present on at least 2v-seta, possibly on other spiniform setae. Outer distal b_{1-3} setae each branched at least twice in asymmetrically dichotomous manner; b_5 seta bifid. Apical 6-setae similar to each other in size.

Oral papilla (Fig. 3A) very large, funnel-shaped, directed ventrally and preceded by pair of simple pores. Pair of tubular pores, with four spines on lip of each pore, situated further anteriorly between posterior ends of bases of antennules. Cluster of three knob-like scars behind base of each antennule, middle knob smaller than others.

Forehead region (Fig. 3A) with pair of circles formed of cuticular ridges just anterodorsal to antennule bases, smaller circle on midline just posterior to these, and pair of pores anterodorsal to large circles (pair of hair-like sensilla seen arising from these pores in some paratypes). Subcircular pit with wrinkled thin cuticle on dorsal midline of forehead, 10 μm in largest diameter (Fig. 3B, C). In an SEM specimen, two pores observed behind this structure, and three pores on each side further laterally (some shown in Fig. 3B); numbers and positions of these pores not necessarily constant in other specimens. Lateral cups of naupliar eye about same size as ventral cup, about 80 μm in diameter.

Three pairs of dorsal pores on cephalothorax at posterior boundary between narrow and broad reticular meshes (Fig. 3D). Arrangement of dorsal pores and dorsal and lateral pit setae from rear of cephalothorax to urosome shown in Figure 29 (see also Fig. 5A–D). Dorsal pores on free pedigers 1–3 only. Dorsal pit setae in one widely separated pair on incorporated pediger; in one, two, two and one pair, respectively, on succeeding four free pedigers. In addition, four pairs of dorsolateral and lateral pit setae on incorporated pediger and two pairs each on first and second free pedigers, anterior pair on each segment located more ventrally than posterior one. Dorsum of first free pediger (Fig. 5A) covered with sharp, posteriorly directed denticles arrayed in six longitudinal rows of rectangular patches, these patches numbering 3-3-7-7-3-3, respectively; those of second free pediger arranged the same (Fig. 5A); denticle patches of third free pediger fewer, 3-2-4-4-2-3 (Fig. 5B); and those of fourth free pediger 2-3-2-2-3-2 (Fig. 5C). Dorsum of genital compound somite (Fig. 5C): anterior third with six rows of three denticle patches each; middle third with grid of cuticular ridges; posterior third with six rows of denticle patches arrayed 1-2-2-2-2-1, followed by band of six arrays of considerably larger denticles, with largest three or four denticles in each array extending beyond somite's posterior margin. Penultimate segment (Fig. 5C) with transverse band of four denticle patches followed by six arrays of large denticles like those on genital compound somite.

Legs 1–4 each with two arcuate sclerites laterally at base of leg (Fig. 2B). Intercoxal sclerites low and wide with ventrally produced outer corners (Fig. 2C). Protopod with longitudinal groove on anterior face; suture separating coxa and basis extending diagonally across posterior face and continuing around onto outer part of anterior face (Fig. 4B–D, F). Sharp, distally pointing denticles on outer faces of coxa and exopod (Figs 5C, 6A), as large as denticles on posterior margin of genital compound segment. Pore just in front of lateral seta on basis (Fig. 6A); this seta short and hair-like in legs 1, 2 and 4, but much longer and plumose in leg 3 (Fig. 4D, plumosity omitted). Posterior faces of rami lightly reticulated (Fig. 5C); distal pore on anterior face of third segment of each ramus (e.g. Fig. 6C). No inner seta on first exopodal or first endopodal segment (Fig. 6B). Outer spiniform seta on first and third exopodal segment in legs 1–4 simple, that of third segment bigger. Sparse spinules as well as two rows of long setules found on natatory setae (Fig. 6C): one inner seta on second segment of each ramus; two inner setae on third segment of each ramus in leg 1, but three inner setae on exopod in legs

2–4; one outer seta on third segment of endopod, and two apical setae on each ramus (Fig. 4B–D, F). Outer apical seta of exopod with outer row of widely spaced, talon-like denticles instead of setules (Figs 4E, 6C). Leg 5 rod-like, distally slightly clavate, with two apical setae (Figs 2B, 4G).

Ovigerous spines arising from conical projection of ventral surface of anterior half of genital compound segment (Fig. 2B, C). Crescent-shaped slit leading to copulatory opening at posterior base of cone (Fig. 2D); slit flanked by pair of small knobs projecting from cone. Tips of ovigerous spines found at any point between legs 2 and midlength of cephalothorax; spines cylindrical and smooth, but slightly thickened and wrinkled at two-thirds length, tips naked and tapered. Posteroventral protrusion of genital compound somite large, subconical, spur-like (Figs 2D, 4G).

Caudal rami (Figs 5C, 6D) lightly reticulate dorsally and with ventromedial condyle articulating to telson; anal slit visible in telson. Each ramus with ventral distal pore and six setae (at least five of them plumose), one arising ventrolaterally and the other five apically; most dorsal apical seta (seta VII of Huys & Boxshall, 1991) shorter than others, appearing smooth in some individuals but setulose in two specimens (perhaps setules orientated dorso-ventrally).

MAEMONSTRILLA POLKA SP. NOV.

FIGURES 1A, 7, 8A, 9–12, 13A, 29

Diagnosis: Spherical spots of red pigment throughout body. Cuticular ridges of cephalothorax sporadically spinulose but lacking side branches, discontinuous in anterior ventrolateral region; reticulations uniform in size, enclosing clusters of small, cuneiform cuticular figures. Spiniform 2v-setae and 3-seta on antennule about twice as long as 4-setae; apical 6-setae minutely spinulose. Outer proximal part of coxa of legs 1–4 produced into two low, oval lobes armed with spinules slightly larger than those on rest of coxa. Posterior dorsal margin of genital compound somite and penultimate segment each slightly produced into six flanges bearing minute spinules of same size and density as those over rest of dorsum. Posteroventral part of genital compound somite produced into apron-like flap.

Etymology: Derived from Polish via English, as in ‘polka dots’, referring to the characteristic red spots throughout the body and legs (cf. Figs 1A, 11, 13A); to be treated as a Latin adjective.

Material examined: Three ovigerous females collected by S. Ohtsuka on south coast of Ishigaki Island (type locality; co-occurring with *M. simplex* and *M. turgida*, see below), 30.iv.1994: holotype intact (KMNH IvR 700 205), used for photography; one paratype intact, but egg mass broken (KMNH IvR 700 215); other paratype used for light microscopic drawings and SEM, egg mass with ovigerous spines in vial and four legs on slide (vial and slide: KMNH IvR 700 216), rest of body on SEM stub (SO lab).

Description: Cephalothorax bulbous anteriorly, in lateral view tapering evenly from rounded front to rear (Figs 1A, 7A, 13A). In dorsal view, incorporated pediger widening only slightly behind ‘waist’. Spherical spots of red pigment throughout body and legs 1–4 (Figs 1A, 11, 13A).

Measurements taken from holotype and non-SEM paratype; widths approximate due to difficulty in orientating these ovigerous specimens for microscopic examination in dorsal view. Body length in lateral view (sum of lengths of cephalothorax, metasome and urosome as defined in Fig 1A) 2.56–2.66 mm, with these body regions contributing 51.6–52.7, 28.6–29.0 and 18.3–19.8%, respectively. Height and greatest width of cephalothorax 45.9–51.3 and 49.4–50.7% of cephalothorax length, respectively. Antennule length 42.5–46.15% that of cephalothorax. Width of incorporated pediger 72.4–79.2% of greatest width. Widths of succeeding three free pedigers relative to that of incorporated pediger 84.2–88.3, 74.7–75.1 and 63.0–63.2%, respectively.

Meshwork of cephalothorax and lateral parts of metasomal pedigers and urosome formed of finer cuticular ridges than in *M. hyottoko*, uniformly polygonal over most of surface (Figs 7A, 9A–D). Abundant small cuticular figures occurring inside meshes, and often fine lineations as well. Polygonal pattern largely replaced by maze-like pattern of discontinuous cuticular figures anterolaterally on cephalothorax (Fig. 7B). Oval, ridge-bounded region between antennules with denser, finer cuticular wrinkling than in regions to its front and rear (Fig. 9A). Oral papilla (Fig. 9A) and ventral side of cephalothorax posterior to it smooth, with very fine cuticular lineations. Dorsal side of telson (Fig. 10C) and caudal rami weakly reticulated.

Antennule clearly four-segmented. Basal part of first segment as in *M. hyottoko*. Distal three segments with fine cuticular ridges forming two rows of ladder-like reticulations (Fig. 7D). Setation generally as in *M. hyottoko* (Fig. 8A). 1-seta arising from medial protrusion of first segment. Spiniform 2v-setae and 3-seta longer than 4-setae, but relatively shorter than in *M. hyottoko*. Outer distal b_5-seta shown by SEM to bifurcate three times (Fig. 7D); b_4- and b_6-setae simple; a few setules apparently present on b_2-seta. Apical 6-setae subequal in size in dissected paratype, but lateral one 50% longer than medial one in undissected paratype; both 6-setae covered with abundant minuscule spinules.

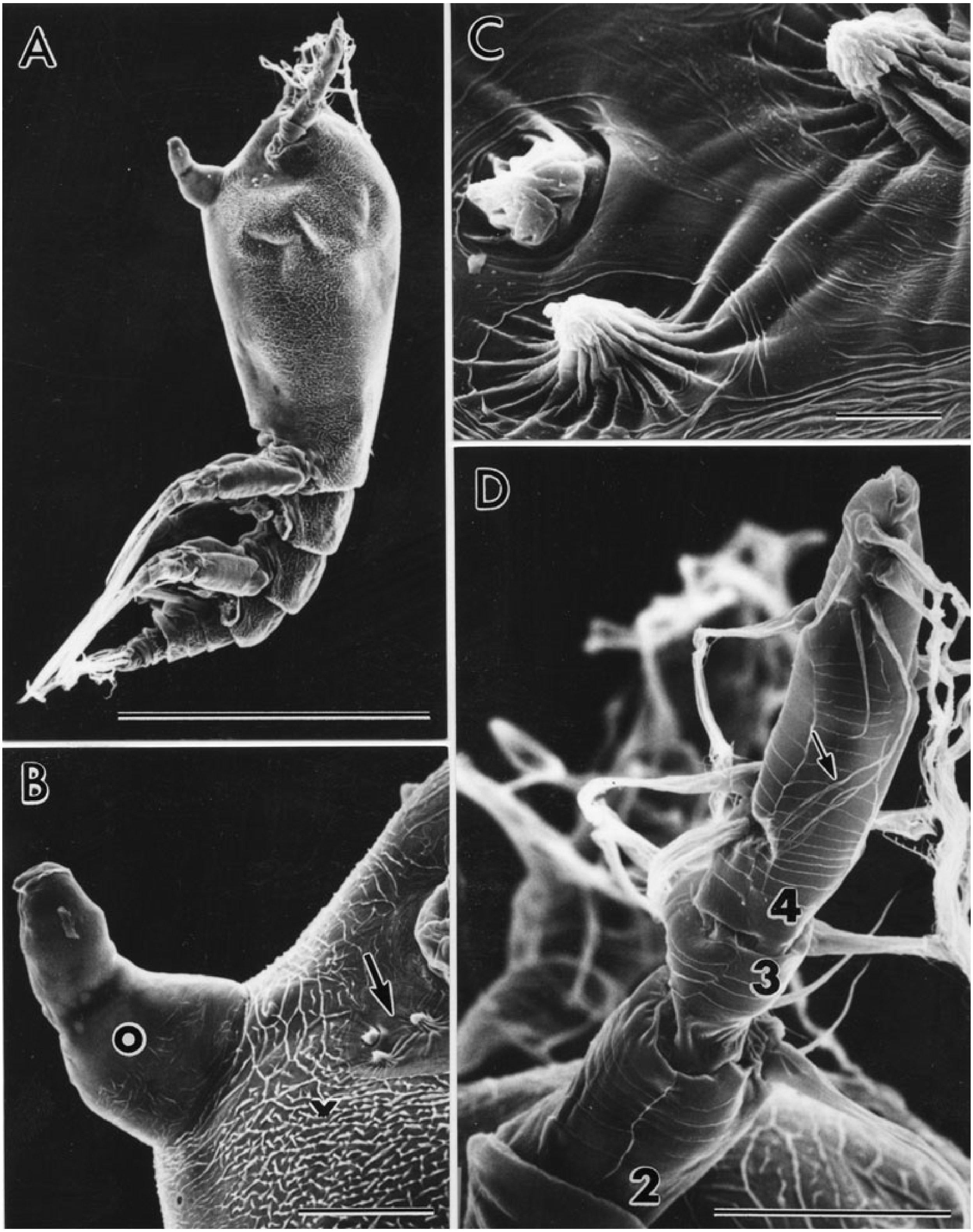


Figure 7. ***Maemonstrilla polka* sp. nov.**, female paratype (SO lab), south coast of Ishigaki Island, 30.iv.1994, SEM. A, habitus, lateral view, some legs removed (same specimen as in Figs 1A, 13A). B, oral papilla (o) and scars (arrow), left lateral view. C, detail of scars from B. D, left antennule, outer view, foreshortened due to viewing angle, more distal segments numbered (2–4), arrow indicating branches of b_5-seta. Scale bars = 1.0 mm in A; 0.1 mm in B, D; 10 μm in C.

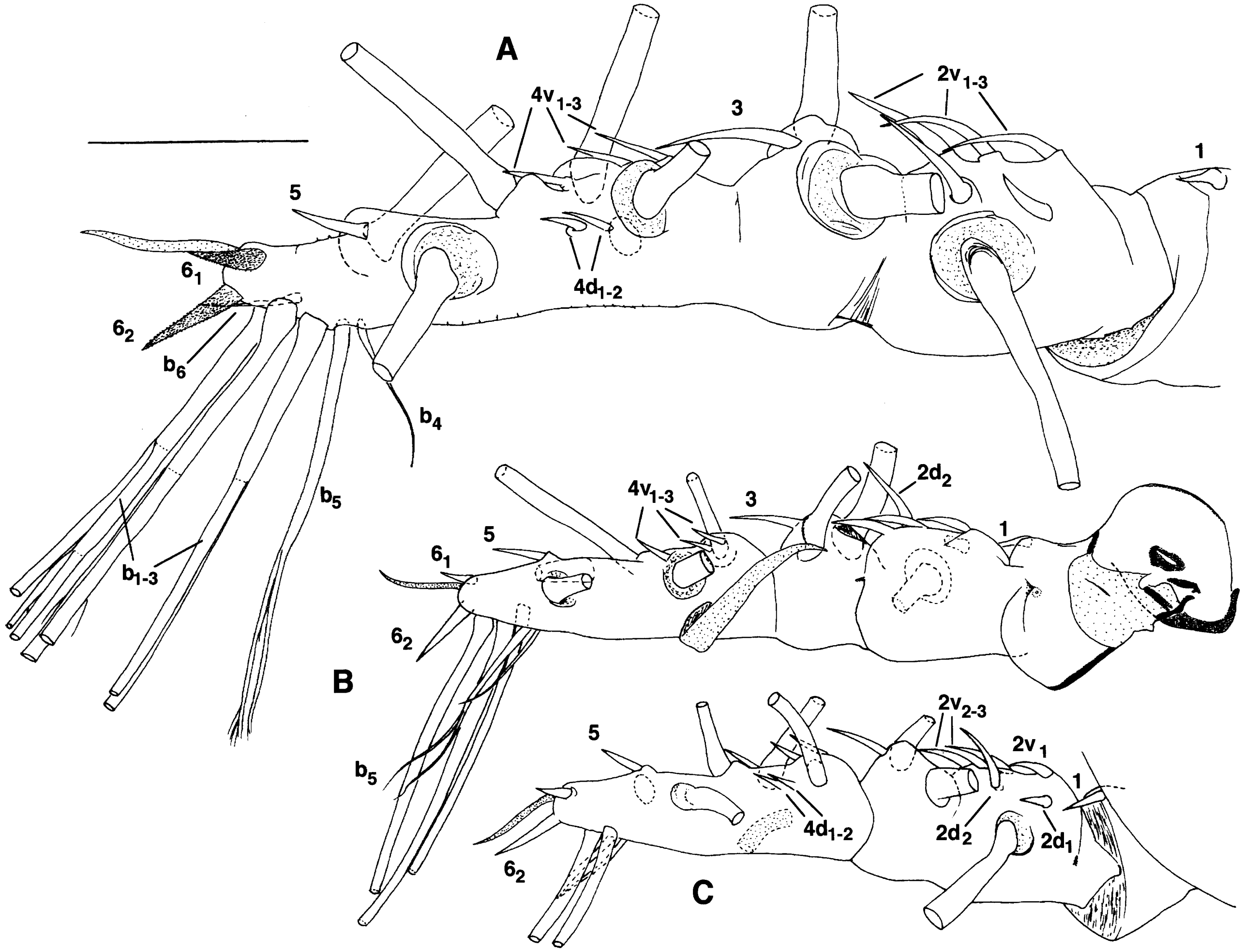


Figure 8. Antennules of two species of ***Maemonstrilla* gen. nov.**, setules omitted, setal designations after Grygier & Ohtsuka (1995: fig. 6). A, ***Maemonstrilla polka* sp. nov.**, female paratype (SO lab), south coast of Ishigaki Island, 30.iv.1994, right antennule, ventral view. B, ***Maemonstrilla spinicoxa* sp. nov.**, female holotype (KMNH IvR 700 217), Sesoko Island, 13.viii.1989, right antennule, ventral view. C, ***M. spinicoxa* sp. nov.**, same specimen, left antennule, dorsal view. Scale bar = 0.1 mm.

Oral papilla large, bent anteriorly at midlength in SEM paratype (Fig. 7B) and in holotype (Fig. 13A). Two pairs of simple pores just behind and just in front of oral papilla, respectively, and two more pairs further anteriorly between scar clusters (Fig. 9A). Medial anterior pair probably homologous to tubular pores of *M. hyottoko*. Three pairs of scars just posterior to bases of antennules, in form of fluted mounds (Fig. 7C). Pair of seta-like sensilla arising from pores between and dorsal to antennules on 'forehead' (Fig. 9A); at least seven pores dorsal to these; no pit similar to that in *M. hyottoko* observed. Naupliar eye as in *M. hyottoko*.

Presence of any dorsal pores along cephalothorax unconfirmed. Incorporated pediger with five pairs of dorsal and lateral pit-setae (Figs 9B, 29). Dorsum of free pedigers covered with very small, posteriorly directed spinules; faint cuticular ridges divide spinulose region into six rows of irregularly quadrangular fields, arranged 3-3-5-5-3-3 on first and second free pedigers (Fig. 10A), 3-2-4-5-2-3 on third (Fig. 10B). Anterior pores on dorsum of first free pediger unconfirmed by SEM, but pair of pores present just beyond midlength, as well as posterior pair of pit-setae (Fig. 10A). Second free pediger with three pairs of pores (anterior, one-third of way from front, and two-thirds of way from front), and two pairs of posterior pit-setae (Fig. 10A). First two free pedigers (but not third and fourth) with two pairs each of lateral pit-setae placed similarly to most lateral pairs of cephalothorax (and as in *M. hyottoko*) (Fig. 9C). Third free pediger with pair of anterior pores, another pair at two-thirds length, and two pairs of posterior pit-setae (Fig. 10B). Fouth free pediger (first urosome segment,

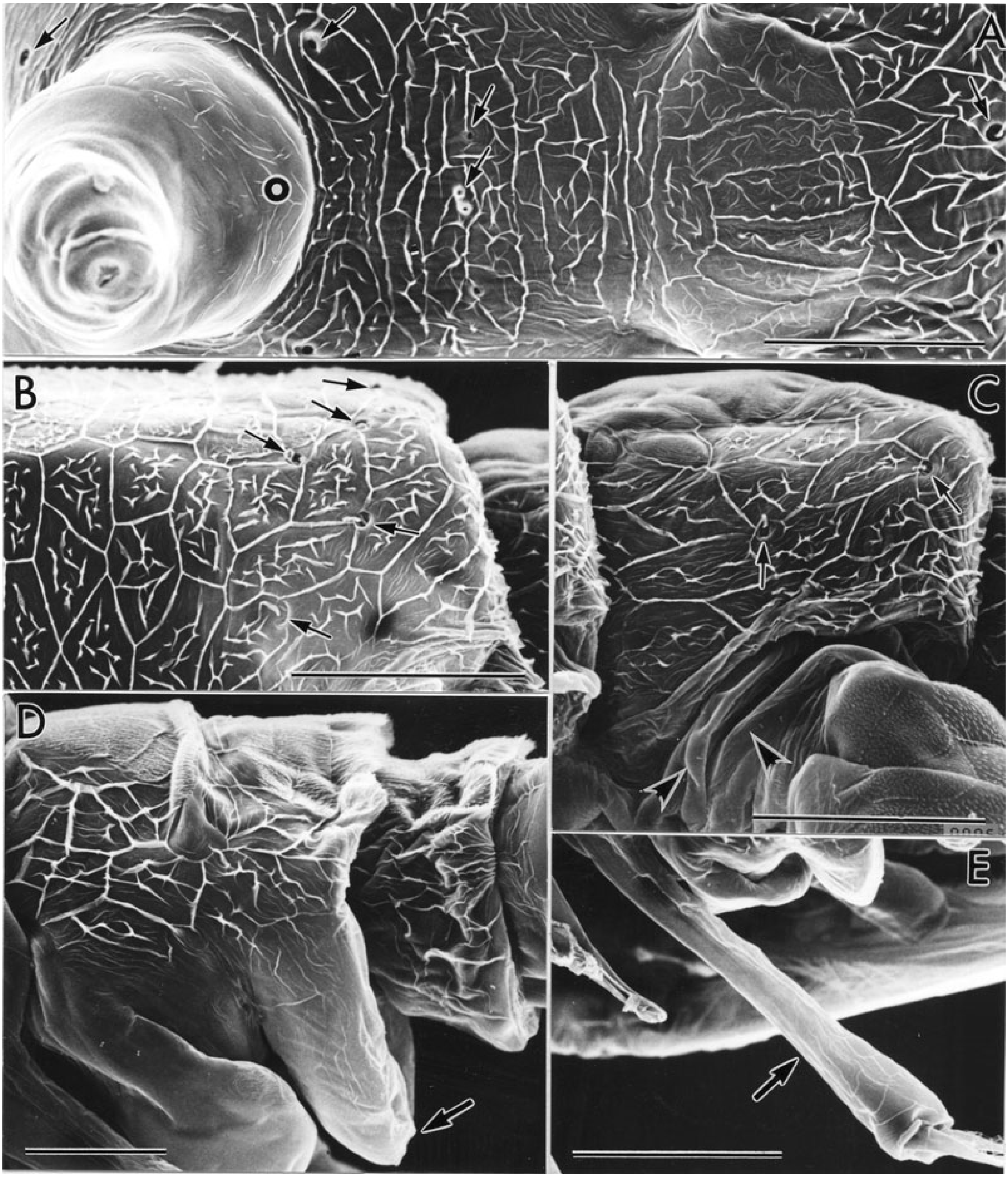


Figure 9. ***Maemonstrilla polka* sp. nov.**, female paratype (SO lab), south coast of Ishigaki Island, 30.iv.1994, SEM. A, anteroventral part of cephalothorax from oral papilla (o) to pair of hair-like sensilla on 'forehead' (far right, arrow), with three pairs of pores (other arrows). B, cephalothorax, right posterodorsal margin, dorsal view, showing five pit setae (arrows). C, free pediger 2, lateral view, showing two lateral pairs of pit setae (arrows) and two arcuate sclerites at base of leg (arrowheads), anterior to left. D, genital compound somite and penultimate segment of urosome, lateral view, anterior to left, showing apron-like posteroventral protrusion of compound somite (arrow). E, leg 5 (arrow). Scale bars = 0.1 mm in A–C, E; 50 μm in D.

