# The Australian Monstrilloida (Crustacea: Copepoda) I. Monstrillopsis Sars, Maemonstrilla Grygier \& Ohtsuka, and Australomonstrillopsis gen. nov. 

EDUARDO SUÁREZ-MORALES ${ }^{1,4} \& A$ A. DAVID MCKINNON ${ }^{2,3}$<br>${ }^{1}$ El Colegio de la Frontera Sur (ECOSUR). Unidad Chetumal. P.O. Box 424. Chetumal, Quintana Roo 77014, Mexico<br>${ }^{2}$ Australian Institute of Marine Science, P.M.B. No. 3, Townsville M.C., Queensland 4810, Australia<br>${ }^{3}$ School of Marine and Tropical Biology, James Cook University, Queensland, Australia<br>${ }^{4}$ Corresponding author. E-mail: esuarez@ecosur.mx

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#### Abstract

Monstrilloid copepods were collected during zooplankton surveys in reef and coastal areas of Australia. Representatives of all four genera of the Monstrilloida (Monstrilla Dana, Monstrillopsis Sars, Cymbasoma Thompson, and Maemonstrilla Grygier \& Ohtsuka) were recorded. In this contribution a taxonomic analysis of specimens belonging to the latter two genera is provided, and a new genus described. The genus Monstrillopsis was represented exclusively by male specimens, on the basis of which three new species are described: Mon. hastata sp. nov., Mon. boonwurrungorum sp. nov., and Mon. nanus sp. nov. These are distinguished from each other and previously described species of this genus by details of the genital complex (or genital apparatus), body size, ornamentation of the cephalic surface, number of caudal setae, and characteristic modifications of the fifth antennular segment. All have distinctive characters not associated with sexual modifications, which will ease the task of matching females collected in future studies. Australomonstrillopsis gen. nov. is proposed to accommodate a male specimen with a unique combination of characters including massively developed caudal rami, cephalic perioral protuberances, and absence of an inner seta on the first exopodal segment of legs $1-4$, among other characters. The new genus is monotypic and contains $A$. crassicaudata $\mathbf{s p}$. nov. Three of the four new species of Maemonstrilla (Mae. ohtsukai sp. nov., Mae. hoi sp. nov., and Mae. protuberans sp. nov.) belong to the Mae. hyottoko species group, and the remaining one, Mae. crenulata sp. nov., belongs to the Mae. turgida group. Each of the new species of Maemonstrilla from Australia can be distinguished from its known congeners by a unique combination of characters


including the type of body reticulation, body size, antennule and body proportions, distinctive characters of the swimming legs, details of the antennular armature, and the presence/absence of a posteroventral process on the genital compound somite. With the addition of the four new species of Monstrillopsis and the four of Maemonstrilla described herein, the number of species in these genera has increased to 13 and 11 species, respectively. In no case did congeneric species cooccur, hinting that there may be a rich species diversity yet to be discovered within the Australian Monstrilloida.

Key words: marine zooplankton, taxonomy, associated Copepoda, reef crustaceans

## Introduction

Monstrilloids are protelean parasites of benthic polychaetes and molluscs; most postnaupliar and preadult stages are endoparasitic (Suárez-Morales 2011; Suárez-Morales et al. 2010, 2014). Only the first naupliar stage, a final, transitory copepodid stage ("subimago"), and the planktonic adults are free-living. The adults are the most conspicuous stage; they are non-feeding, reproductive forms that lack second antennae and mouthparts. These copepods are part of the zooplankton community in coastal-neritic waters at all latitudes, including Arctic and Antarctic waters (Razouls, 1996; Suárez-Morales \& Ivanenko 2004; Suárez-Morales 2011). Monstrilloids are frequently collected during routine plankton surveys but are rarely found in large numbers, although high densities in samples collected at night in and around coral reefs have been reported (Sale et al. 1976, 1978; Suárez-Morales 2001, 2011). The systematic position of the Monstrilloida is unclear: Huys et al. (2007) regarded the group as belonging within the Siphonostomatoida, a case considered unproven by Suárez-Morales (2011) and Suárez-Morales et al. (2014). For the purposes of the present work we retain the ordinal status of the Monstrilloida. Currently, the order is known to contain over 120 nominal species arranged in four valid genera: Monstrilla Dana, Monstrillopsis Sars, Cymbasoma Thompson, and Maemonstrilla Grygier and Ohtsuka (Suárez-Morales et al. 2006; Grygier \& Ohtsuka 2008; Suárez-Morales 2011). The taxonomic status of all valid and invalid genera of the Monstrilloida was briefly reviewed by Grygier and Ohtsuka (2008). Except for Maemonstrilla, the valid genera can be identified following Boxshall and Halsey's (2004) key.