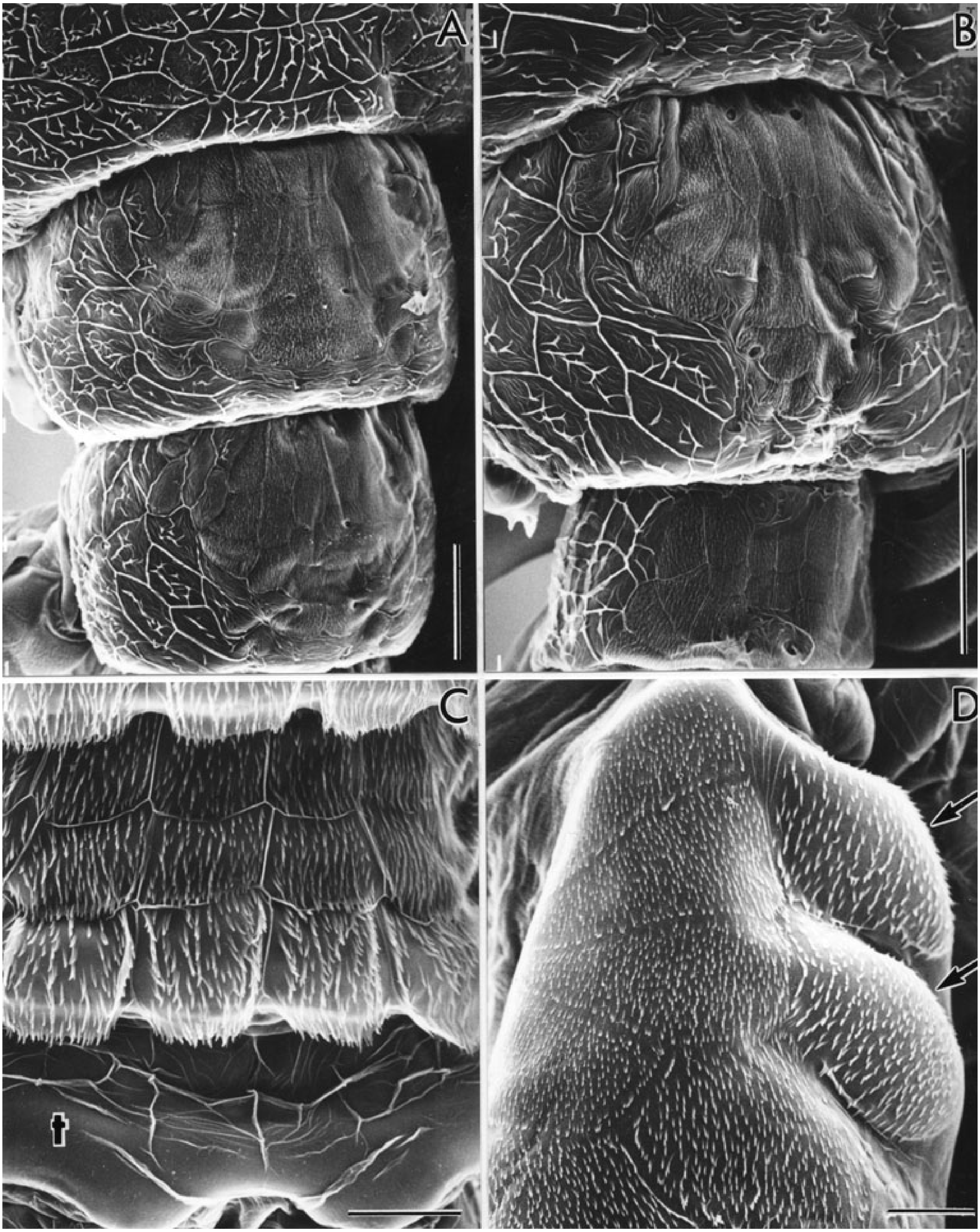


Figure 10. ***Maemonstrilla polka* sp. nov.**, female paratype (SO lab), south coast of Ishigaki Island, 30.iv.1994, SEM. A, dorsal surface of posterior part of cephalothorax and free pedigers 1 and 2, anterior at top. B, dorsal surface of free pedigers 3 and 4, anterior at top. C, dorsal surface of penultimate segment and telson (t) of urosome, anterior at top. D, proximal part of coxa of leg 1, showing spinulose outer lobes (arrows), anterior to left. Scale bars = 100 μm in A, B; 20 μm in C, D.

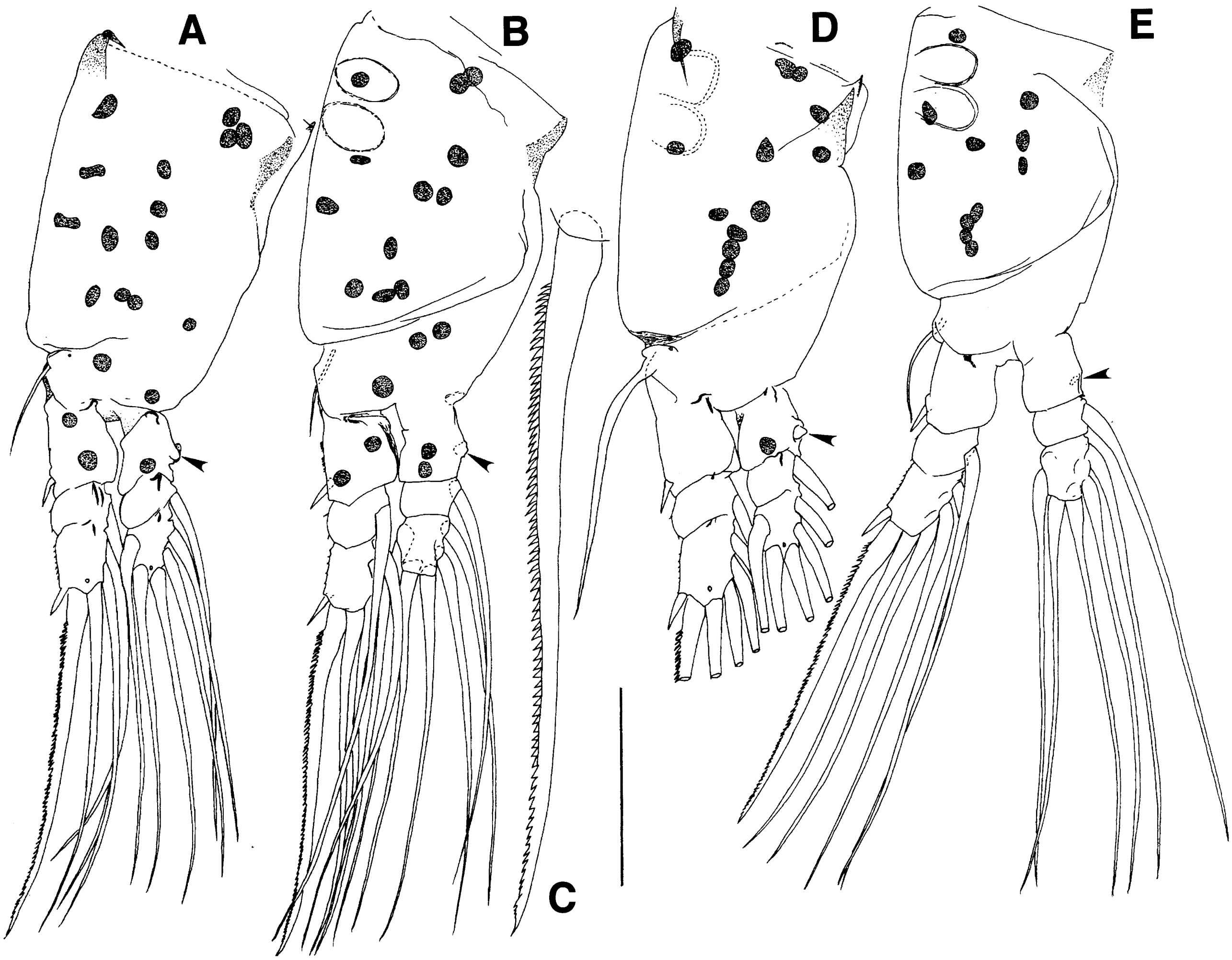


Figure 11. ***Maemonstrilla polka* sp. nov.**, female paratype (slide-mount of legs, KMNH IvR 700 216), south coast of Ishigaki Island, 30.iv.1994, legs 1–4, showing diagnostic red spots and invaginations or vestigial buttons replacing proximal inner endopodal seta of each leg (arrows), setules omitted and some setae cut short. A, right leg 1, anterior. B, left leg 2, posterior. C, outer apical exopodal seta of left leg two (see also Fig. 12D). D, right leg 3, anterior. E, left leg 4, posterior. Scale bar = 0.2 mm in A, B, D, E; 0.1 mm in C.

bearing legs 5) with dorsal surface divided by ridges into spinulose patches as follows (Fig. 10B): 4-4-2-2-4-4, with non-spinulose area anteromedially and additional pair of spinulose fields behind posterior pair of pit-setae; no dorsal pores.

Compound genital somite with spinulose, transverse dorsal ridge at midlength (Fig. 9D; dorsal view not illustrated). Six longitudinal rows of three square, spinulose reticulations each found anterior to this ridge. Six longitudinal rows of four rectangular meshes each found behind this ridge: first mesh in each row short and smooth; second mesh square with smooth anterior half and spinulose posterior half; third and fourth meshes square and spinulose, with fourth slightly produced into plate overhanging posterior edge of somite (Fig. 10C). Penultimate somite with six longitudinal rows of three square, spinulose regions each; posterior margin as in genital compound somite (Fig. 10C).

Latero-basal arcuate sclerites (Fig. 9C), intercoxal sclerites, and protopodal segmentation of legs 1–4 as in *M. hyottoko*. Outer side of each coxa with about 15 spinulose fields separated by narrow bare strips (Fig. 10D); spinules much smaller and more numerous than in *M. hyottoko*, all pointing distally; posterior basal part of coxa produced into two low, oval lobes bearing slightly larger spinules (see also Fig. 11B, D, E). Basis with lateral seta (small and hair-like in legs 1, 2 and 4, long and plumose in leg 3; Figs 11, 12A) and anterolateral pore (double pore in at least one examined leg; Fig. 12A). Each segment of each ramus articulated to more proximal limb

Figure 12. ***Maemonstrilla polka*** **sp. nov.**, female paratype (SO lab), south coast of Ishigaki Island, 30.iv.1994, details of swimming legs, SEM. A, basis and first exopodal segment of leg 1, outer view, proximal at top and anterior to right, showing one seta on each segment, anterior pore near basis seta (arrow), and spinule patches on exopod. B, third segments of endopod (right) and exopod (left) of leg 2, anterior view showing distal pore on each segment (arrows). C, proximal endopodal segment of leg 2, anterior view, showing vestigial button-like seta (arrow). D, detail of outer apical exopodal seta. Scale bars = 20 μm in A–C; 10 μm in D.

segment by prominent, anteromedial condyle at base (Fig. 12B, C); third segment of each ramus with distal pore on anterior side (Figs 11A, D, 12B). Patches of distally directed spinules on outer face of exopodal segments; three such patches on first segment, two on second, five on third (Fig. 12A). Distal edge of each patch marked by row of slightly larger spinules and continuing as simple ridge onto posterior side of exopod. Setation of legs 1–4 as in *M. hyottoko* (Fig. 11). First endopodal segment with button-like vestigial seta or socket-like structure on inner side (Figs 11, 12C). Outer spiniform setae of first and third exopodal segments similar in size (Fig. 11), at least proximal one bearing minute spinules. Outer apical seta of exopod with long setules along inner side and row of conical, curved denticles along outer side (Figs 11C, 12D); these denticles relatively shorter and more closely spaced than in *M. hyottoko*. Leg 5 as in *M. hyottoko* (Fig. 9E).

Posterior part of genital compound somite protruding ventrally as simple, apron-like flap (Fig. 9D). Anteriorly directed ovigerous spines broken off in examined paratype, and not visible due to adhering egg masses in other specimens, but medial copulatory pore visible posteriorly at base of prominence bearing them (not illustrated). Caudal rami (not

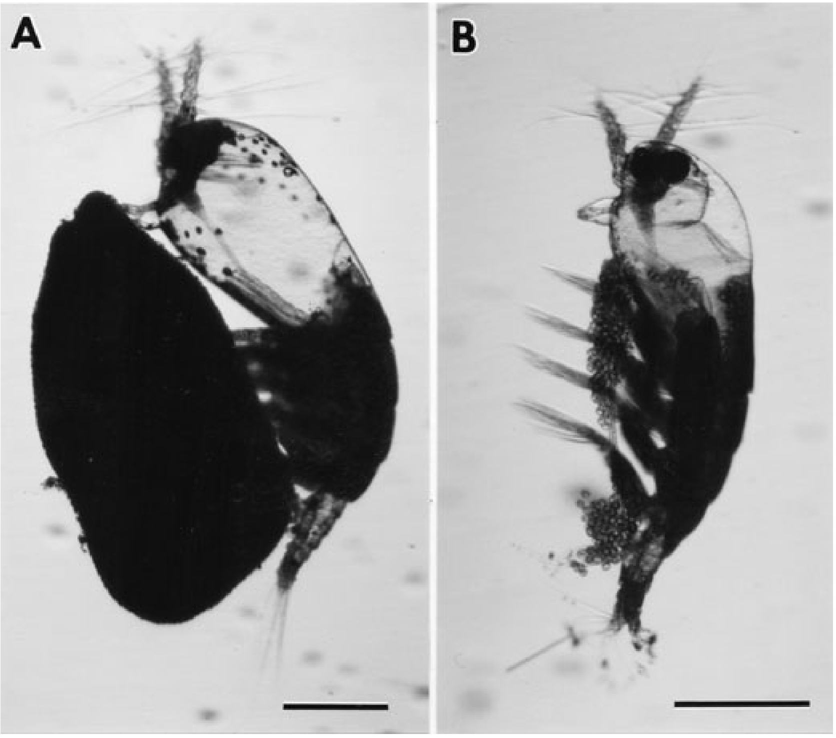


Figure 13. Ovigerous females of ***Maemonstrilla* gen. nov.**, south coast of Ishigaki Island, 30.iv.1994, photomicrographs of preserved specimens. A, ***Maemonstrilla polka* sp. nov.**, holotype (KMNH IvR 700 205). B, ***Maemonstrilla turgida*** (A. Scott, 1909) **comb. nov.** (KMNH IvR 700 226). Scale bars = 0.5 mm.

illustrated) as in *M. hyottoko*, but socket of dorsal apical seta somewhat set off from rest of ramus. In undissected paratype, dorsal apical seta seen to be plumose, with medium-short setules spaced as in other caudal setae.

Eggs: Large egg mass somewhat oval in lateral view with more pointed anterior end, laterally compressed with flat sides, and reaching ventrally further than the tips of the leg setae (Fig. 13A). In lateral view, egg mass appearing bigger than copepod itself (e.g. 2.07 mm long, 1.28 m high), but width slightly less than half that of cephalothorax (within which all eggs were formerly stored). Mean egg diameter 34.4 μm (n = 15).

MAEMONSTRILLA SPINICOXA SP. NOV.

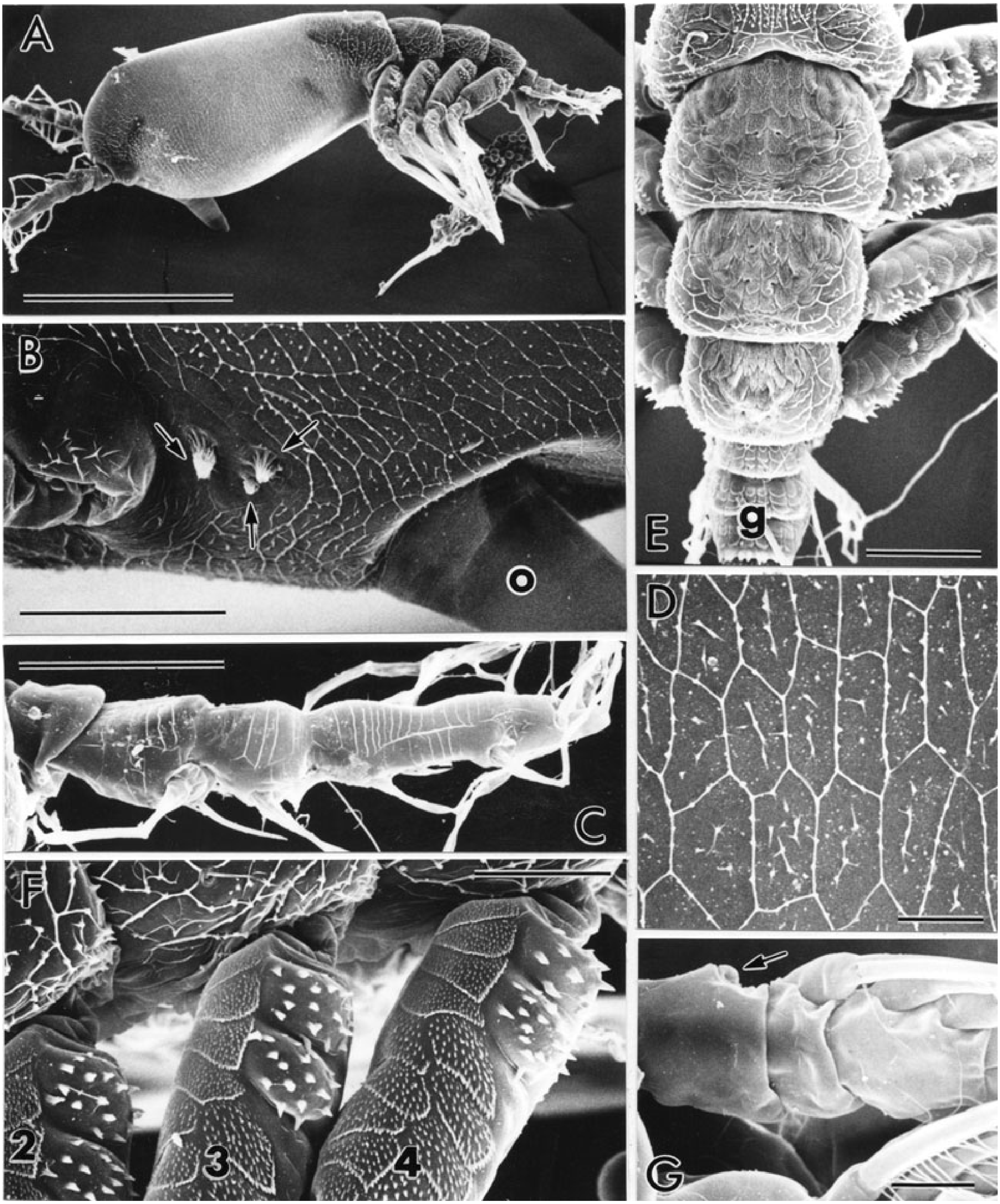
FIGURES 8B, C, 14–16, 21A, 29

Diagnosis: Cephalothoracic reticulation of unbranched fine ridges with occasional minute spinules; additional minute spinules sparsely distributed within meshes. Spiniform antennular 2- and 3-setae less than twice as long as 4-setae; apical 6_1-seta distinctly shorter than 6_2-seta. Oral papilla prominent and straight; base narrower than in preceding two species. Proximal outer part of coxa of legs 1–4 produced into two low, rounded lobes bearing numerous large, bluntly rounded denticles; remainder of coxa with nubbly texture as seen by light microscopy, and outer side of exopod armed with denticles smaller than those on lobes. Genital compound somite with large, rounded anteroventral protrusion and small, rounded posteroventral spur.

Etymology: Noun in apposition, referring to the two spinose lobes on the coxa of legs 1–4.

Material examined: Four females: holotype (KMNH IvR 700 217) in vial with left legs 1–4 mounted on slide, collected by M. J. Grygier at Sesoko Island (type locality), 13.viii.1989; paratype (SO lab) used for microscopical drawings, then SEM, collected by A. Murase off Kabira, Ishigaki Island, in light-trap at 18 m depth, 14.iv.1996; paratype (USNM 1093748), intact, collected by S. Kubota at Shirahama, Iriomote Island, 11–13.xi.1992; paratype (LBM Reg. No. 1430000929), intact, collected by M. J. Grygier at Sesoko Island, 14.x.2003.

Description: In lateral view (Fig. 14A), cephalothorax distinctly bulbous anteriorly, widening again in dorsal view at rear behind distinct ‘waist’ (incorporated



pediger; Fig. 14E). Measurements taken from all three non-SEM specimens, but dorsal view not available for dissected holotype. Body length in lateral view (sum of lengths of cephalothorax, metasome and urosome as defined in Fig. 1A) 1.48–1.70 mm, with these body regions contributing 53.0–55.3, 26.3–29.5 and 17.5–19.5%, respectively. Height and greatest width of cephalothorax nearly equal, 43.4–46.3 and

Figure 14. ***Maemonstrilla spinicoxa* sp. nov.**, ovigerous female paratype (SO lab), off Kabira, Ishigaki Island, 14.iv.1996, SEM. A, habitus, lateral view. B, anteroventral part of cephalothorax between oral papilla (o, its base artificially depressed) and base of antennule (left), lateral view, showing three scars (arrows). C, left antennule, dorsal view. D, detail of reticulation pattern of cephalothorax. E, dorsal view of body from rear of cephalothorax (top) to genital double somite (g, letter placed on this segment's dorsal suture) and coxae of right legs 1–4. F, proximal parts of coxae of left legs 2–4, showing spiny outer lobes. G, endopod of left leg 4, posterior view, showing button-like vestige of inner seta of first segment (arrow), and absence of inner seta of first exopodal segment (below). Scale bars = 0.5 mm in A; 0.1 mm in B, C, E; 20 μm in D, G; 50 μm in F.

44.3–44.7% of cephalothorax length, respectively. Antennule length 43.7–49.6% that of cephalothorax. Width of incorporated pediger 76.3–82.2% of greatest width. Widths of succeeding three free pedigers and genital compound somite relative to that of incorporated pediger 76.1–81.8, 67.0–70.2, 53.4–54.9 and 32.5–33.4%, respectively.

Cephalothorax ornamented with delicate, polygonal reticulation without side branches (Fig. 14A, B, D), polygons higher than long on sides but more or less equilateral on dorsum. Occasional minute spinules on mesh-bounding ridges in dorsolateral region around midlength, but not elsewhere; only a few isolated spinules, or groups of two or three linked spinules, found within meshes (Fig. 14D), but rearwards, dorsal meshes containing more complex figures and lateral meshes containing swirls of fine ridges. Posterolateral reticulations on tergites of free pedigers 1–3 like those on dorsum of cephalothorax, but swirls of fine ridges found within anterodorsolateral meshes on these tergites (Fig. 15A, B).

Antennules 4-segmented (Figs 8B, C, 14C), with clear boundaries between first three segments (that between second and third segment on outer side only, as seen by SEM) and incomplete or partial articulation (constriction only, as seen by SEM) between third and fourth segments; fourth segment very indistinctly divided into proximal and distal parts. Ornamentation of antennule including weak, fine reticulation (Fig. 14C). Full setal armature as set forth by Grygier & Ohtsuka (1995) present, except for subapical, fine b_6-seta (not seen in three examined antennules). Neighbouring b_5-seta bifid. All spiniform setae (series 1–6) appearing simple by light microscopy; 2- and 3-setae not more than twice as long as 4-setae, and apical 6_1-seta distinctly shorter than 6_2-seta.

Oral papilla prominent, narrowly conical (Fig. 14A, B); two pairs of simple pores preceding it, and one pair behind, all three pairs similarly far from midline and none produced as tubes (not illustrated). Three pairs of small, knob-like scars in cluster behind bases of antennules (Fig. 14B). Cups of naupliar eye well separated, 60–73 μm in diameter. Pair of hair-like sensilla on 'forehead' between antennules; more dorsally, anterior pair of closely set large pores, pair of minute pores widely flanking them, and three pores on midline behind (middle one might be sensillum or sensory pit). Another pair of large pores far laterally behind antennular bases. Two pairs of dorsal pores, one at two-thirds length and flanked by anterior end of swirly mesh area, other halfway between there and posterior margin (none of these pores or sensilla illustrated). Rear of cephalothorax (incorporated pediger) with widely spaced pair of dorsal pit setae, three pairs more laterally arranged in equilateral triangles, and at least one pair further ventrolaterally (Fig. 29).

Distribution of more posterior cuticular organs (Fig. 29) based on both light microscopy and SEM of specimen from Ishigaki Island. First free pediger with pair of large, close-set pores under overhang of cephalothorax, pair of minute pores between them, pair of dorsal pores at midlength, and one pair (at least) of posterior pit setae (Fig. 15A). Second free pediger with two anterior pairs of large pores (mostly hidden in SEM photo, Fig. 15A), two pairs of small middorsal pores with very small pore on midline at their centre, and (at least) two pairs of posterior pit setae. Second free pediger also with two pairs of lateral pit setae, as in *M. hyottoko*, but only posterior counterpart of them seen on first free pediger (SEM field of view, Fig. 14F, not reaching far enough forward). Third free pediger with anterior pair of large dorsal pores (hidden in SEM photo, Fig. 15B), pair of dorsal pores at about two-thirds length, and two pairs of posterior pit setae in transverse row. Fourth free pediger with one pair of posterior pit setae (Fig. 15C).

Trunk somites with dorsal ornamentation of fields of small spinules, much as in *M. hyottoko*, with six rows of spinule fields arranged as follows on free pedigers 1–4 (Fig. 15A–C): 3-3-5-5-3-3, 3-4-6-6-4-3, 3-2-4-4-2-3 and 3-3-3-3-3-3. On first free pediger, each row of fields widening posteriorly, like fish-tail; on second, most fields coming to point posteriorly, but most posterior field of outer and inner rows truncate posteriorly; above-mentioned middorsal pores found in notches of second and fifth fields of innermost rows, and on midline at anterior end of fourth fields (Fig. 15A). On third free pediger, outermost rows of spinule fields partly separated from others by areas of swirly ornamentation (Fig. 15B); above-mentioned dorsal pores in notches at outer base of fourth pair of fields of innermost rows. Genital compound somite

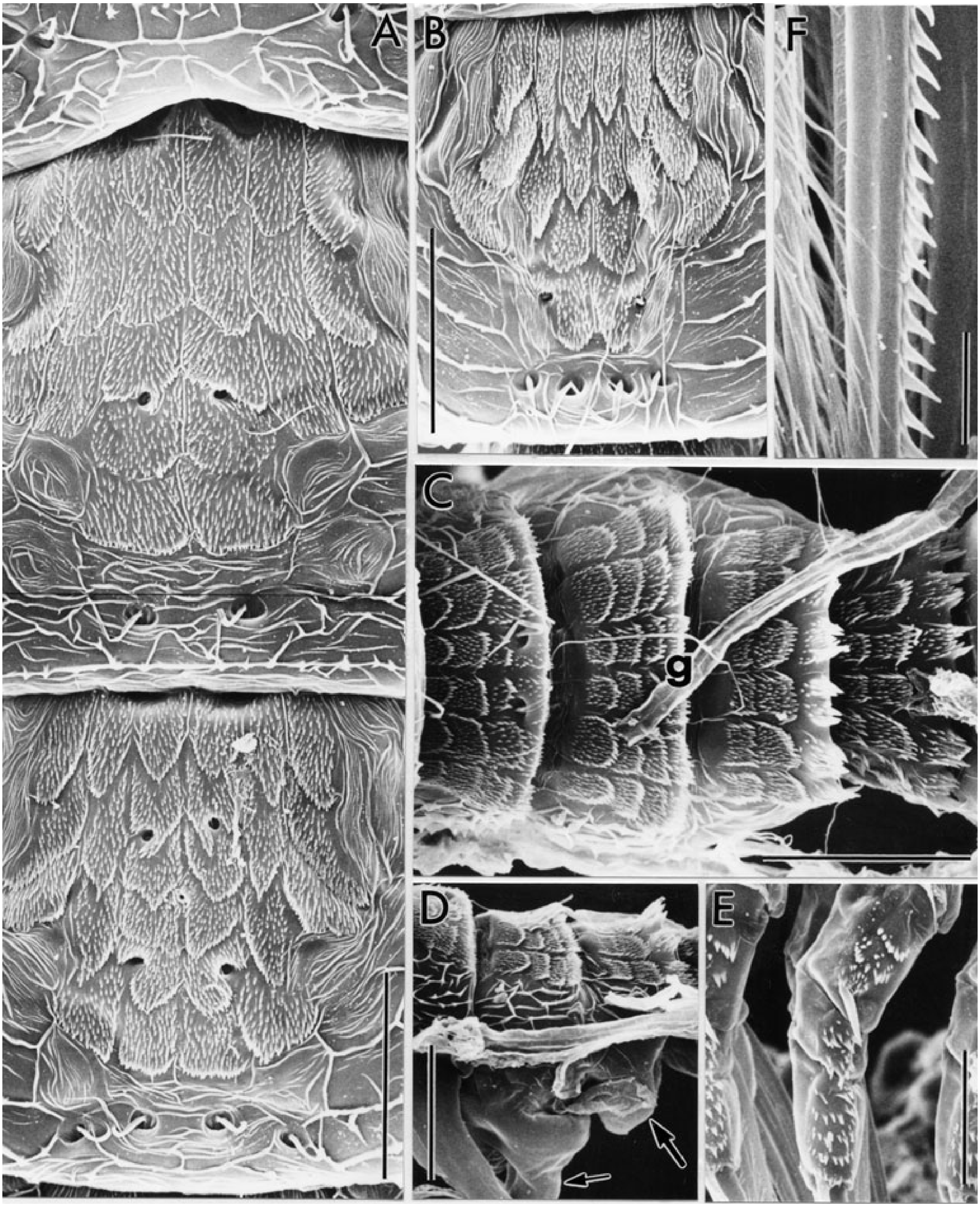


Figure 15. ***Maemonstrilla spinicoxa*** **sp. nov.**, ovigerous female paratype (SO lab), off Kabira, Ishigaki Island, 14.iv.1996, SEM. A, dorsal surface of free pedigers 1 and 2, anterior at top. B, dorsal surface of free pediger 3, anterior at top. C, dorsal surface of free pediger 4, genital compound somite (g, letter placed on this segment's dorsal suture), and penultimate segment, anterior to left. D, genital compound somite, lateral view, anterior to left, showing bases of ovigerous spines (small arrow) and ventroposterior process (large arrow). E, exopod of left leg 2 or 3, lateral view, anterior to left. F, detail of outer apical exopodal seta of swimmng leg. Scale bars = 50 μm in A–E; 10 μm in F.

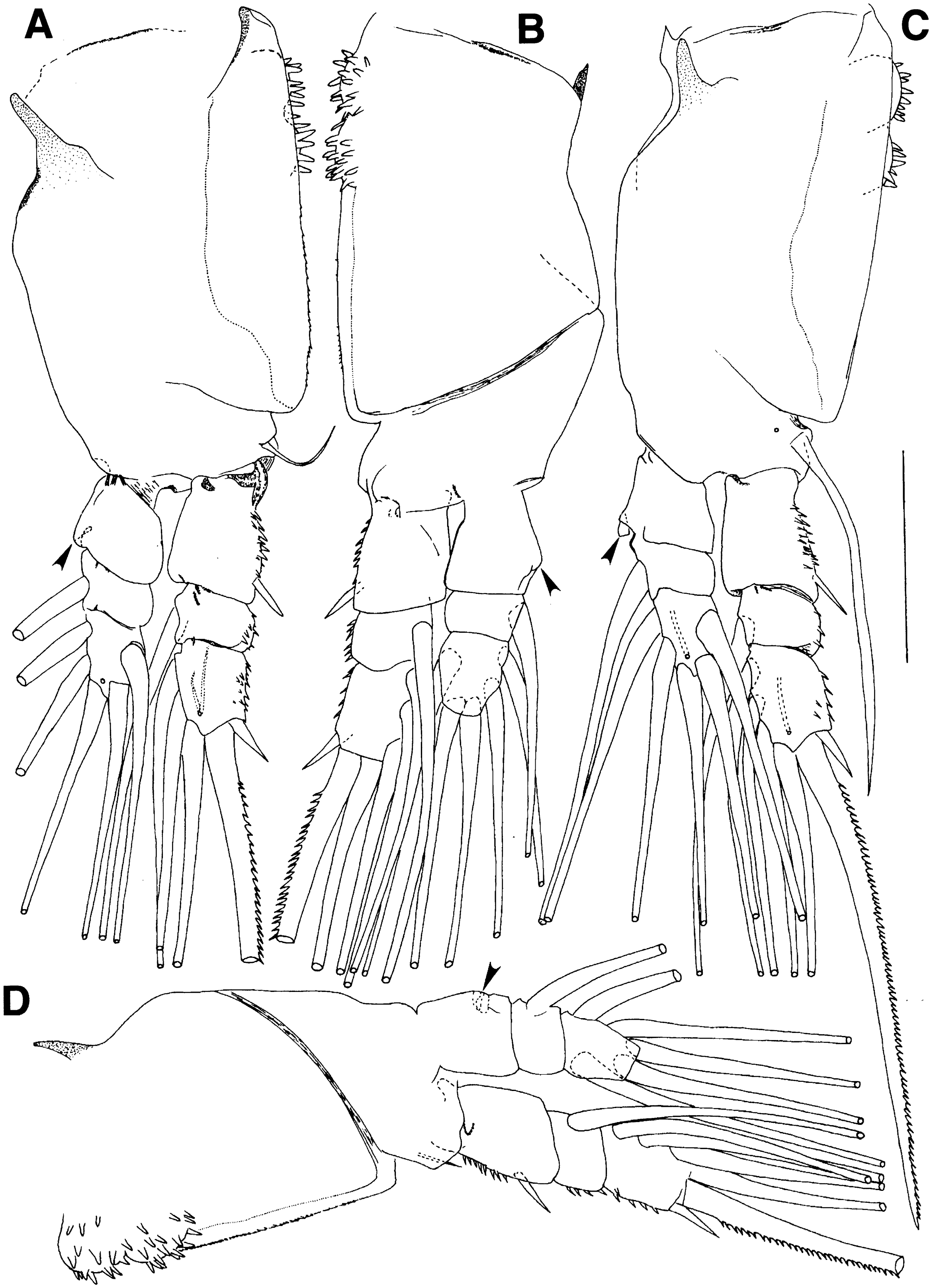


Figure 16. ***Maemonstrilla spinicoxa*** **sp. nov.**, female holotype (KMNH IvR 700 217), Sesoko Island, 13.viii.1989, left legs 1–4, setules omitted and most setae cut short, showing invaginations or vestigial buttons in place of proximal inner endopodal seta of each leg (arrows). A, leg 1, anterior. B, leg 2, posterior. C, leg 3, anterior. D, leg 4, posterior. Scale 0.1 mm.

(Fig. 15C) with spinule fields arranged 3-3-3-3-3-3 in anterior half, rearmost field of each row continuing onto transverse ridge; 2-2-2-2-2-2 in posterior half, plus six sets of several large denticles each on rear margin, preceded by some small denticles. Penultimate somite with 3-3-3-3-3-3 arrangement of spinule fields (Fig. 15C); posteriormost denticles in each field like others in front rank, larger than others but regular in second rank, and larger than others but irregular in third rank (on rear margin of somite). Telson unornamented; caudal rami with weak anteroposterior striations on dorsal side.

Intercoxal sclerites of legs 1–4 low and wide. Two low, rounded knobs at outer posterior base of each coxa, each knob bearing 17–18 large, pointed denticles (Figs 14E, F, 16). Anterior to knobs, row of four spinule fields found, each field outlined distally and posteriorly by close-set row of spinules (imparting a scale-like appearance to the array); similar spinule fields found in two rows more distally, but observed clearly only in leg four (Fig. 14F): five fields in anterior row, four in posterior row, the distalmost posterior field lacking the bounding palisade. By light microscopy, these spinule arrays appear nubbly, not coarsely spinulose as in *M. hyottoko*. Outer margin of exopod armed with denticles smaller than those on knobs but much larger than spinules on rest of coxa (Fig. 15E). Pore present in front of outer basis seta; this seta long and plumose in leg 3, short and hair-like in legs 1, 2 and 4 (Fig. 16). Leg setation as in *M. hyottoko*, and minute pore found on anterior side of third segment of each ramus (Fig. 16). Outer spiniform setae on exopodal segments 1 and 3 similar in size, that of segment 1 (at least) with double row of minute serrations. Outer side of outer apical seta of third segment with row of large, distally orientated, somewhat widely spaced denticles (Figs 15F, 16). Proximal segment of endopod with invaginated, socket-like structure or projecting, button-like setal vestige (Figs 14G, 16); proximal segment of exopod lacking any trace of inner seta. Leg 5 as in *M. hyottoko* (Fig. 14A).

Genital compound somite with large, rounded protrusion anterior to base of ovigerous spines, as well as small, rounded posteroventral spur (Fig. 15D). Ovigerous spines directed anteriorly, with blunt tips reaching beyond first pair of legs to rear of cephalic part of cephalothorax (Fig. 14A), those of Sesoko paratype 49.2% as long as body length.

Caudal rami with six setae arranged as in *M. hyottoko* (not illustrated), dorsal apical seta about two-thirds as long as others, apparently simple.

Eggs: Those attached to ovigerous spines of SEM specimen nearly spherical, 24 µm in diameter (Figs 14A, 21A).

MAEMONSTRILLA OKAME SP. NOV.

FIGURES 17, 18A, B, 19, 20, 21B–F, 29

Diagnosis: Cuticular meshwork of cephalothorax consisting of high, thin ridges; at least anterolaterally and laterally, edges of ridges thorny. Cuticle within meshes ornamented with many specks and short, fine arcs (lateral meshes with several minute spinules only). Antennules with same defining setal characters as *M. hyottoko* (see above), but $4v_1$ seta longer, at least 70% as long as 3-seta. Oral papilla small, directed more anteriorly than ventrally, region lateral and posterior to it expanded like puffed cheeks. Genital compound somite lacking obvious dorsal suture. Spinules of outer face of coxa of legs 1–4 arranged, in part, in about eight transverse rows. Small posteroventral bump on compound genital somite.

Etymology: Noun in apposition, named for the Japanese festival mask called ‘Okame’ because of a putative resemblance between the copepod’s ‘face’ and the mask’s small mouth and puffed cheeks.

Material examined: Nine females collected by M. J. Grygier at Sesoko Island (type locality): holotype (KMNH IvR 700 218), 22.v.1996, intact, used for microscopic drawings; two non-ovigerous paratypes (SO lab), 22.v.1996, used for SEM; one ovigerous paratype (ZMA Co. 205909), 22.v.1996, intact but its egg mass decayed without hatching; one non-ovigerous paratype (USNM 1093749), 22.v.1996, intact; two ovigerous paratypes (KMNH IvR 700 219, IvR 700 220), collected 2.v.1996, 20:00 h, fixed on 5 May after death and partial decay, latter used for microscopic drawings with right legs 1–4 mounted on slide, hatched nauplii from both used in failed SEM effort; one ovigerous paratype (LBM Reg. No. 1430000930), 13.v.1996, 19:45–20:00 h, used for microscopic drawings with right legs 1–4 mounted on slide, rest of body in vial, hatched nauplii used for SEM; one paratype (KMNH IvR 700 221), 22.xii.1996, intact, used for microscopic drawings.