Because of their relative rarity in plankton samples and the taxonomic complexity of the group, there are large geographic areas in which the monstrilloid copepod fauna remains practically unknown (Suárez-Morales 2011). One of these is Australia. Nicholls (1944) illustrated two specimens of Monstrilla sp. from Spencer Gulf, for which Davis (1949) later proposed the new species M. nicholsii Davis, 1949. According to Grygier (1995), Razouls (1981) stated that this species was "peu reconnaissable" because of the lack of data on many important morphological details. Its taxonomical status should be revised by checking the type specimens if they are available, or by examining collections from the type locality. There are additional Australian records of two widespread species of Cymbasoma, C. longispinosum (Bourne, 1890) and C. thompsoni (Giesbrecht, 1893) (Razouls et al. 2013).

In this contribution we present a taxonomic analysis of the Australian species of Monstrillopsis Sars, 1921 and Maemonstrilla Grygier \& Ohtsuka, 2008, and describe three new species of the former genus and four of the latter. We also describe a new genus to which a single new species is herein assigned. Ecological and distributional comments of the species are also provided.

## Materials and methods

Monstrilloid copepods were isolated from plankton samples collected in ecological studies of Australian coastal and shelf seas during the career of the second author. In all, monstrilloids occurred in 76 samples taken between November 1982 and November 2009. The source plankton samples were fixed in formaldehyde solution. Once isolated, monstrilloid copepods were transferred to $70 \%$ ethanol for taxonomic examination and long-term preservation.

The taxonomic descriptions presented here accord with the upgraded descriptive standards proposed by Grygier and Ohtsuka (1995) for monstrilloid copepods. New micro-characters were recently proposed by Grygier and Ohtsuka (2008) to further upgrade these standards, particularly in Maemonstrilla, but some of them require SEM analysis and others are not practical to check or evaluate with a small set of specimens or with only a single specimen available, as is the case for most of the Australian material considered here. Huys et al.'s (2007) nomenclature for the terminal
segment of the male antennule is followed; however, given the highly modified structure of this appendage in Monstrillopsis, setal elements are designated based on their position. Total body lengths are measured from the anterior end of the cephalothorax to the posterior end of the anal somite. Armament formulae for swimming legs are presented from basis to most distal segment and as outer margin first; Roman numerals indicate spines (i.e. spiniform setae), Arabic numerals indicate (ordinary) setae. The specimens were lightly stained with methylene blue, and semipermanent mounts of whole specimens or dissected appendages in glycerine were sealed with acrylic nail varnish or with Entellan $\circledR^{\circledR}$. Drawings were prepared at $400-1000 \mathrm{X}$ magnification with the aid of a camera lucida mounted on an Olympus CR31 microscope. Type specimens are deposited in the collections of the Museum of Tropical Queensland (MTQ), Townsville, Australia and the Museum of Western Australia, Perth (WAMC).

## Systematics

## Order Monstrilloida Sars, 1901

## Family Monstrillidae Dana, 1849

## Genus Monstrillopsis Sars, 1921

## Monstrillopsis hastata sp. nov.

(Figs 1-3)

Material examined: Holotype: adult male from Western Port Bay (Station G2VA of Kimmerer \& McKinnon 1985), Victoria, Australia ( $38^{\circ} 35.344^{\prime}$ S $144^{\circ} 59.687^{\prime} E$ ), partially dissected, slide-mounted in glycerine, sealed with Entellan®. Date of collection: 15 May 1983. Slide deposited in MTQ, Australia (cat. MTQW34268).