Description: Anteriorly bulbous cephalothorax distinctly swollen at and behind small, anteriorly directed oral papilla, entire anteroventral side resembling a face with pursed lips and bulging cheeks (Fig. 17A). In dorsal view, slight expansion (incorporated pediger) behind ‘waist’ towards rear of cephalothorax. Measurements taken from six specimens in lateral and dorsal view (one from 2 May, three from 22 May, one from 22 December, one from 13 May). Body length in lateral view (sum of lengths of cephalothorax, metasome and urosome as defined in Fig. 1A) 1.20–1.67 mm, with these body

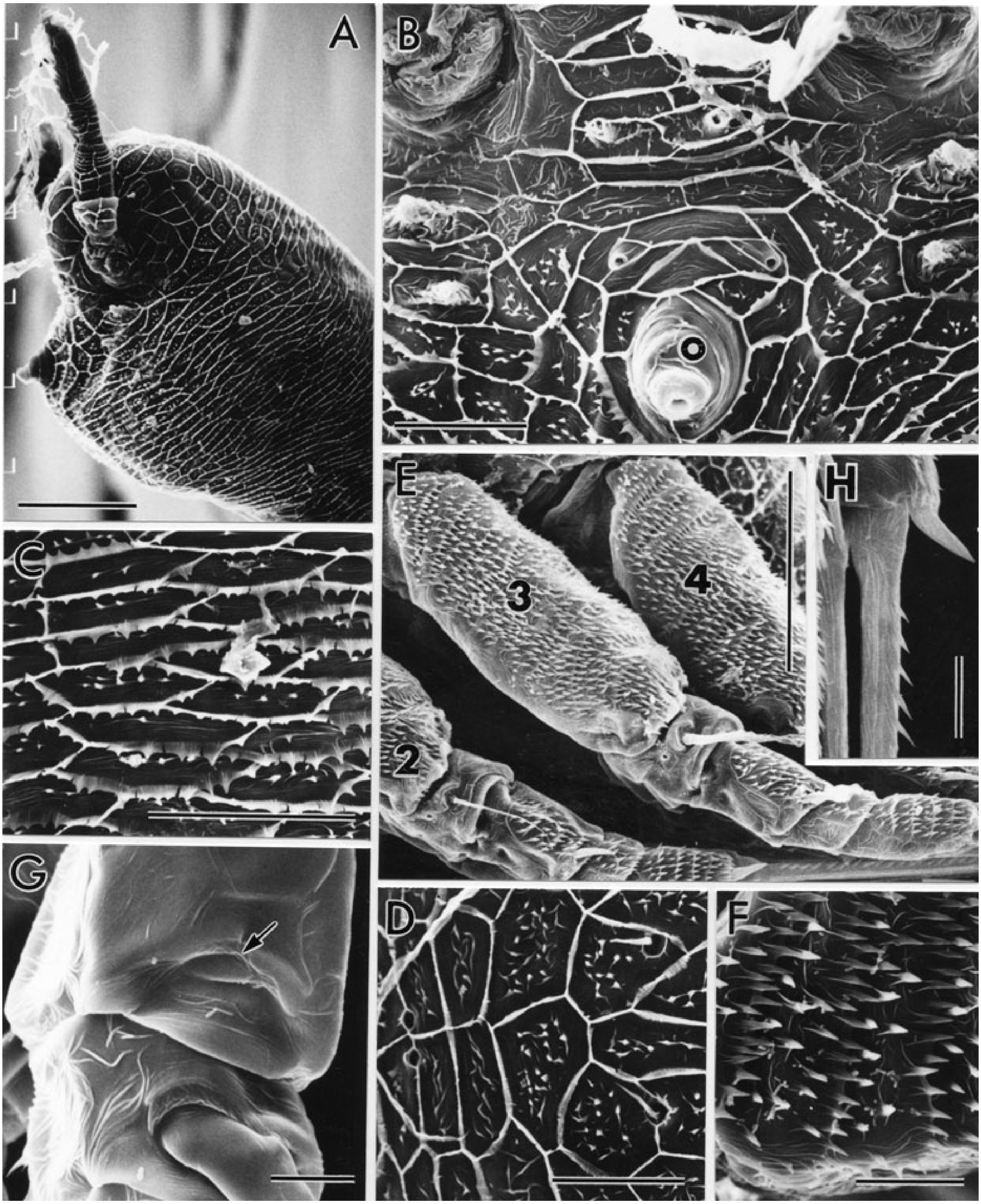


Figure 17. ***Maemonstrilla okame* sp. nov.**, two non-ovigerous female paratypes (SO lab), Sesoko Island, 22.v.1996, SEM. A, anterior half of cephalothorax, lateral view. B, anteroventral part of cephalothorax (i.e. 'face') between oral papilla (o) and bases of antennules (top corners), showing two pairs of pores and two pairs of scars. C, reticulations of lateral side of cephalothorax. D, reticulations of 'forehead', showing pair of hair-like sensilla and pair of pores, dorsal to left. E, legs 2–4, lateral view. F, detail of coxal spinulation of a right swimming leg, proximal to left. G, site of absent inner seta (arrow) of first endopodal segment of right leg 1. Scale bars = 100 μm in A, E; 50 μm in B–D; 20 μm in F, H; 10 μm in G.

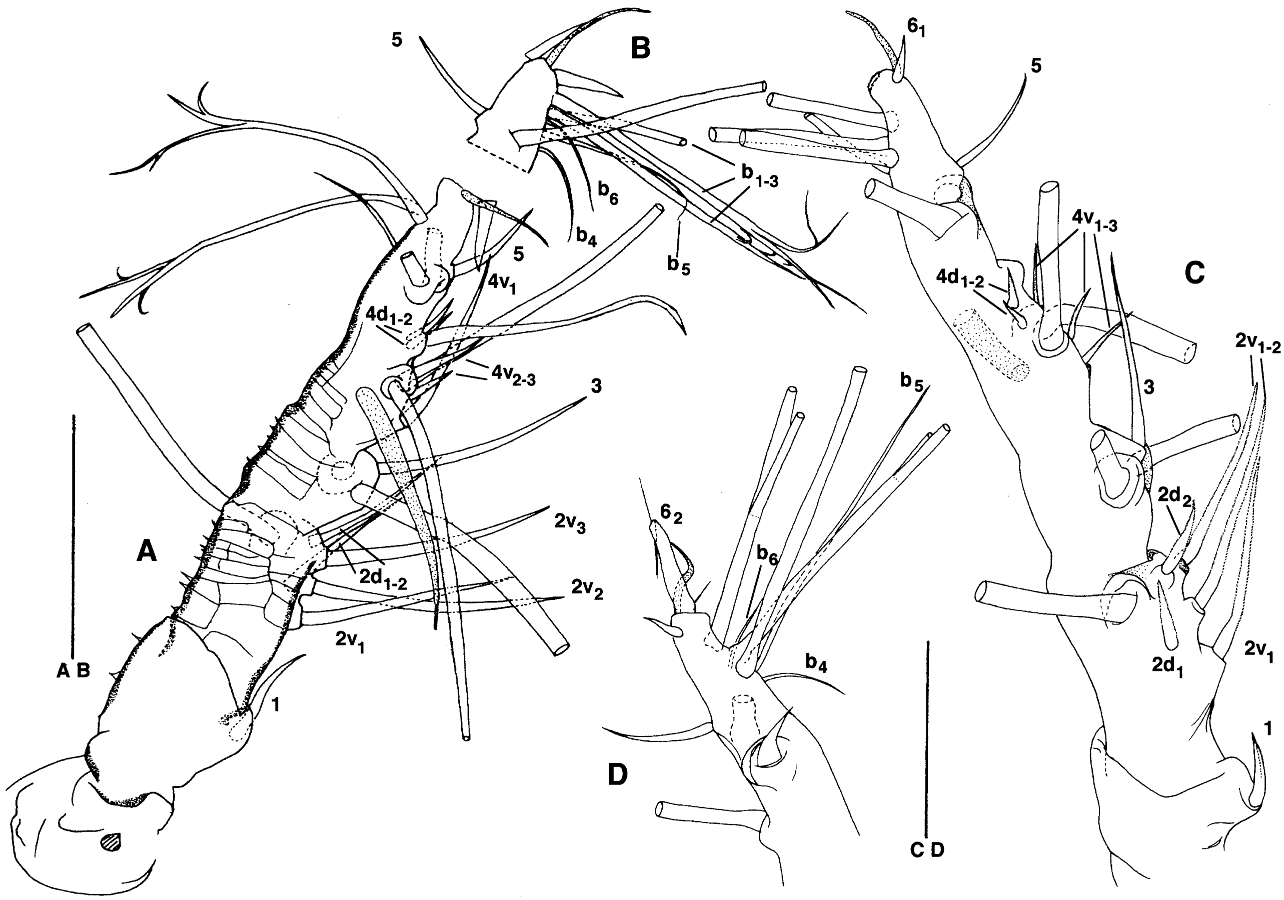


Figure 18. Antennules of two species of ***Maemonstrilla* gen. nov.**, setules omitted, setal designations after Grygier & Ohtsuka (1995: fig. 6). A, ***Maemonstrilla okame* sp. nov.**, female holotype (KMNH IvR 700 218), Sesoko Island, 22.v.1996, right antennule, ventral view. B, same, more fully armed tip of left antennule, ventral view (b_5-seta seen to be bifid in another specimen). C, ***Maemonstrilla simplex* sp. nov.**, female holotype (KMNH IvR 700 222), south coast of Ishigaki Island, 30.iv.1994, left antennule, dorsal view. D, same, more fully armed tip of right antennule, dorsal view. Scale bars = 0.1 mm.

regions contributing 49.3–54.2, 27.9–30.8 and 17.4–20.7%, respectively. Height and width of cephalothorax 50.0–61.2 and 48.6–53.7% of cephalothorax length, respectively. Antennule length 29.6–47.3% that of cephalothorax. Width of waist of cephalothorax 63.3–75.6% that of greatest width; width of incorporated pediger 72.9–87.8% of greatest width. Widths of succeeding three pedigers and genital compound somite relative to that of incorporated pediger 82.6–84.6, 65.2–74.5, 53.7–56.1 and 31.0–33.2%, respectively.

Oral papilla preceded immediately by pair of pores and, further anteriorly at same distance from midline, another pair of pores at ends of small tubes (Fig. 17B). Probably only two pairs of scars present. Naupliar eye extremely large, lateral and ventral cups approximately equal, 102 × 126 μm diameter in one specimen, 106 × 134 μm in another. Lateral meshes of cephalothoracic reticulation higher than wide (Fig. 17C), but antero- and posterodorsal ones more equally dimensioned (Fig. 17D). Mesh borders and interiors as described in diagnosis.

Antennule with distinct first joint, second joint (between second and third segments) distinct ventrally, third joint represented by constriction only (Figs 17A, 18A). Cuticular reticulations present, height of ridges decreasing distally. Spiniform $2v_{1-3}$-setae, 3-seta and $4v_1$-seta very long, with two rows of short, spiky setules, $4v_1$-seta at least 70% as long as 3-seta (Fig. 18A). Position and size of other setae and aesthetascs as in *M. hyottoko*; in one case (not Fig. 18B) b_5-seta clearly bifid.

Anterior part of cephalothorax with pair of anterodorsal setae followed by closely spaced pair of pores (Fig. 17D). Most of rest of cephalothorax not examined for such structures, but transverse row of at least four pores present mid-dorsally just in front of 'waist'. Incorporated pediger with at least four pairs

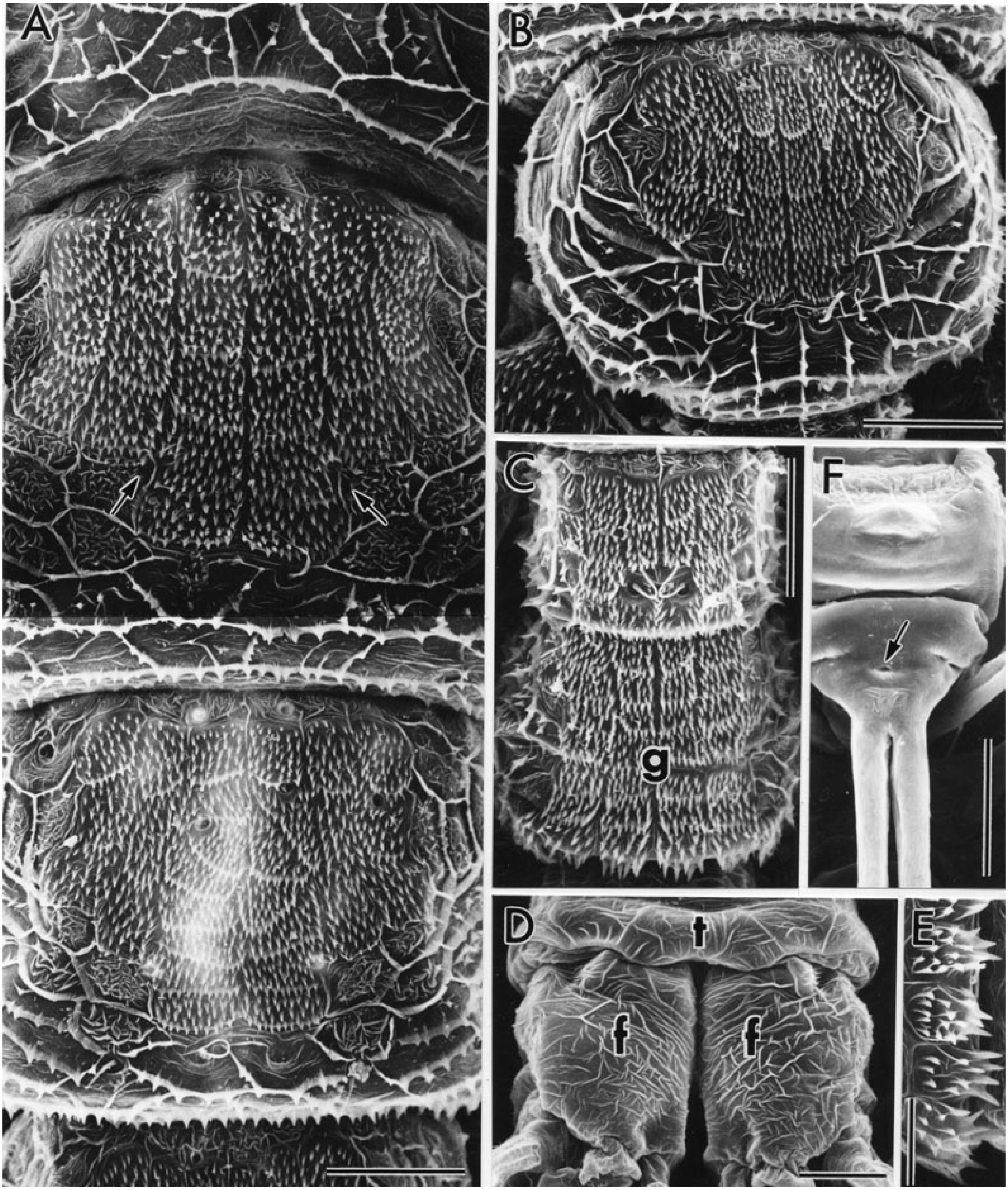


Figure 19. ***Maemonstrilla okame* sp. nov.**, two non-ovigerous female paratypes (SO lab), Sesoko Island, 22.v.1996, metasome and urosome, SEM. A, dorsal surface of free pedigers 1 and 2, anterior at top, arrows indicating obscured pair of large pores. B, dorsal surface of free pediger 3, anterior at top. C, dorsal surface of free pediger 4 and genital compound somite (g; letter placed on indistinct dorsal suture), anterior at top. D, telson (t) and caudal rami (f), dorsal view. E, part of posterior margin of penultimate segment of urosome, posterior to right. F, genital compound somite, ventral view, anterior at bottom, showing copulatory pore (arrow) and small ventral knob on posterior part (above). Scale bars = 50 µm in A–C, F; 20 µm in D, E.

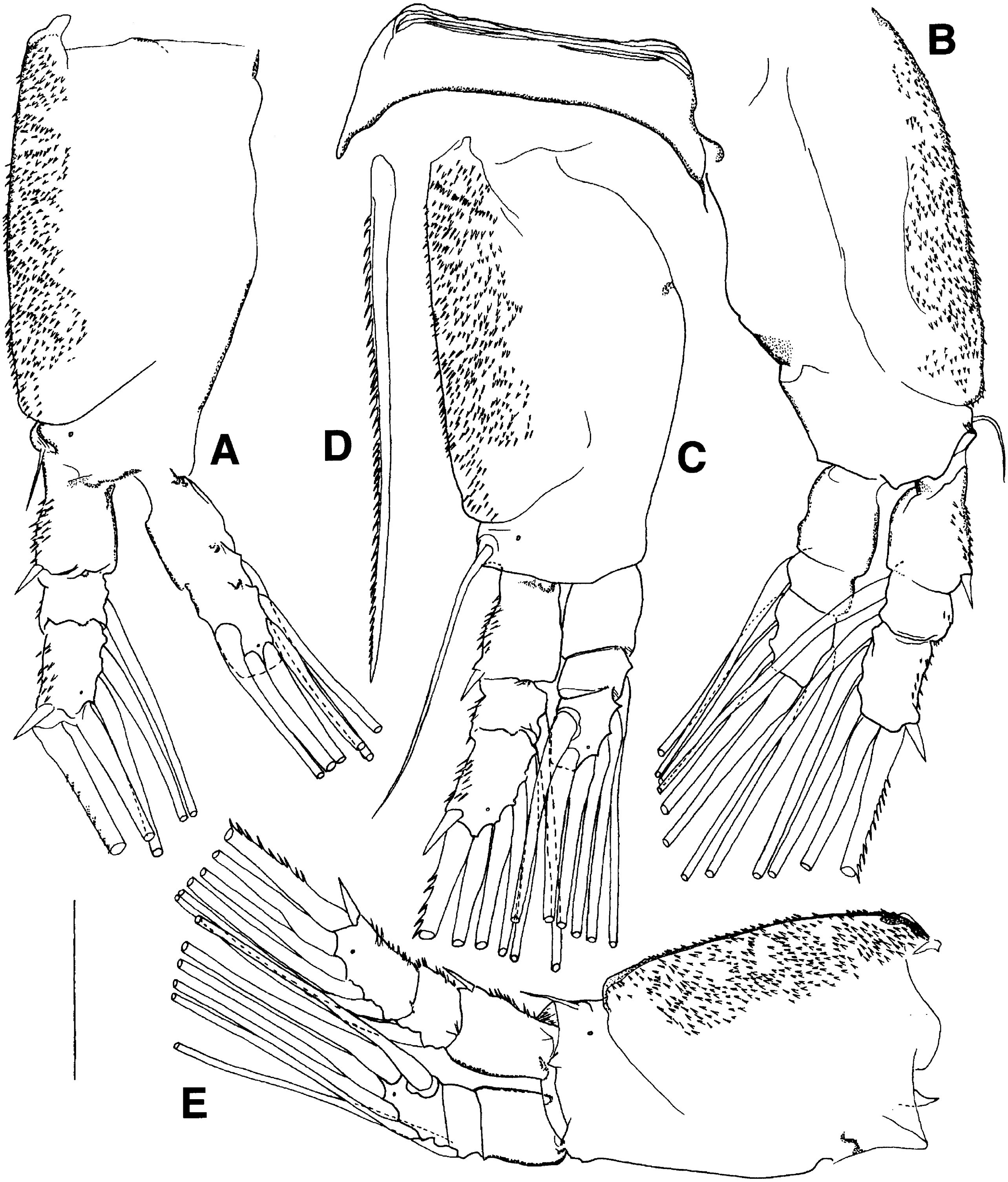


Figure 20. ***Maemonstrilla okame* sp. nov.**, ovigerous female paratype (KMNH IvR 700 220), Sesoko Island, 2.v.1996, right legs 1–4, setules omitted and setae cut short. A, leg 1, anterior. B, leg 2 and intercoxal sclerite, posterior. C, leg 3, anterior. D, outer distal exopodal seta of leg 3. E, leg 4, anterior. Scale bar = 0.1 mm.

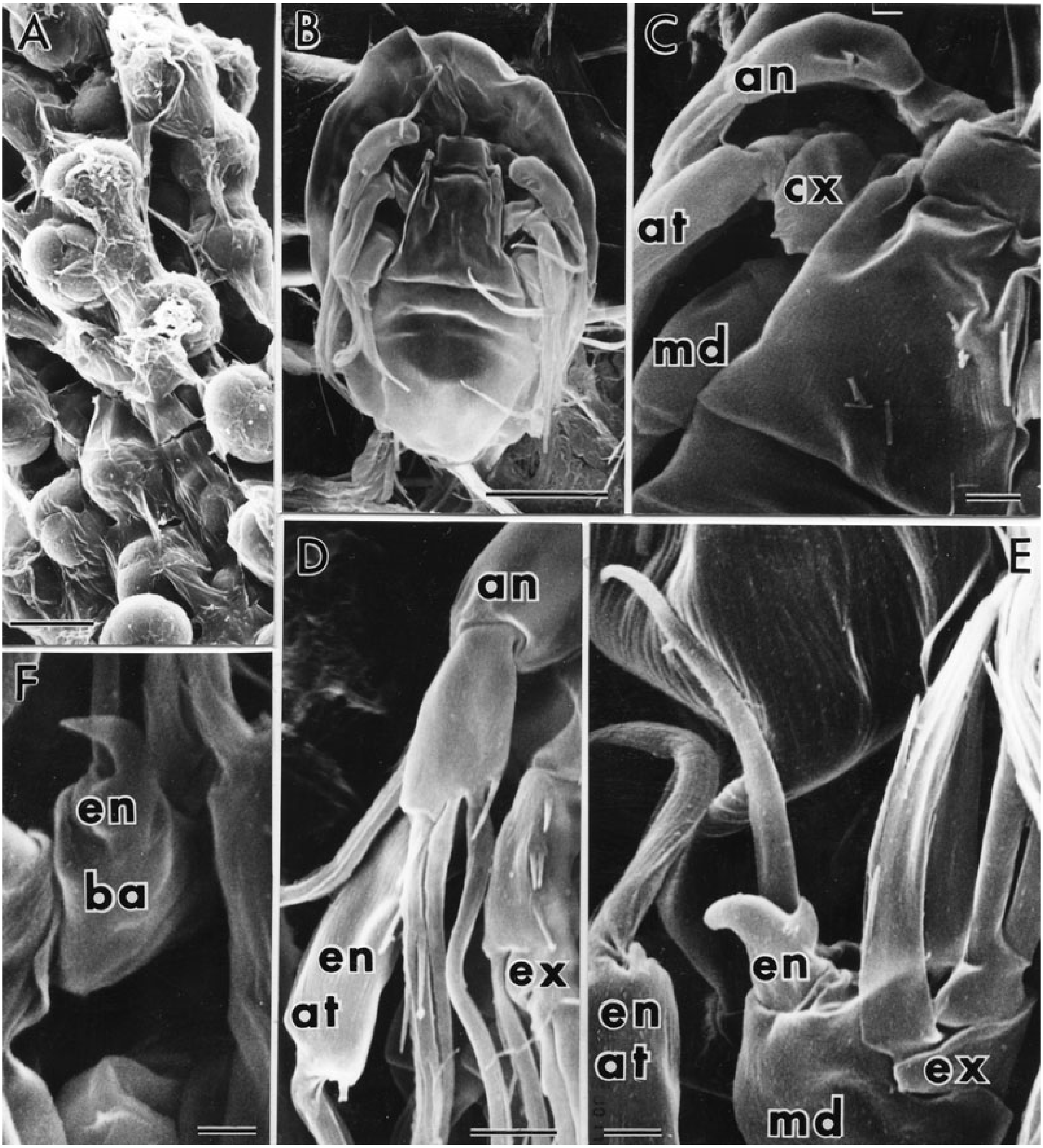


Figure 21. Eggs and nauplius of ***Maemonstrilla* gen. nov.**, SEM. A, eggs of female paratype of ***Maemonstrilla spinicoxa* sp. nov.** adhering to ovigerous spines (same specimen as Fig. 14A, *q.v.*). B–F, first nauplius hatched from egg mass of paratype female (LBM Reg. no. 1430000930) of ***Maemonstrilla okame* sp. nov.**, Sesoko Island, 13.v.1996. B, habitus, ventral view. C, labral bulge and parts of right appendages. D, distal parts of antennule and antennal endopod and exopod. E, distal parts of mandible and of antennal endopod. F, mandible, apical view, showing insertion of seta on base of claw, thus confirming that the claw represents the endopod. Abbreviations: an, antennule; at, antenna; ba, basis; cx, coxal endite; en, endopod; ex, exopod; md, mandible. Scale bars = 20 μm in A; 10 μm in B; 2 μm in C, D; 1 μm in E, F.

of dorsolateral and lateral pit setae, medial-most ones being very widely separated from each other (Figs 19A, 29); rear dorsal meshes not much ornamented. On first free pediger (Fig. 19A), spinule field formula apparently 3-3-5-5-3-3, but boundaries between fields hard to see, each field being bounded posteriorly by comb of spinules of same size as others in field; spinulose region surrounded by reticulate region, its meshes full of squiggly figures. Pores on this segment not clearly seen, possibly a tiny anterior one just right of midline and a large one at midlength just left of midline, definitely a pair at two-thirds length. Pit setae including dorsal posterior pair and two lateral pairs, anterior one of which located further ventrally. On second free pediger (Fig. 19A), spinule fields and surrounding meshes as above, former with formula 3-3-8-7-3-3 (some of the 7 being triangular in shape). Anterior pair of large pores, another pair at one-third length, single pore far to right of these, and final pair at two-thirds length; two pairs of posterodorsal pit setae and two lateral pairs, anterior of latter being further ventral. On third free pediger (Fig. 19B), spinule fields better defined than above, formula 3-2-4-4-2-3; one pair of large anterior pores, possibly another pair (or 1 + 2) in front of them; two pairs of posterodorsal pit setae. On all three of these pedigers, lateral meshes of tergites containing several small cuticular figures each. On fourth free pediger (Fig. 19C), posterior pair of pit setae present, spinule fields as 1-4-3-3-4-1 (lateralmost single field at same level as second field of other rows; third field in innermost rows considered to include spinule areas behind pit setae).

Genital compound somite with no or very little hint of dorsal division (Fig. 19C), ventral side with medial pore at base of ovigerous spines, two pairs of lateral pores (or combinations of pore and groove), and posterior small, medial bump (Fig. 19F). Spinule fields (as seen in dorsal view; possibly more lateral fields exist) with formula 7-7-7-7, with four fields in each row anterior to the purported dorsal division. Rearmost spinules on this segment about twice as long as other spinules (Fig. 19C). In dorsal view, anterior half of penultimate segment and all of telson ornamented with weak, wavy, transverse ridges (Fig. 19D). Posterior part of penultimate segment with transverse array of six spinule fields, each ending posteriorly in 2–4 largish spines (Fig. 19E). Caudal rami with more-or-less rectilinear pattern of short, weak ridges (Fig. 19D), armed with six setae, five of them long and biserially plumose, but dorsalmost seta shorter with single, dorsal row of setules.

Segmentation and setation of legs 1–4 as in *M. hyottoko* (Fig. 20). Outer anterior face of coxa of legs 1–4 spinulose (Fig. 17E), these spinules about twice as large as dorsal ones on trunk somites, arranged in about eight transverse combs with many others between combs (Fig. 17F). Two ‘pads’ of unexplained nature at distal end of spinulose area, another found subapically anterior to these (barely visible in Fig. 17E, leg 2). Basis seta of leg three much longer than that of legs 1, 2 and 4; single pore anterior to base of this seta in each leg (Fig. 20). Outer margin of all three exopodal segments spinulose; about four rows on third segment (Fig. 17E). No inner seta on first segment of either ramus, at most a ‘scar’ on endopod (Fig. 17G). Tiny pore distally on anterior face of third segment of each ramus (Fig. 20A, C, E). Outer apical seta of third exopodal segment with widely spaced, rather weak, distally directed denticles (Figs 17H, 20D). Intercoxal plates about 40% wider than leg coxae, and 5–6 times wider than their height at midline (Fig. 20B). Leg 5 as in *M. hyottoko* (not illustrated).

Ovigerous spines arising from conical ventral protuberance of anterior half of genital double somite (Fig. 19F), 24.1–36.7% of body length in lateral view. Spines tapering to fine distal points with slight irregular thickening at midlength.

Eggs: Spherical, 29 μm in mean diameter in one ovigerous specimen ($n = 10$), 37 μm in another ($n = 9$).

Nauplius: Oval, 38 μm long, 25 μm wide, with smooth dorsal surface and large, trapezoidal, labral bulge in middle of ventral side between bases of limbs (Fig. 21B). Antennule possibly three-segmented, but small, proximal ‘first segment’ not seen clearly (Fig. 21C, D). Second segment moderately elongate and curved, with two long medial setae (one near base and other one distal and setulose). Third segment smaller than second, with setulose seta on inner apical corner, two outer subapical setae (at least outermost of these setulose), and subapical outer spinule. Protopod of antenna not well seen; coxal endite rounded with a few blunt teeth on margin (Fig. 21C). Endopod two-segmented; first segment short, cylindrical; second segment long, straight, and thin, with short sensillum or duct on outer apical corner, next to long, hook-like seta bent inwards at up to right angle to axis of segment (Fig. 21C, D; presence of any subapical sensillum not confirmed). Exopod four-segmented (Fig. 21D); first segment short; second segment elongate, rectangular, with four spinules arranged 1-2-1 on anterior margin and long inner distal seta with setules; third segment short, its armament, if any, unconfirmed; tiny fourth segment with two long setae, at least inner one with setules. Mandible with short, unarmed coxa and oblong basis, neither seen clearly (e.g. Fig. 21C). Exopod two-segmented, both segments very short, bearing one and two long setae, respectively, at least that of first segment setulose (Fig. 21E). Endopod (see Discussion) consisting of small hook with spur on its outer side and simple seta inserting at its base posteriorly (Fig. 21E, F). Furcal setae ('balancers') arising from raised cylindrical sockets, examined one apparently bifid near its base (not illustrated).

MAEMONSTRILLA SIMPLEX SP. NOV.

FIGURES 18C, D, 22, 23, 29

Diagnosis: Cephalothorax less bulbous and more cylindrical than in other species of this genus. Its polygonal reticulation simple and completely non-spinulose. No reticulation or spinulation noted on other body regions by light microscopy (SEM not attempted due to scarcity of material). Articulations between antennular segments 2–4 not distinct. Spiniform 2_v- and 3-setae more than three times longer than 4-setae; 1-seta and all 2-setae appearing minutely spinulose even by light microscopy, and 6-setae differing greatly in size. Oral papilla relatively smaller than in other species except *M. okame*, preceded by parallel grooves and pair of tubular pores. Basis of legs 1–4 slightly protruding on inner side. Two large, rounded, ventral lobes on anterior and posterior parts of genital compound somite.

Etymology: Named for the simple appearance of the trunk cuticle.

Material examined: Three females: Holotype (KMNH IvR 700 222) and ovigerous paratype (KMNH IvR 700 223) collected by S. Ohtsuka on south coast of Ishigaki Island, 30.iv.1994, holotype used for microscopic drawings with all legs 1–4 mounted on slide, body in vial, paratype also used for microscopic drawings; one paratype (LBM Reg. No. 1430000931), collected by M. J. Grygier from Kabira Bay, Ishigaki Island, 9.iii.1993, intact.

Description: Cephalothorax only moderately bulbous, cylindrical with rounded anterior end and slightly tapered posterior half (Fig. 22A, B). In dorsal view, modest 'waist' evident before incorporated pediger. Dorsal and lateral measurements made from all three specimens. Body length in lateral view (sum of lengths of cephalothorax, metasome and urosome as defined in Fig. 1A) 1.80–1.98 mm, with these body regions contributing 58.6–59.9, 25.7–26.6 and 14.2–15.5%, respectively; thus, overall size larger, cephalothorax relatively longer, and urosome relatively shorter than in other members of this species group. Height and greatest width of cephalothorax close to equal, 40.4–42.8 and 41.1–42.1% of cephalothorax length, respectively, lower than in other members of this species group. Antennule length 45.1–48.3% that of cephalothorax. Width of cephalothorax at waist 70.8–83.0% of greatest width, that of incorporated pediger 86.0–91.9%. Widths of succeeding three free pedigers and genital compound somite relative to that of incorporated pediger 72.9–78.0, 63.5–70.2, 49.5–55.6 and 30.6–35.5%, respectively. Ovigerous spines 67.4–71.9% as long as cephalothorax.

Cephalothorax reticulate posterior to level of naupliar eye (Fig. 22A, B). Reticulations polygonal, similar in shape and size throughout, smooth inside and bounded by fine, simple, cuticular riges. No reticulations noted elsewhere on body. No beds of denticles or spinules noted on dorsum of trunk by light microscopy, nor any projecting armament along rear margins of genital compound somite and penultimate somite. Outer face of coxa and exopod in legs 1–4 also seemingly smooth, except for three transverse rows of spinules observed on outer side of third exopodal segment of left leg 1 (Fig. 23A).

Antennules (Fig. 18C, D) with three small sclerites for muscle attachment amidst wrinkled arthrodial membrane at base of first segment. Second to fourth segments not clearly separated from each other. All setal elements as shown in Grygier & Ohtsuka (1995) present on right antennule of examined specimen, some distal elements lost from left antennule. Two apical 6-setae greatly differing in size, 6_1 being smaller and 6_2 apparently bearing some long setules. 2_v-setae and 3-setae more than three times longer than 2_d-setae and 4-setae; 1-seta and 2-setae with two rows of minute spinules discernible by light microscopy, 3-seta and 4-setae with even smaller spinules, and 5-seta seemingly smooth.

Oral papilla conical, nearly straight and protruding ventrally (Fig. 22A, B), relatively the smallest among the species of *Maemonstrilla* introduced in this paper except that of *M. okame*. Anteroventral surface of cephalothorax between oral papilla and bases of antennules longitudinally wrinkled, with pair of conical tubular pores, presumably homologous to tubular pores of *M. hyottoko* (Fig. 22C). Post-antennular scars expressed as two pairs of small, radially rayed knobs level with conical pores, each pair accompanied by pore (or minute third knob?) (Fig. 22C). 'Forehead' transversely wrinkled, with pair of hair-like sensilla among wrinkles (Fig. 22D); button-like structure present anterodorsally (presumably homologous to wrinkled pit in *M. hyottoko*), followed by two medial pores and two pairs of more lateral pores. One pair of pores close behind oral papilla (Fig. 22C). Three cups of naupliar eye well developed, diameters 110–139 μm, lateral ones separated from each other and slightly larger than ventral cup.

More posterior pores and pit setae shown in Figure 22A (in part) and Figure 29. Cephalothorax with five pairs of dorsolateral and lateral pit setae on incorporated pediger (mostly only their pits observed).

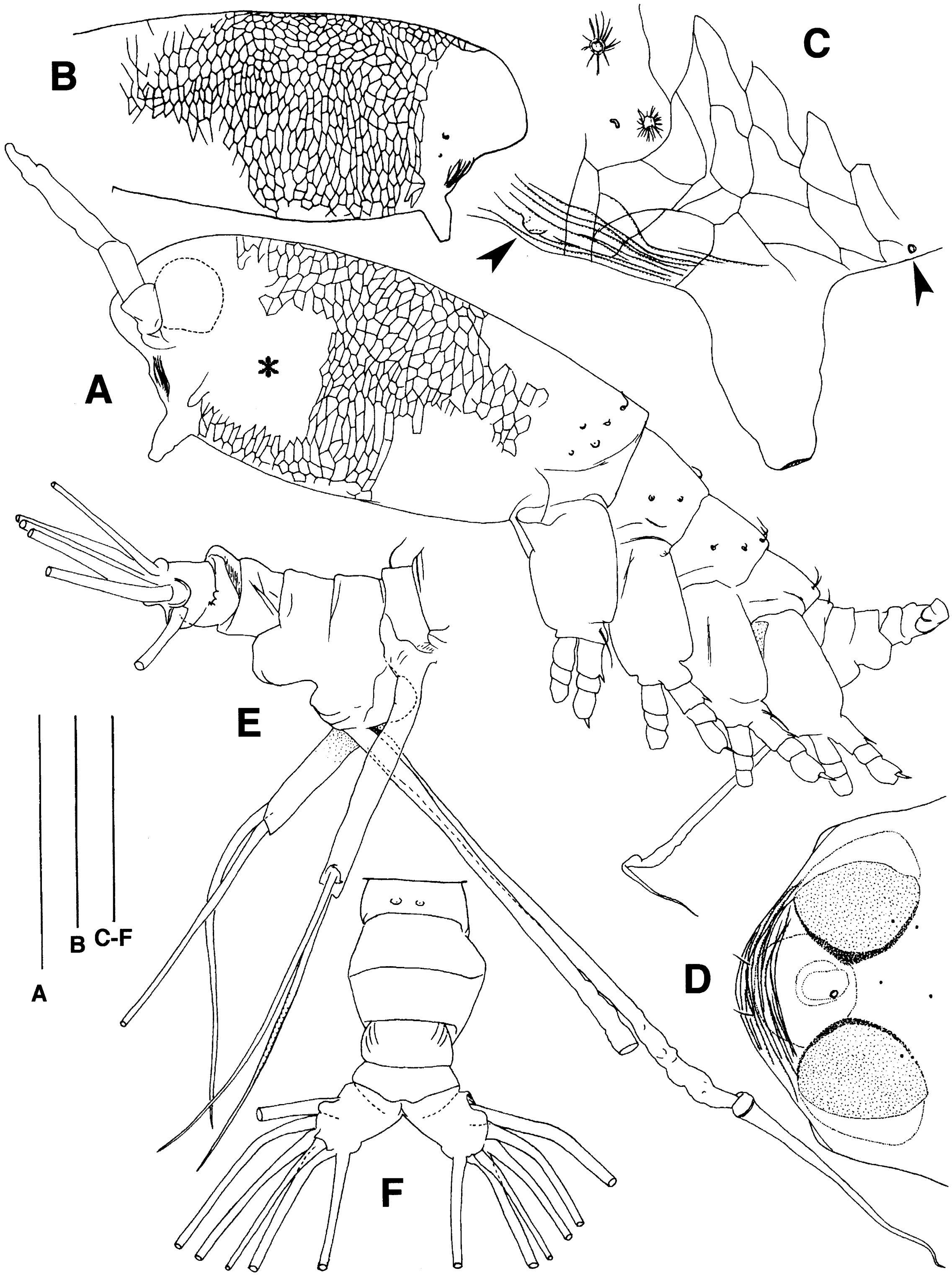


Figure 22. ***Maemonstrilla simplex* sp. nov.** A, C–F, female holotype (KMNH IvR 700 222); B, female paratype (KMNH IvR 700 223), both south coast of Ishigaki Island, 30.iv.1994. A, habitus, reticulations in area marked with asterisk (*) obscured. B, cephalothorax showing full extent of obvious reticulation. C, detail of oral papilla region, showing scars and two pairs of pores (arrowheads). D, anterior end of cephalothorax, dorsal view. E, urosome, lateral view, with legs 5 and ovigerous spines (one of latter broken), setules of setae omitted, furcal setae cut short. F, urosome, dorsal view, furcal setae cut short and with setules omitted. Scale bars = 0.5 mm in A, B; 0.1 mm in C; 0.2 mm in D–F.

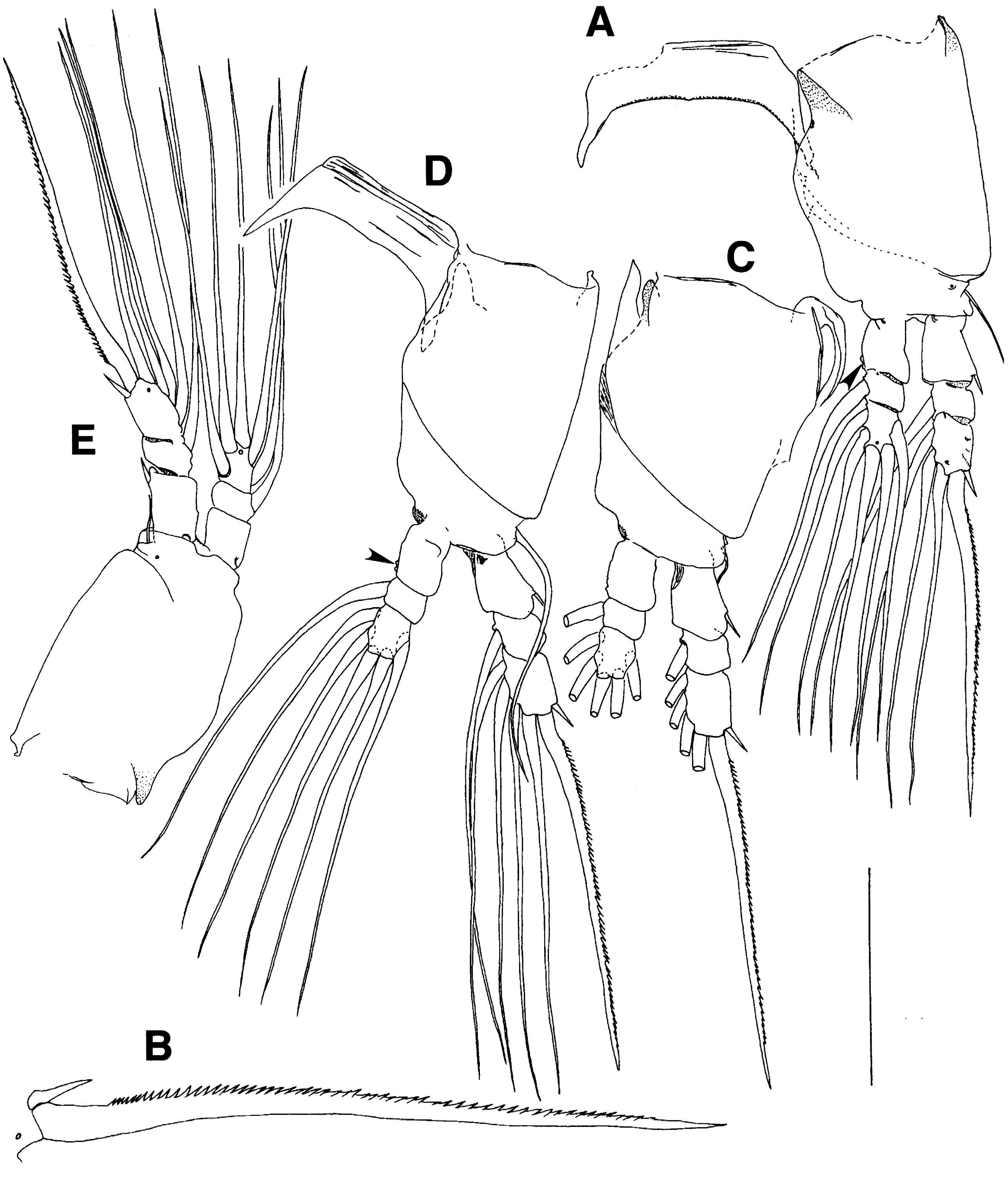


Figure 23. ***Maemonstrilla simplex* sp. nov.**, female holotype (KMNH IvR 700 222), south coast of Ishigaki Island, 30.iv.1994, left legs 1–4, setules omitted, some setae cut short. A, leg 1 and intercoxal sclerite, anterior. B, detail of outer apical exopodal setae (and distal pore) of leg 1 (see also Fig. 6C). C, leg 2, posterior. D, leg 3 and intercoxal sclerite, posterior. E, leg 4, anterior. Arrows in A and D indicating vestige of proximal inner endopodal seta. Scale bars = 0.2 mm in A, C–E; 0.1 mm in B.

First free pediger with one dorsal and two lateral pairs of pit setae, and second free pediger with two dorsal and two lateral pairs; more anterior of lateral pit setae also most ventral on these two somites. Third free pediger with two pairs of dorsal pit setae, and fourth free pediger with one pair. Each free pediger with pair of anterior dorsal pores hidden under rear margin of preceding segment or cephalothorax. Second free pediger with additional pair of double pores at one-third length and pair of simple pores at two-thirds length. Third free pediger with pair of dorsal pores at about two-thirds length.

Legs 1–4 (Fig. 23) with low and wide intercoxal sclerite, as wide as or wider than legs, with very slight projection at midline and distally directed processes at outer corners. Inner margin of basis rounded and slightly protruding. Outer seta and pore of basis, as well as segmentation and setation of rami, and pore in distal segment of each ramus, as in *M. hyottoko*. Outer spiniform setae on exopod simple, that on third segment slightly larger than that on first. Inner distal corner of first endopodal segment with protruding, socket-like structure (Fig. 23A, D). Outer margin of outer apical exopodal seta with row of small, sharp, distally pointing, closely spaced denticles (Fig. 23B). Leg 5 as in *M. hyottoko* (Fig. 22E).

Dorsum of genital compound somite with transverse partial articulation (Fig. 22F). Ventrally, posterior part and portion anterior to bases of ovigerous spines each produced into round swelling (Fig. 22E). Anteriorly directed ovigerous spines cylindrical but tapering to naked tips from slightly swollen, wrinkled region at two-thirds length, reaching perhaps just beyond first legs (Fig. 22A, E). Caudal rami armed as in *M. hyottoko*, dorsal seta originally with setules, but these now all broken off (Fig. 22F); ventral pore present.

Eggs: Mean diameter of eggs from ovigerous specimen from south coast of Ishigaki Island 32 μm ($n = 15$).

MAEMONSTRILLA LONGIPES (A. SCOTT, 1909) **COMB. NOV.**

Monstrilla longipes A. Scott, 1909: 238, pl. LVIII, figs 3–4. Davis 1949: 248(footnote), 249; Sewell 1949: 141; Wickstead 1961: 61, 62; Zheng, Li & Xu 1984, 1989: both fig. 141H.
Monostrilla longipes – Al-Kholy 1963: 130, fig. I, 1–4.

Remarks: Scott (1909) described and illustrated (habitus dorsal view, detail of reticulation and legs 5) this species based on a single, 1.85-mm-long female captured during the Siboga Expedition at sta. 142, off Laiwui, coast of Obi Major, 0°24′S, 127°36′E, northern part of Ceram Sea, Indonesia. In 1994 this holotype was not found together with the other Siboga monstrilloids that are deposited in the Institute for Systematics and Population Biology, University of Amsterdam, and it is presumed lost. The description is detailed enough to recognize *Monstrilla longipes* as a member of *Maemonstrilla* (*M. hyottoko* species group) on the basis of its body form, the spinose-reticulate cuticle of the cephalothorax and free metasomal pedigers, and the form and setation of leg 5. A suture crosses the dorsum of the genital segment, as in most species of *Maemonstrilla*. The ovigerous spines were not described. It is possible that one of the newly described species of the *M. hyottoko* species group described herein (but not *M. simplex*) is synonymous with *M. longipes*, but this cannot be demonstrated conclusively.

More recent, non-illustrated records of supposed female *Monstrilla longipes* from Nankauri Harbour, Nicobar Islands (Sewell, 1949; 2.25 mm long with a groove subdividing the genital segment) and the Singapore Strait (Wickstead, 1961), and a poorly illustrated record from Ghardaqa, Egypt, on the Red Sea (Al-Kholy, 1963), must be considered unsubstantiated at the specific level, although the specimens involved presumably do belong to the *Maemonstrilla hyottoko* species group. The 1.55-mm-long Egyptian specimen has a minute, non-setose, endopodal lobe on leg 5 (Al-Kholy, 1963: fig. I, 4), and so it very likely represents an undescribed species. Perhaps the ‘short hairs’ along the outer surface of the antennule are optically sectioned, high cuticular ridges such as those present in *M. hyottoko*. The ovigerous spines are 0.63 mm long but their direction was not mentioned. We have not tried to borrow this specimen for redescription.

MAEMONSTRILLA TURGIDA SPECIES GROUP (MONOTYPIC)

MAEMONSTRILLA TURGIDA (A. SCOTT, 1909) **COMB. NOV.**

FIGURES 1B, 13B, 24–29

Monstrilla turgida A. Scott, 1909: 239, pl. LVIII, figs 5–6. Davis, 1949: 248(footnote), 250; Wickstead, 1961: 61, 62; Martin Thompson & Meiyappan, 1980: 207, fig. 1.
[?] *Monstrilla* sp. – Krishnaswamy 1953: 75, text-figs 17–18.

Diagnosis: Cephalothorax non-reticulated, but with faint encircling striations. Cuticle appearing smooth by light microscopy, but patches of minute spinules revealed by SEM dorsally on metasomal pedigers and all urosomal segments except telson, and on outer face of coxa of legs 1–4. Pair of spinulose, spine-like scales posteriorly near dorsal midline on both first and second free pedigers. Outer basis seta of leg three shorter than exopod. Inner seta present on first segment of each ramus of legs 1–4. Leg 5 bilobed, its exopodal lobe with three setae and endopodal lobe with one seta (perhaps

KEY TO THE RYUKYU SPECIES OF THE *MAEMONSTRILLA HYOTTOKO* SPECIES GROUP

1. (a) Cuticle of cephalothorax, antenules, lateral sides of trunk, dorsum of telson, and caudal rami reticulated; outer faces of legs 1–4 and dorsum of free pedigers, genital compound somite, and penultimate somite spinulose. Cephalothoracic reticulations comprising ridges with abundant or sparse spinules; simple or complex cuticular ornamentation within at least some meshes……2
   (b) Only cephalothorax reticulated, and no obviously spinulose regions present. Ridges of cuticular meshwork lacking spinules, and cuticular surface within meshes plain……*M. simplex*
2. (a) Oral papilla large and conical, directed ventrally. Genital compound somite distinctly divided by transverse ridge……3
   (b) Oral papilla small, directed more anteriorly than ventral and flanked by ‘puffed cheeks’. Genital compound somite lacking dorsal transverse ridge……*M. okame*
3. (a) Legs 1–4 each with two low, rounded lobes on outer proximal part of coxa; rest of outer face of coxa with fields of minute spinules separated by bare lanes. Cephalothoracic reticulatations lacking side branches but bearing sporadic or sparse spinules; meshes uniformly polygonal over most of surface……4
   (b) Legs 1–4 lacking such coxal lobes; outer face of coxa evenly covered with larger spines. Cephalothoracic reticulatations with many side branches; besides polygonal meshes anteriorly and posteriorly, wide zone of narrow meshes present behind level of oral papilla……*M. hyottoko*
4. (a) Proximal coxal lobes of legs 1–4 bearing spinules only slightly larger than those on rest of coxa. Body length (as defined herein) > 2 mm. Spherical pigmented spots (red when fresh) found throughout body. Posteroventral part of genital compound somite produced into apron-like flap; posterodorsal margins of this somite and penultimate somite not denticulate……*M. polka*
   (b) Proximal coxal lobes of legs 1–4 bearing large, bluntly rounded denticles. Body length < 2 mm, and pigment spots absent. Posteroventral part of genital compound somite produced into spur; posterodorsal margins of this somite and penultimate somite distinctly denticulate……*M. spinicoxa*

up to two setae). No ventral protrusion of posterior part of genital compound segment.

Distribution: ‘Siboga’ Expedition sta. 142, northern Ceram Sea, Indonesia; Kundugal Channel and Minicoy Island lagoon, India; east of Linggau Archipelago, South China Sea; Ryukyu Islands.

Material examined: Syntype female, ‘Siboga’ Expedition sta. 142, off Laiwui, coast of Obi Major, 0°24′S, 127°36′E, northern part of Ceram Sea, Indonesia, on loan from Institute for Systematics and Population Biology (Zoölogisch Museum), University of Amsterdam (Cat. no. ZMA Co. 201478).

Twelve females collected at Sesoko Island by M. J. Grygier (on first occasion, with H. Ueda), intact unless otherwise noted: one on 12.vii.1988 (USNM 1093750), one on 26.xii.1988 (LBM Reg. No. 1430000932); two on 7.vii.1989 (SO lab; both used for SEM), three on 13.viii.1989 (ZMA Co. 205910), two on 31.viii.1989 (KMNH IvR 700 224, 700 225; latter including slide with legs 1–4, used for microscopic drawings), one on 28.ix.1992 (USNM 1093751), one on 2.x.1992 (NHM Reg. No. 2006. 1912), one on 9.vii.1996 (LBM Reg. No. 1430000933).

Twelve females collected at Ishigaki Island, all intact: one at Kabira Bay, 9.iii.1993, by M. J. Grygier (NHM Reg. no. 2006. 1913); two on south coast, 30.iv.1994, by S. Ohtsuka (KMNH IvR 700 226, 700 227; former used for photography); 9 off Kabira, 14.iv.1996, by A. Murase (intended for LBM, but now misplaced).

Description of Ryukyuan specimens: Overall appearance with bulbous cephalothorax much the same as in *M. hyottoko*, but considerably larger and with relatively longer ovigerous spines (Figs 1B, 13B, 24A, 25A). Measurements taken from ten or (for some) 11 specimens, excluding specimens from Kabira in 1996. Length in lateral view (sum of lengths of cephalothorax, metasome and urosome as defined in Fig. 1A) 1.38–2.21 mm, with these body regions contributing 49.4–54.8, 26.1–30.4 and 17.2–20.8%, respectively (this sum exceeding body length as seen in dorsal view by 2.4–8.7%; largest individual 2.11 mm long in dorsal view). Height and greatest width of cephalothorax, respectively, 40.9–57.9 and 41.9–57.9% of cephalothorax length; in several specimens height and width equal. Antennule length 41.6–51.3% that of cephalothorax. Width of incorporated pediger 68.4–88.5% of greatest width. Widths of succeeding three free pedigers and genital compound somite relative to that of incorporated pediger 76.1–89.1, 64.8–77.2, 53.8–63.5 and 30.7–40.3%, respectively. Ovigerous spines (seven pairs measured) 45.1–56.1% as long as body in dorsal view.

Cuticular reticulation completely absent, but cephalothorax with faint but dense circular striae (Fig. 25C); scattered minute dots also seen by phase

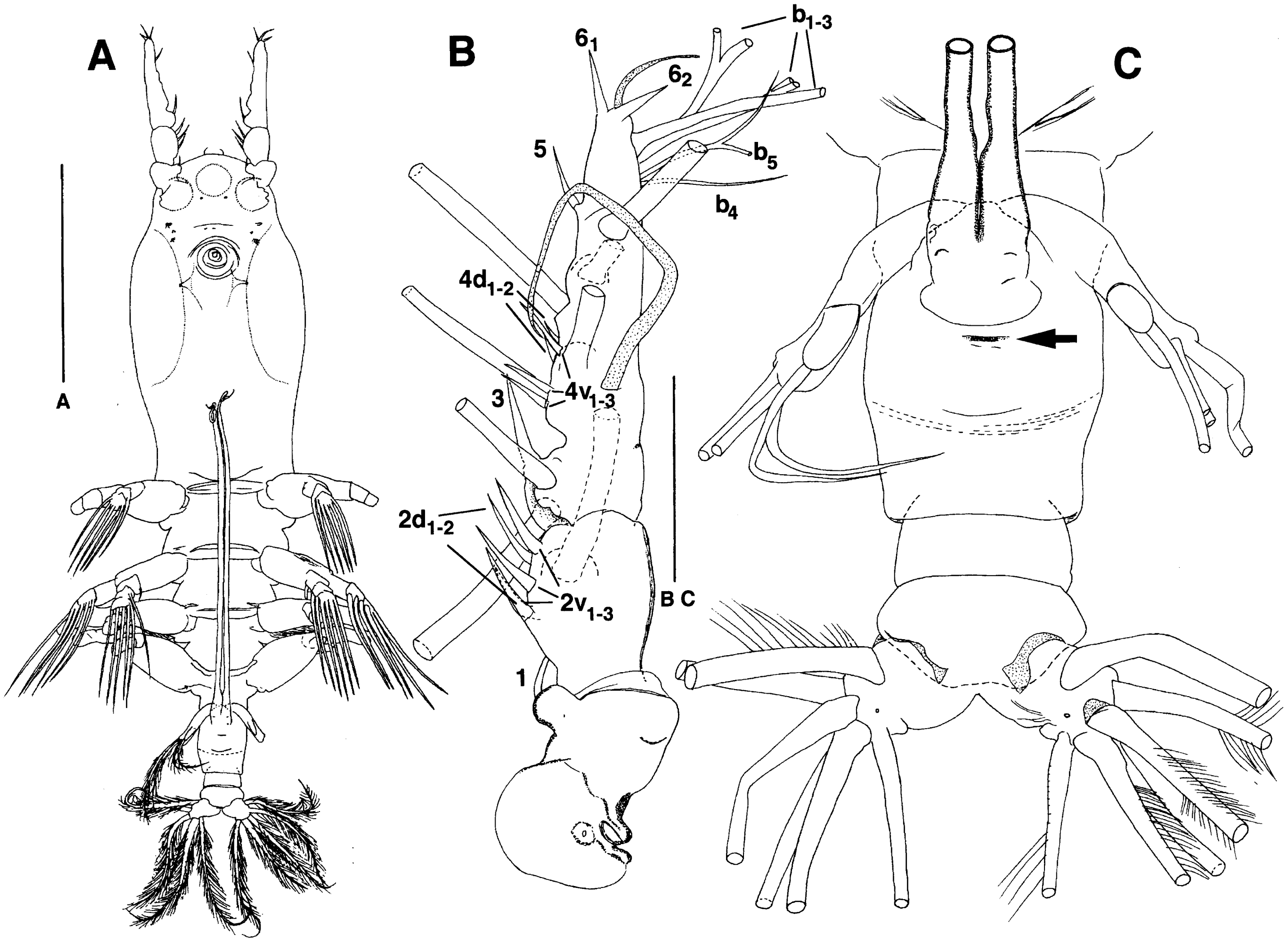


Figure 24. ***Maemonstrilla turgida*** (A. Scott, 1909) **comb. nov.**, female (KMNH IvR 700 225), Sesoko Island, 31.viii.1989. A, habitus, ventral view, only representative seta and setules shown (cf. Fig. 1B for dorsal view of same specimen). B, left antennule, ventral view, setules omitted, setal designations after Grygier & Ohtsuka (1995: fig. 6). C, urosome, ventral view, ovigerous spines and most setae cut short, some representative setules shown on furcal setae, copulatory pore arrowed. Scale bars = 0.5 mm in A, 0.1 mm in B, C.

contrast. Oral papilla long, straight, conical, directed ventrally (Fig. 25A, B). Pair of closely spaced pores just in front of it; another pair, further apart, at level of posterior bases of antennules (Fig. 25B). Two more pairs of pores, even further apart, behind oral papilla (Fig. 25C). Three or four small scars behind base of each antennule, middle one(s) smallest, anterior and posterior ones surrounded by radiating ridges (Fig. 25B). Pair of hair-like sensilla on forehead; dorsal to them, symmetical pattern of about nine small pores and dorsolateral pair of larger pores (not illustrated); apparently no wrinkled pit like that of *M. hyottoko*. Three cups of naupliar eye large, equal in size (Fig. 24A).

Antennules with non-articulating boundary between third and fourth segments suggested by constriction; first and second segments distinct (Fig. 24B). Full setation probably present in life (Grygier & Ohtsuka, 1995), but one or two setae missing on each antennule observed. Among spiniform setae, 2-setae all rather short, less than twice as long as longest 4-seta; 3-seta a little longer than 2-setae; near tip, b-setae all bifurcating twice with first split rather far out; apical 6-setae short and equal.

Patches of minute, bluntly conical teeth separated by smooth lanes present dorsally beginning with first free pediger (Fig. 26A, C–E). Patches arrayed in six rows, with numbers per row as follows: 2-3-6-6-3-2 on first free pediger, 4-4-7-7-4-4 on second, 3-3-4-4-3-3 on third, fourth unknown due to wrinkling, ?(3-3-3-3-3-3) + (3-3-3-3-3-3) on genital compound somite before and after transverse dorsal suture (suture: Fig. 26E) and 2-2-2-2-2-2 on penultimate segment. Patches generally square to oblong, but all patches on second free pediger and outer ones on third free pediger irregular in shape (Fig. 26D). Rear-most patches of middle two

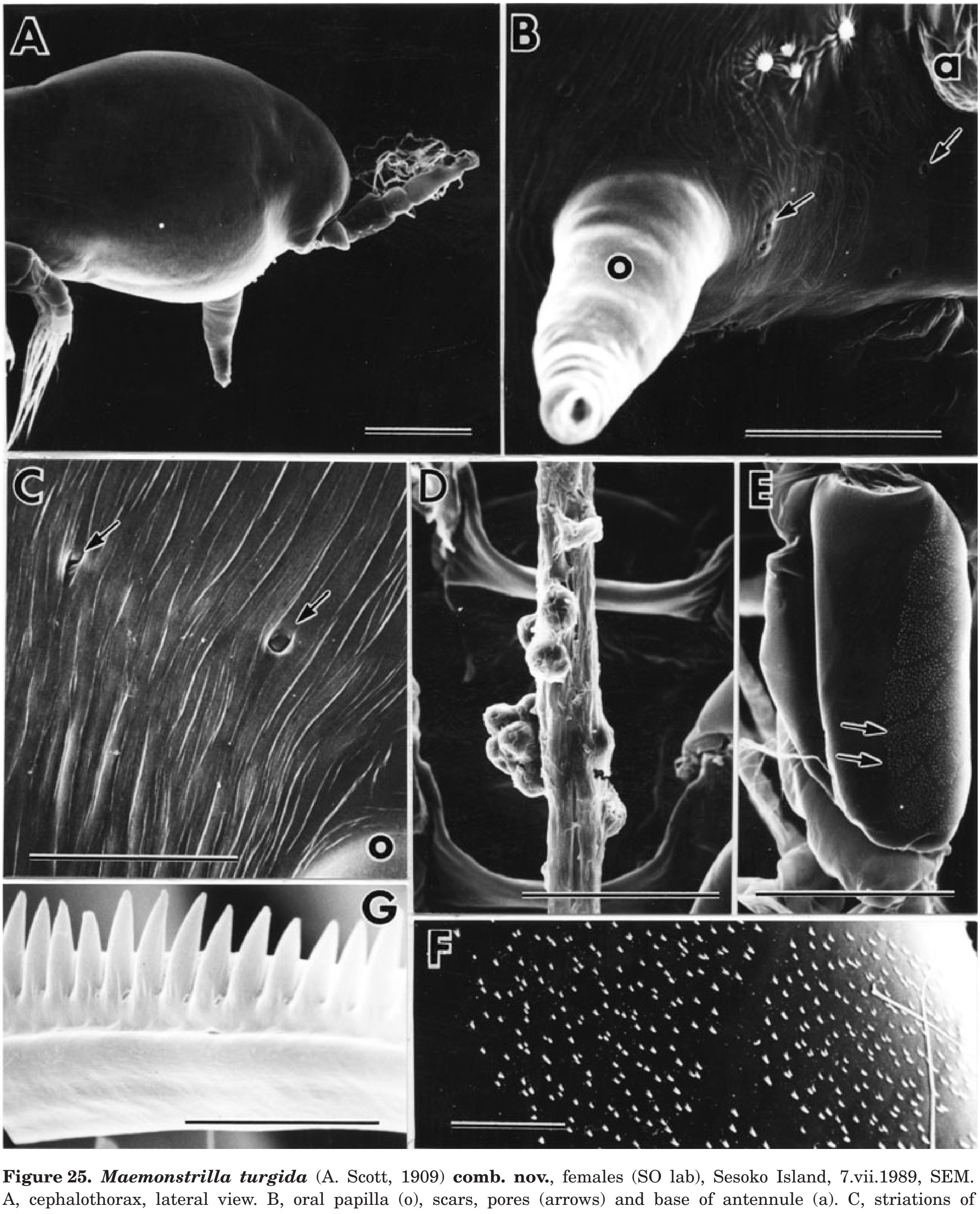


Figure 25. ***Maemonstrilla turgida*** (A. Scott, 1909) **comb. nov.**, females (SO lab), Sesoko Island, 7.vii.1989, SEM. A, cephalothorax, lateral view. B, oral papilla (o), scars, pores (arrows) and base of antennule (a). C, striations of cephalothorax and two left-hand pores (arrows) behind oral papilla. D, ovigerous spines with attached eggs overlying two intercoxal sclerites. E, protopod of leg 4, lateral view showing patches of denticles, arrows bounding region enlarged in F. F, detail of E. G, detail of outer apical exopodal seta of leg 2. Scale bars = 200 μm in A; 100 μm in B, D, E; 5 μm in C; 10 μm in F, G.

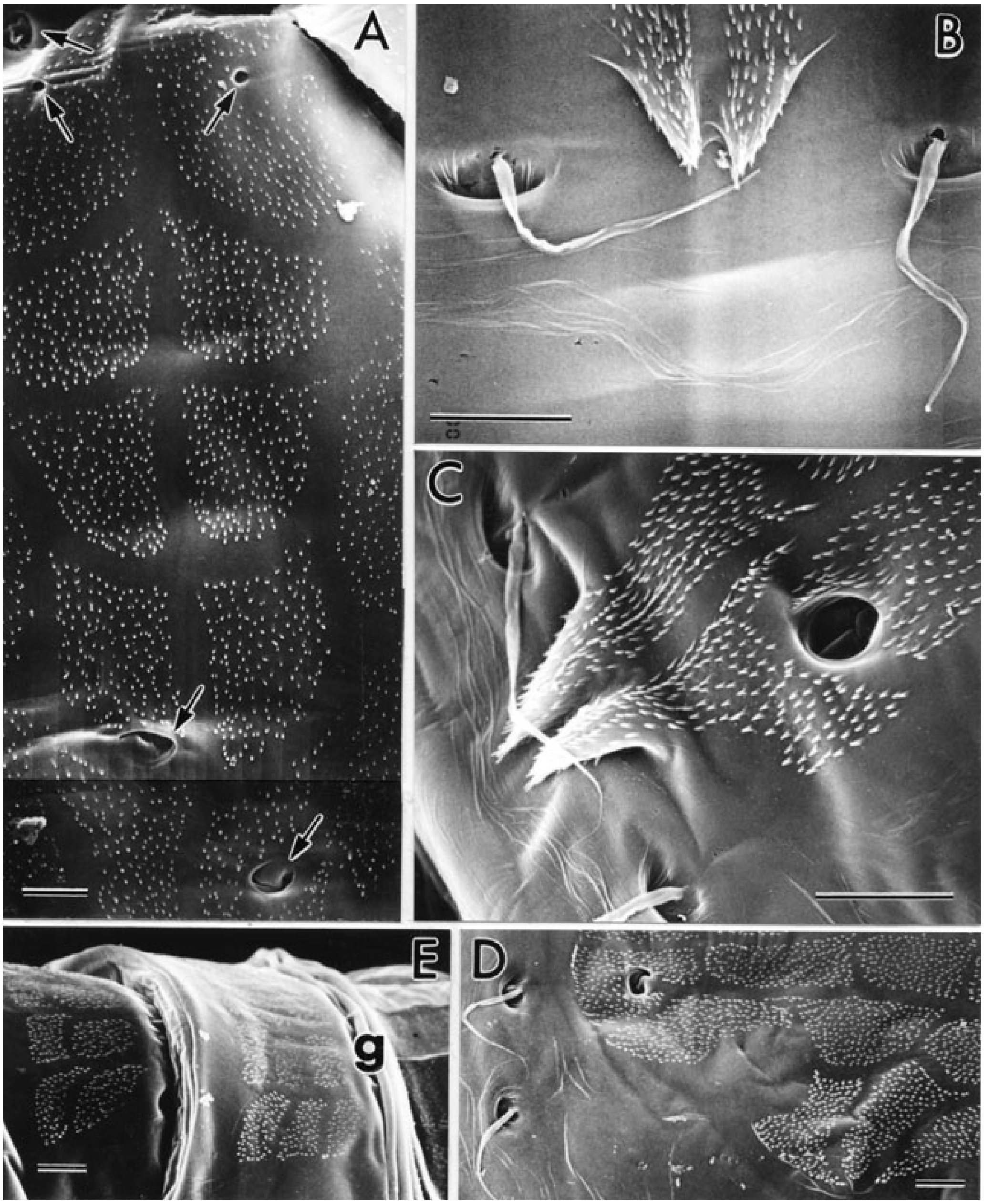


Figure 26. ***Maemonstrilla turgida*** (A. Scott, 1909) **comb. nov.**, females (SO lab), Sesoko Island, 7.vii.1989, SEM. A, dorsal spinulation and pores (arrows) of first free pediger, anterior at top. B, spiniform scales and pit setae at centre rear of dorsum of free pediger 1, posterior at bottom. C, pore, spiniform scales, and pit setae at centre rear of dorsum of free pediger 2, posterior at bottom left. D, right dorsal spinulation, pore and pit setae of free pediger 3, anterior at right. E, spinulation of genital compound somite (g, letter placed on this segment's dorsal suture) and penultimate segment of urosome, dorsolateral view, anterior at right. Scale bars = 10 μm.

rows of first and second free pedigers extending onto pair of posteriorly directed, spine-like scales (Fig. 26B, C).

Several pores near dorsal midline at two-thirds length of cephalothorax. Distribution of more posterior dorsal pores and dorsal and lateral pit-setae shown in Figure 29; essentially as in *M. hyottoko*, but anterior dorsal pores of first free pediger in two rows with medial pair small (Fig. 26A), and anterior dorsal pores of third free pediger not confirmed. Larger pores of first three free pedigers apparently provided with valves (Fig. 26A, C, D).

Intercoxal sclerites and segmentation of legs 1–4 as in *M. hyotokko* (Figs 25D, 27A–F). About 12 patches of

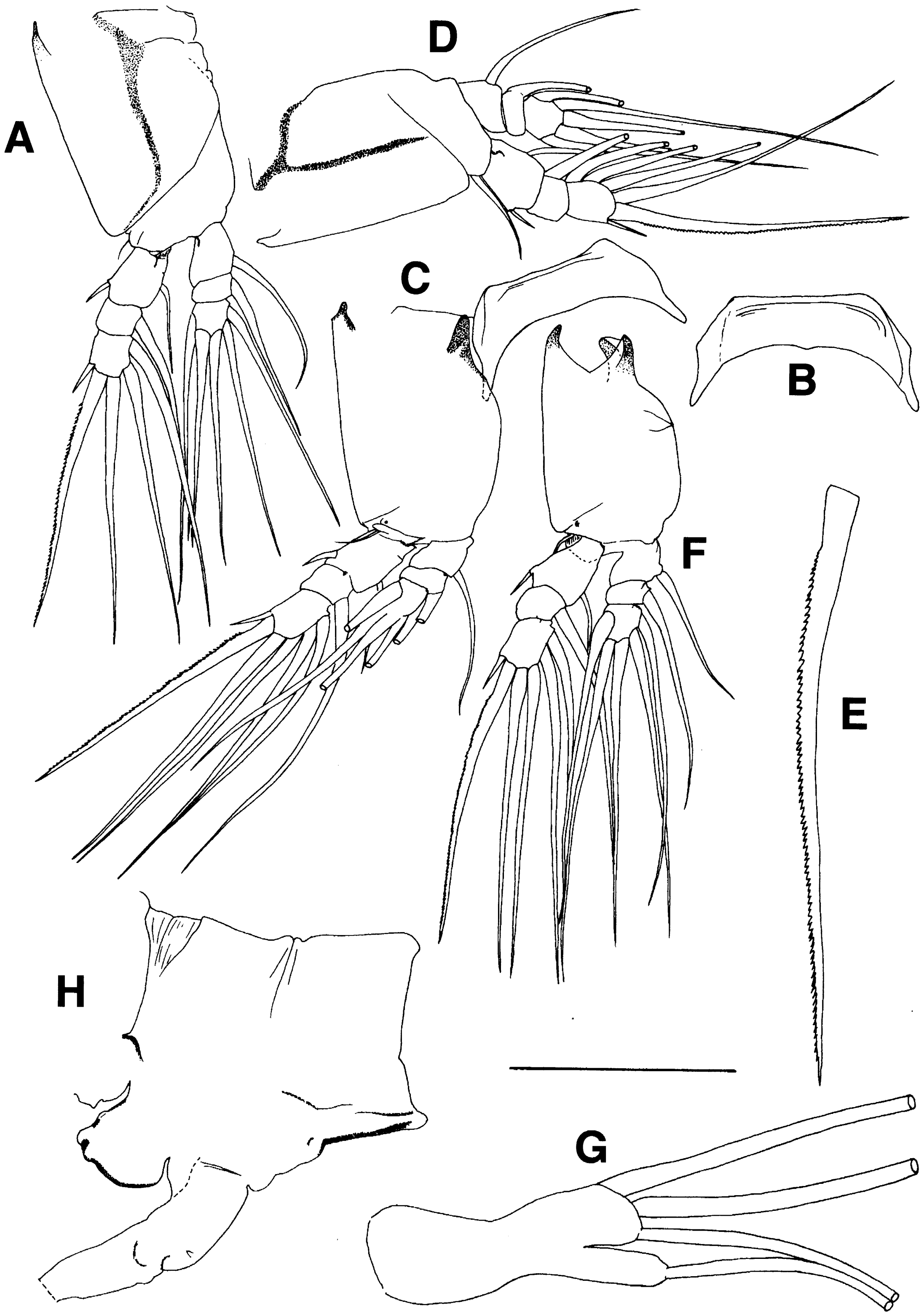


Figure 27. ***Maemonstrilla turgida*** (A. Scott, 1909) **comb. nov.**, female (KMNH IvR 700 225), Sesoko Island, 31.viii.1989. A, left leg 1, posterior. B, intercoxal sclerite of legs 1, anterior. C, right leg 2, anterior. D, left leg 3, posterior. E, outer apical exopodal seta of left leg 3. F, right leg 4, anterior. G, right leg 5, medial view. H, compound genital somite, lateral view, anterior to left, showing prominence at anterior base of ovigerous spines (latter cut short). In A, C, D, F and G, setules omitted, some setae cut short. Scale bars = 0.2 mm in A–D, F; 0.1 mm in E, G, H.

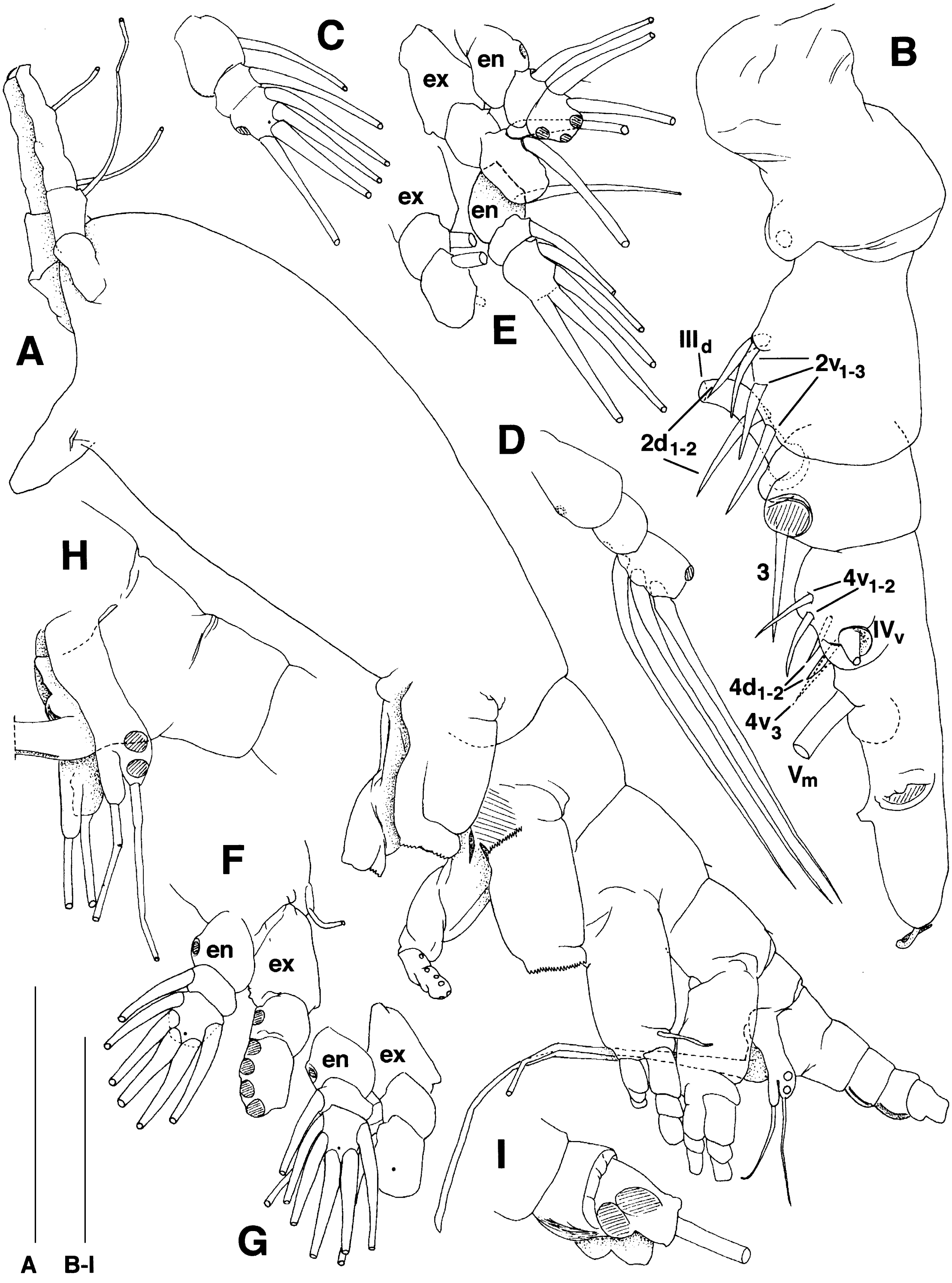


Figure 28. ***Maemonstrilla turgida*** (A. Scott, 1909) **comb. nov.**, syntype, 'Siboga' Expedition sta. 142 (ZMA Co. 201478), most longer setae cut short in drawings, setules almost entirely lost. A, habitus. B, right antennule, ventral view, setal designations after Grygier & Ohtsuka (1995: fig. 6); dotted $4v_3$-seta missing, but drawn in based on its presence in left antennule. C, right leg 2, endopod. D, loose, broken-off exopod of leg 2, 3 or 4. E, rami of left legs 3 (above) and 4 (below), anterior view. F, basis and rami of right leg 3, anterior view. G, rami of right leg 4, anterior view. H, legs 5 and genital compound somite, lateral view. I, telson and caudal rami, lateral view. Scale bars = 0.5 mm in A; 0.1 mm in B; 0.2 mm in C–I.

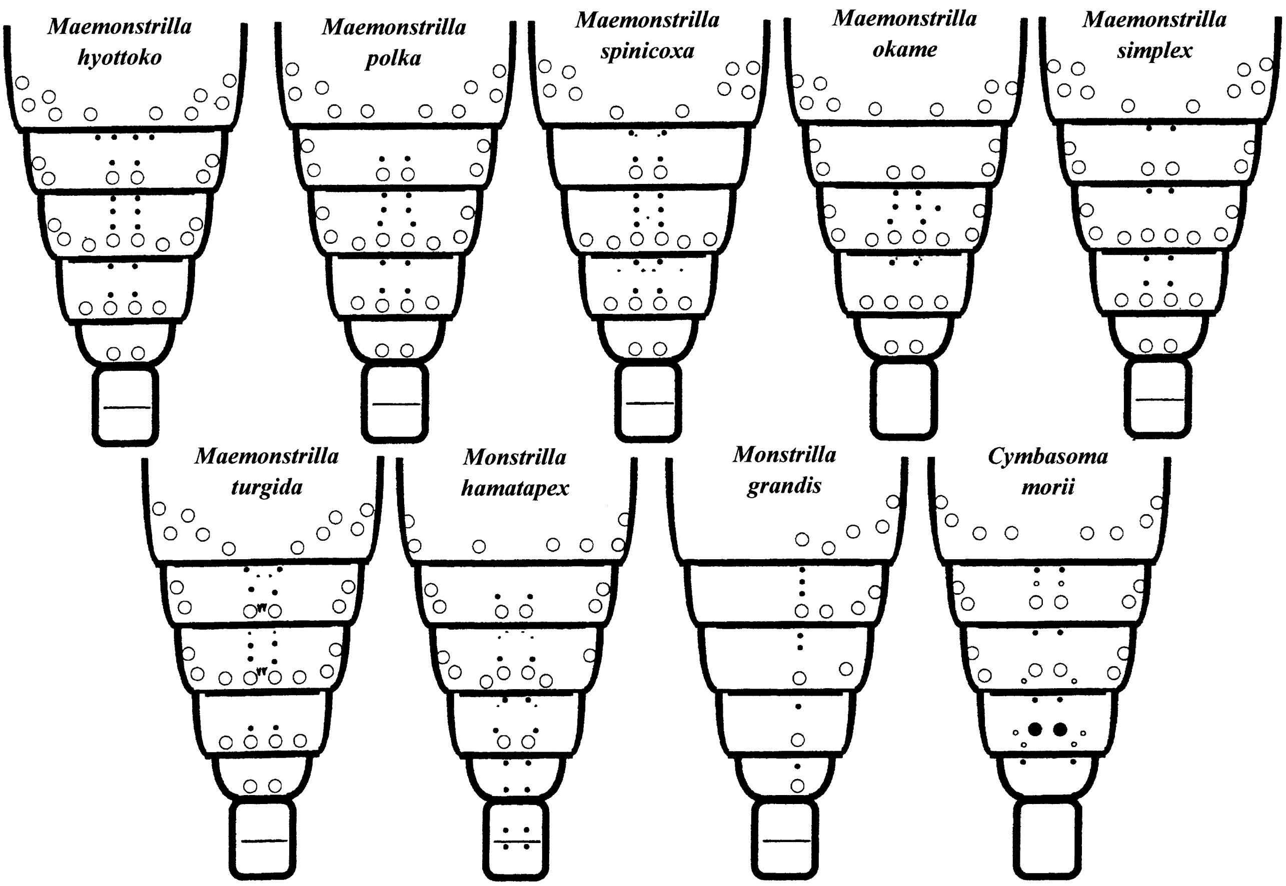


Figure 29. Comparison of dorsal and lateral pore and pit seta patterns, from rear of cephalothorax through genital compound somite, among six species of ***Maemonstrilla* gen. nov.** (present study), two of *Monstrilla*, and one of *Cymbasoma*. Explanation of symbols: dots (three sizes) = pores; larger circles = pits of pit setae; smaller circles = structures of uncertain type observed by light microscopy (*Cymbasoma morii* only); arrowheads = spiniform scales (*Maemonstrilla turgida* only). *Maemonstrilla* patterns based on SEM and light microscopical examination, frequently representing composites and in some cases probably incomplete. *Monstrilla hamatapex* Grygier & Ohtsuka, 1995 after Grygier & Ohtsuka (1995: fig. 5B, E); *Monstrilla grandis* Giesbrecht, 1891 after Huys & Boxshall (1991: fig. 2.5.1A; lateral view, so only right-side structures shown); *Cymbasoma morii* Sekiguchi, 1982 after Grygier (1994b: fig. 1E).

minute, rather widely spaced denticles along outer face of coxa (Fig. 25E, F); these patches in two interdigitating rows and separated by bare lanes. Similar spinules present on outer face of at least least first exopodal segment. Full plesiomorphic setation of legs 1–4 present as outlined by Huys & Boxshall (1991), including inner seta of first endopodal segment and weak inner seta of first exopodal segment (Fig. 27A, C, D, F). Outer basis seta short and hair-like in legs 1, 2 and 4, longer and plumose in leg three but shorter than exopod; pore anterior to this seta in each leg. Tiny pore on anterior face of third segment of each ramus (illustrations all in posterior view, so pore not shown). Outer spiniform setae of exopod simple, that on third segment a little longer than that on first. Outer side of outer apical exopodal seta lined with closely adjacent, bluntly conical denticles (Figs 25G, 27E).

Leg 5 with wide exopodal lobe bearing two apical setae and one subapical outer seta; narrower but longer endopodal lobe with one apical seta; all setae biserially plumose, outer two exopodal setae longer than others (Figs 24C, 27G).

Round copulatory pore on midline within crescent-shaped slot at posterior base of conical process bearing ovigerous spines (Fig. 24C). Spines extending to halfway between legs 1 and oral papilla, slender and cylindrical with tapered tips (Figs 13B, 24A). Caudal rami with ventral pore and six setae distributed as in *M. hyottoko* (Fig. 24A); short dorsal seta usually simple, but sometimes with distal setules; other setae biserially plumose and medial one longest.

Description of syntype: Damaged (Fig. 28A), lacking most leg setae besides those of endopods of legs 3 and

4 (Fig. 28E–G), lacking many antennular setae, especially distal to 4-setae and Vm (Fig. 28B), and lacking all except one pair of furcal setae (Fig. 28I). In addition, all rami of legs 1 and left leg 2 torn away, along with exopod of right leg 2 (a few loose pieces of these legs found; Fig. 28C, D). Dimensions in lateral view as follows: length (sum of lengths of cephalothorax, metasome and urosome as defined in Fig. 1A) 2.39 mm, with these body regions contributing 53.3, 28.1 and 18.6%, respectively; height of cephalothorax 42.1% of cephalothorax length; antennule length 37.0% that of cephalothorax; unbroken part of longer ovigerous spine 34.1% as long as body. Cephalothorax full of unlaid brood. Three pairs of scars behind bases of antennules. Inner seta of first exopod segment not retained on any leg; that of first endopodal segment retained on right leg 2 and left leg 4 (Fig. 28C, E), represented by socket on some other legs. Leg 5 biramous, at least left one originally with three setae on exopod (1 remaining) and one setae on endopod (Fig. 24H). Ovigerous spines arising from process with large, rounded, anterior protrusion (Fig. 24H).

Remarks: The full setation of legs 1–4 and the biramous condition of leg 5 are plesiomorphic features compared with the *M. hyottoko* species group. The spine-like scales of the first two free pedigers are similar to but much smaller and closer together than the pairs of spines present on the same segments in the eponymous *Monstrilla spinosa* Park, 1967 (see Park, 1967; Suárez-Morales & Vásquez-Yeomans, 1996). *Monstrilla spinosa* is an odd species with an assortment of other unique specializations, none of which indicates any relationship with *Maemonstrilla turgida*.

Scott (1909) reported two syntypes of his *Monstrilla turgida* from the same sample, but only one was in the vial obtained on loan from Amsterdam; the other must be assumed lost. The remaining syntype (original description and present observations) shows enough of the distictive features of the present Ryukyuan specimens so as to allow assignment of the latter to *M. turgida* for the time being. It was not possible to confrm in the syntype the inner seta of the first exopodal segment of legs 1–4, nor the presence of the pair of spine-like scales dorsally on the first two free pedigers. Although the first antennae of the syntype are relatively shorter than in the measured Ryukyuan specimens, other measurements and proportions fall within the range of the latter.

The unidentified *Monstrilla* figured by Krishnaswamy (1953) from Kundugal Channel, India, seems to be a female of *Maemonstrilla turgida* or a similar species, to judge from the bulbous cephalothorax and bilobed leg 5. The ovigerous spines were neither mentioned nor drawn; possible differences from the Ryukyuan specimens are the supposed presence of two setae, not one, on the endopod of leg 5 and five setae, not six, on the caudal rami.

Suárez-Morales & Dias (2001b) compared two new or redescibed species of *Monstrilla*, both with ordinary ovigerous spines and swimming legs, with what was then called *Monstrilla turgida*, while citing A. Scott (1909) and Grygier & Ohtsuka (1996) in regard to the latter. In particular they judged that *M. pustulata* Suárez & Dias, 2001 from Brazil shows ‘some affinities’ to *M. turgida*, i.e. a similar cephalothoracic shape and a bilobed female leg 5 with 3 + 1 setation. But they noted several differences as well, especially the opposed direction of the ovigerous spines, and did not press a case for a phyletic connection.

DISCUSSION

MONSTRILLOID SYSTEMATICS

According to the keys of Davis (1949) and Isaac (1975), the presence of two clearly defined segments behind the genital compound somite refers the present female specimens to *Monstrilla* or *Monstrillopsis*, and the well-developed eyes and rather anterior position of the oral papilla specify *Monstrillopsis*. The key of Boxshall & Halsey (2004) also assigns all the present species to *Monstrillopsis*. Recently, however, Suárez-Morales *et al*. (2006) excluded most species with other than four setae on each caudal ramus from *Monstrillopsis*, leaving nine nominal species currently assigned to it firmly or tentatively based on one or both sexes. If strictly applied, this criterion would also exclude all species of *Maemonstrilla*, which have six such setae. In *Monstrillopsis* females, leg 5 resembles that of *Maemonstrilla turgida* in being bilobed with three setae on the exopodal lobe.

Of the five species of *Monstrillopsis* that are known from females, no relevant information is available concerning one originally described as *Haemocera filogranarum* Malaquin, 1901 but tentatively assigned here by Suárez-Morales *et al*. (2006). Three others, *M. dubia* (T. Scott, 1904) (the type species), *M. ferrarii* Suárez-Morales & Ivanenko, 2004 and *M. dubioides* Suárez-Morales *in* Suárez-Morales & Ivanenko, 2004 have a narrow, elongate cephalothorax, not a bulbous one. The cephalothorax of *M. chilensis* Suárez-Morales, Bella-Smith & Palma, 2006 is somewhat thicker, but still not anteriorly bulbous in the fashion of *Maemonstrilla*. These last four species, considered morphologically closest to each other by Suárez-Morales *et al*. (2006), all have posteriorly directed ovigerous spines, an unarmed inner lobe of leg 5 and four setae on each caudal ramus (see also

Scott, 1904; Sars, 1921; Suárez-Morales & Ivanenko, 2004). Legs 1–4 are also normal in regard to degree of separation across the midline, shape of the intercoxal sclerites and setation (cf. discussion below of subthoracic egg brooding).

Two other species merit attention as possibly closer relatives than these to the species herein assigned to *Maemonstrilla*. *Monstrillopsis zernovi* Dolgopol'skaya, 1948, otherwise quite similar to the four species mentioned above, differs from them but agrees with *Maemonstrilla* species in having five long, plumose setae and one short, supposedly simple seta on each caudal ramus (see Dolgopol'skaya, 1948). Despite this, Suárez-Morales *et al*. (2006) retained *M. zernowi* in *Monstrillopsis* as an 'aberrant form'. The female of *Monstrilla reticulata* Davis, 1949, a species that was assigned to *Monstrillopsis* by Isaac (1975), was returned to *Monstrilla* by Suárez-Morales *et al*. (2006). The latter authors considered the male described by Davis (1949) not to be conspecific with the female, and probably belonging to *Monstrillopis*. To formally assign the species name *reticulata* to one sex or the other will require the designation of a lectotype. The female has a reticulated cephalothorax, as in *Maemonstrilla hyottoko*, and its leg 5 is bilobed with 3 + 1 setation, as in *M. turgida* (see Davis, 1949); also, its oral papilla protrudes somewhat. By contrast, the female of *M. reticulata* is very small (maximum length 0.74 mm), its cephalothorax is cylindrical, not bulbous, its urosome is relatively slender, its ovigerous spines point posteriorly, and it supposedly has no branched setae on the antennules and only five setae on each caudal ramus. *Monstrillopis zernowi* and females of *M. reticulata* cannot now be assigned to *Maemonstrilla*, but they might be the closest relations among other known monstrillids. A full cladistic analysis is beyond the scope of the present paper.

Suárez-Morales *et al*. (2006: 104) proposed that an undescribed species from Jersey in the Channel Islands, which was given the manuscript name of '*Monstrillopsis latipes*' in a doctoral thesis (Isaac, 1974b), has 'an anteriorly directed pair of ovigerous spines, a character presumably relegating it to a long known but as yet formally undescribed genus', i.e. to *Maemonstrilla*. The shape and armament of its leg 5 appear consistent with an assignment to *Monstrillopsis* (*sensu* Suárez-Morales *et al*., 2006). The ovigerous spines were described and illustrated as perpendicular to the body axis, not anteriorly directed. Provisional assignment of this form to *Maemonstrilla* is, in our opinion, premature. Such a step will require clarification of the original orientation of these spines as well as knowledge of the morphology of legs 1–4. Being stuck together, the legs of the sole available specimen were not described by Isaac (1974b).

INTEGUMENTAL ORGANS

The chapter on the Monstrilloida by Huys & Boxshall (1991) incidentally showed some integumental organs, in particular in drawings of *Monstrilla grandis* Giesbrecht, 1891, and Grygier (1994b) and Grygier & Ohtsuka (1995) took care to note the occurrence of such organs in other species at the light microscopical level. These descriptions together with the present ones (compiled in Fig. 29) suggest that monstrilloids have a rather limited, and to a degree stereotypical, arrangement of such structures. While not greatly dissimilar to patterns in certain cyclopoids (e.g. Rocha *et al*., 2000), this is in strong contrast to the much more elaborate cuticular pore signatures of calanoid and some other cyclopoid copepods (e.g. Vaupel Klein, 1982; Mauchline, 1987; Koomen, 1992; Park & Mauchline, 1994; Baribwegure & Dumont, 2003; Alekseev *et al*., 2006). In the Monstrilloida it would be premature to try to use these structures seriously in systematics, as light microscopical observations of them are somewhat unreliable. Furthermore, Park (1996) has suggested that at least five individuals of a species should be checked to be sure of finding most of the potential pore sites. It is notable, however, that all species of *Maemonstrilla* lack dorsal pores on the genital compound somite, where *Monstrilla hamatapex* Grygier & Ohtsuka, 1995 has two pairs (Fig. 29). Species of *Maemonstrilla* furthermore have pit setae posteriorly on the fourth free pediger, where *Monstrilla hamatapex* has pores.

Based on the present study and some of our unpublished observations on other monstrillids from the Ryukyu Islands, we here list the integumental organs one might expect to find in any female monstrillid. We hope that later workers will take the trouble to check other species and document exceptions and variations.

1. Pair of hair-like sensilla arising from anterior pores on 'forehead'.
2. Up to three pairs of pores anterior to oral papilla and two pairs close behind, one anterior pair sometimes produced as conical tubes.
3. Various paired arrangements of anteroventral scars.
4. Various pore patterns anterodorsally on cephalothorax, sometimes including a medial cuticular pit of unknown function.
5. Few pores dorsally along cephalothorax, perhaps concentrated in front of former anterior margin of incorporated first pediger.
6. Four or five pairs of dorsal and lateral pit setae at rear of cephalothorax, one dorsal and two lateral pairs at rear of first free pediger, two dorsal and two lateral pairs at rear of second free pediger,

two dorsal pairs at rear of third free pediger, one dorsal pair at rear of fourth free pediger.

7. One or two pairs of pores near anterior margin of all four free pedigers, often hidden by overlapping rear margin of preceding somite or cephalothorax.
8. Additional one or two dorsal pairs of pores, some simple and some valved, on some segments as far posteriorly as each half of genital compound segment.
9. In legs 1–4, outer anterior pore or pair of pores near basis seta, and one or two distal pores anteriorly on third segment of each ramus.
10. Ventral pore on caudal ramus.

The present SEM micrographs also show cuticular ornamentations, such as reticulate ridges and beds of spinules and denticles, which have only occasionally been mentioned and illustrated until now. Several previously described species in genera other than *Maemonstrilla* have more or less extensive cuticular reticulations: *Cymbasoma reticulatum* (Giesbrecht, 1893), *Monstrilla wandelii* Stephensen, 1913, *Monstrillopsis reticulata* and *Monstrilla careli* Suárez-Morales & Dias, 2000 (see Giesbrecht, 1893; Stephensen, 1913; Davis, 1949; Suárez-Morales & Dias, 2000). Huys & Boxshall (1991) showed with SEM the dense, irregular ridges that ornament the trunk cuticle of *Monstrilla helgolandica*, and Suárez-Morales & Ivanenko (2004) similarly showed with SEM various sets of wrinkles found anteriorly on the cephalothorax of *Monstrillopsis ferrarii*. Grygier & Ohtsuka (1995) reported but did not illustrate extensive beds of minute spinules on the metasomal dorsum, urosome and outer faces of legs 1–4 in *Monstrilla hamatapex*. We expect that such structures will prove to be widely distributed at least on larger species of monstrillids. Because we observed by SEM the spinule patch pattern on just one or two specimens each of the five SEM-examined species in the present paper, we cannot yet judge the intraspecific variability, nor the utility of this kind of feature in systematics. Only a few grosser features, such as spinules or denticles that are clearly visible by light microscopy, are used in the key herein.

SUBTHORACIC EGG BROODING

Free-living adult female copepods ordinarily release eggs freely into the water (some Calanoida) or they carry the eggs in one or two sacs hanging from the genital segment (remaining Calanoida, other orders except for Monstrilloida) (Huys & Boxshall, 1991). Female monstrilloids carry the eggs on a pair of ovigerous spines that arise from the ventral side of the genital compound somite (Huys & Boxshall, 1991). These spines trail posteriorly in all monstrilloids aside from the forms described herein.

The unusual direction of the spines suggests that species of *Maemonstrilla* practise subthoracic brooding. Although it is conceivable that the spines point forward only after the final moult and bend backwards to the ‘normal’ position when the eggs are deposited, several examples refute this. A few eggs (about 23 μm in diameter) were found attached to the anteriorly pointing spines of two specimens of *M. turgida* (Fig. 25D), and there were two larger clusters (part of a single larger original mass?) on the spines of another specimen of this species (Fig. 13B). All three specimens of *M. polka* bore very large egg masses held beneath, and matching in length, the cephalothorax and metasome (Fig. 13B); each mass consisted of thousands of eggs. Five specimens of *M. okame* also were carrying eggs beneath the thorax (not illustrated). The egg mass is somewhat oval in lateral view with a more pointed anterior end, it is laterally compressed with flat sides, and it reaches ventrally further than the tips of the leg setae. In lateral view the egg mass appears bigger than the copepod, but it is a little less than half as wide as the cephalothorax, within which all the eggs were stored before deposition.

In comparison with other copepods, legs 1–4 of all species of *Maemonstrilla* treated here are very widely separated across the midline, and the intercoxal sclerites are very low as well as very wide (Figs 2C, 20B, 23A, D, 24A, 25D, 27C). These features are surely adaptations that make room for a large egg mass borne beneath the thorax. The loss of the inner seta of the first segment of each leg ramus in all species of the *Maemonstrilla hyottoko* species group may be a further adaptation to avoid interference between the legs and the egg mass while swimming. Subthoracic brooding may avoid the problem of egg stripping from trailing spines, either by friction against some obstacle or by predators. Secondly, a subthoracic egg mass is likely to have a different effect on the female’s swimming hydrodynamics than the trailing mass of eggs of other monstrilloids. Both of these points require confirmation by observation and recording of living animals.

Specialized brooding in enclosed or semi-enclosed chambers formed from body somites and/or appendages has evolved independently many times in copepods (Table 1). This tendency is particularly remarkable in symbiotic copepods. This may be due to the restricted space for the symbiont on the host and/or a need to avoid loss of eggs within the host. All examples listed here are podoplean copepods, which generally carry egg-sacs, as opposed to free release of eggs into water, which is characteristic of many gymnopleans (= calanoid copepods). Possession of egg-sacs seems to have encouraged the development of specialized brooding in some lineages of podopleans.

Table 1. Specialized brooding in copepods. Although the order Poecilostomatoida has been synonymized with the order Cyclopoida by Boxshall & Halsey (2004), this classification is not adopted here

Brooding type	Order	Taxon	References
1. Egg mass borne between legs on urosomal ovigerous spines.	Monstrilloida	*Maemonstrilla*	Present study
2. Egg mass covered by foliaceous leg 5.	Harpacticoida	*Phyllopodopsyllus*, *Eudactylopus*, *Parathalestris*, *Parmenophia*, Tetragonicipitidae	Lang (1965), Gamô (1969), Itô (1970, 1972, 1973, 1974), Boxshall & Halsey (2004)
	Cyclopoida	*Ascidicola*	Gotto (1993), Boxshall & Halsey (2004)
3. Brood pouch formed by thoracic somites.	Cyclopoida	Notodelphyidae, Buproridae	Gotto (1993), Boxshall and Halsey (2004)
	Poecilostomatoida	Gastrodelphyidae	Boxshall & Halsey (2004)
Siphonostomatoida	(?) *Pectenophilus ornatus*	Nagasawa *et al*. (1988)	
4. Brood pouch formed by body processes (as cage).	Cyclopoida	Chordeumiidae	Boxshall (1988), Boxshall & Halsey (2004)
5. Tube formed by host.	Poecilostomatoida	Chitonophilidae	Lamb *et al*. (1996)

Four types of special brooding can be recognized in copepods (Table 1). Some free-living harpacticoids and a commensal cyclopoid have foliaceous legs 5 that shield the developing eggs, which are attached to or held in a ventral pocket of the genital area. A brood pouch that is formed dorsally or dorsolaterally within one or more thoracic somites is present in parasitic or commensal notodelphyid cyclopoids and a parasitic poecilostomatoid. Although the origin of the brood pouch of the highly modified parasitic siphonostomatoid *Pectenophilus ornatus* Nagasawa, Bresciani & Lützen, 1988 is unknown, its brooding may also be of this type. Maintenance of loose egg sacs in a subthoracic 'cage' formed from modified and ventrally downturned cephalic appendages and thoracic outgrowths occurs in certain highly modified chordeumiid cyclopoids, endoparasites of ophiuroids. A special case is known in the poecilostomatoid family Nucellicolidae, endoparasitic in gastropods. The vermiform female is enveloped in a membranous tube that is possibly of host origin, and the tube becomes filled with eggs and developing nauplii (Lamb *et al*., 1996). If the tube is induced by the parasite, it can be regarded as an additional kind of brooding apparatus. Other examples, particularly among parasites, can be adduced; however, *Maemonstrilla* represents the only example of subthoracic brooding among planktonic copepods.

COXAL LOBES

Maemonstrilla polka and *M. spinicoxa* share an apparent synapomorphy, namely two spinulose or denticulate lobes at the outer base of the coxa in legs 1–4 (Figs 10D, 14F). The location of these lobes suggests a similarity with exites such as gills or epipods, found on the thoracic limbs of many crustaceans but never in copepods (Huys & Boxshall, 1991). However, they are not articulated to the limb, are low and dome-shaped rather than lamelliform or branched, and do not have thinner cuticle than the rest of the limb, and we do not consider them to represent exites. Depending on species, the spinules on the lobes are either slightly or much more robust than those elsewhere on the outer side of the coxa. Perhaps they as well as the other coxal and exopodal denticles have a role in a non-planktonic phase of the female copepod's life. Such an occasion may be while seeking a potential host for its ready-to-hatch brood, e.g. within the narrow confines of a polychaete tube, where such spinules would provide a grip on the walls.

NAUPLIAR MORPHOLOGY

The nauplius of *Maemonstrilla okame* is quite similar to that of *Monstrilla hamatapex*, described by Grygier & Ohtsuka (1995) on the basis of SEM micrographs. It is smaller (38 μm versus 48.7 μm in length), the dorsal surface is smoother, the second segment of the antennule is curved rather than straight, the labral bulge is narrower anteriorly than in *M. hamatapex* and extends further posteriorly (to the distal rather than proximal end of the mandibular basis), and there are no labial spinule rows in the present nauplius. The most important difference concerns the mandible, which has a relatively smaller basis, a much smaller claw than in *M. hamatapex* and a two-segmented exopod with three setae instead of a one-segmented exopod with five setae. Grygier & Ohtsuka (1995) could not confirm the origin of the hook-associated mandibular seta in *M. hamatapex* and left the homology of the hook unresolved. The fact that the seta posterior to the claw arises from the base of the claw in *Maemonstrilla okame* (Fig. 21F), and not from the distal end of the basis, demonstrates that the claw represents the endopod, not a modified basis seta.

THE UNKNOWN MALES

To match males to females of a given monstrillid species, four methods are available, and most are difficult to apply. In a region with a demonstrated impoverishment of species, co-occurrence of males and females in the plankton may be an indication of conspecificity. If both sexes can be reared from the same host species, and only one species of each sex appears, the two sexes may be assumed to be conspecific. Distinctive morphological features, if shared between the sexes, may serve as markers to help match them up. Finally, genetic matching may be tried, using various molecular biological techniques. Co-occurrence has been used most frequently, but unreliably, in areas such as the British seas or the Mediterranean where many species occur in low numbers, and capture *in copulo* has never been reported. Some Pacific coral reefs are characterized by a great abundance of monstrillids, particularly in the nighttime plankton (e.g. Sale, McWilliams & Anderson, 1976, 1978). The Ryukyu Islands are such a place. In the samples examined for the present study, mostly taken over or near coral reefs, monstrillid specimens and species of various genera were usually abundant, and up to three species of *Maemonstrilla* females co-occurred in samples (see 'Material examined' for *M. hyottoko* and *M. polka*). Matching sexes by co-occurrence cannot be done in these circumstances. Although females of *Maemonstrilla*, especially those of the *M. hyottoko* species group, have an abundance of very distinctive morphological features compared with other monstrillid genera, most are connected with subthoracic brooding and unlikely to have any expression in males. By contrast, certain species-specific features, such as the coxal lobes of *M. polka* and *M. spinicoxa* and the red dots of the former, or the dorsal spiniform scales of *M. turgida*, might well be found in the respective males. None of the Ryukyu males we have examined, mostly of various larger species comparable in size with the *Maemonstrilla* females, shows any such feature, however, and none is distinctly reticulated, but many smaller males remain unexamined.

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