Description. Male: Total body length of adult male holotype: 0.81 mm . Cephalothorax 0.42 mm long, representing $51 \%$ of total body length. Antennule 0.38 mm long, representing $47 \%$ of total body length and $85 \%$ of cephalothorax length (Fig. 1A, B). Oral papilla small, located anteriorly, about $27 \%$ of way back along ventral surface of cephalothorax (Fig. 1A). Pair of relatively large ocelli present, pigment cups moderately developed, separated by less than half eye diameter, weakly pigmented; ventral cup and lateral cups equally sized. Forehead widely rounded, with two large sensilla and field of small cuticular papillae extending to most of cephalic area, including ventral and dorsal surfaces (Fig. 2A, B). Ventral surface of cephalic area bearing two pairs of nipple-like cuticular processes between antennule bases and oral papilla, one pair being small (Fig. 2A). Light pattern of cuticular striation present surrounding these structures, transverse striae reaching also middle ventral surface between nipple-like processes (Fig. 2A).

As usual in male monstrilloids, antennules five-segmented, geniculate (Fig. 1C). In terms of pattern described by Grygier and Ohtsuka (1995), element 1 present on first segment; elements $2 \mathrm{~d}_{1}, 2 \mathrm{~d}_{2}, 2 \mathrm{v}_{1}, 2 \mathrm{v}_{2}, 2 \mathrm{v}_{3}$, and IId present on second segment. Third segment with elements 3, IIId, and IIIv, the latter being unusually stiff and slender (Fig. $1 C$ ). Fourth segment bearing elements $4 d_{1,2}$ and $4 \mathrm{v}_{1-3}$ as well as IVd. Inner middle margin of segment with pair of subtriangular protuberances near insertion of element 4 v (Fig. 1D). Terminal segment with elements 1-6, unbranched elements A-D (on posterior margin), and short medial aesthetasc (Fig. 1D). As usual in male Monstrillopsis, terminal antennular segment modified, with inner rounded expansion and elongate, sabre-like distal half representing $58 \%$ of segment length; inner expansion ornamented with four spinules (arrowed in Fig. 1C).

First pedigerous somite incorporated into cephalothorax; this and succeeding three free pedigerous somites each bearing pair of biramous swimming legs. Pedigerous somites 2-4 together accounting for $33 \%$ of total body length in dorsal view. Intercoxal sclerites of legs 1-4 sub-rectangular, without ornamentation on surface or along distal margin. Basis of legs articulating with rectangular coxa along diagonal line. Basis with thin, simple lateral seta on legs 1,2 , and 4 ; on leg 3, this seta thicker, lightly setulate and four times longer than on other legs. Endopodites and exopodites of swimming legs 1-4 triarticulate (Fig. 3A-C). Ramus setae all lightly and biserially plumose except for spiniform outer setae on exopodal segments 1 and 3, and inner seta of first exopodal segment, these all being short and slender. Also, outer apical exopodal seta of swimming legs 1-4 with outer margin smooth, inner margin lightly setose.

Armature formula of swimming legs:

|  | basis | endopodite | exopodite |
| :--- | :--- | :--- | :--- |
| leg 1 | $1-0$ | $0-1 ; 0-1 ; 1,2,2$ | $\mathrm{I}-1 ; 0-1 ; \mathrm{I}, 2,2$ |
| legs $2-4$ | $1-0$ | $0-1 ; 0-1 ; 1,2,2$ | $\mathrm{I}-1 ; 0-1 ; \mathrm{I}, 1,2,2$ |

Fifth legs absent. Urosome consisting of four somites: fifth pedigerous somite, genital somite with genital apparatus, one free postgenital somite, and large anal somite possibly incorporating fused preanal somite (Fig. 2E). Ventral surface of genital somite forming enlarged base of cylindrical shaft with distal genital lappets. Lappets represented by divergent pair of posteriorly directed cylindrical processes, each tapering distally into nipple-like process and reaching distal margin of anal somite (Fig. 2C-E). Anal+preanal somite large, representing 37\% of urosome, ornamented with posterior hyaline fringe of short spines on dorsal surface; similar ornamentation also present on dorsal surface of succeeding free postgenital somite (arrows in Fig. 2C). Anal+preanal somite with irregular posterior margin in dorsal view (Fig. 2E). Caudal rami subrectangular, symmetrical, divergent, approximately 1.3 times longer than wide, each ramus bearing four setae (Fig. 2C,E).

Female: unknown.
Type locality. Western Port Bay, Victoria, Australia ( $38^{\circ} 35.344^{\prime}$ S $144^{\circ} 59.687^{\prime} \mathrm{E}$ ).
Etymology. An adjective derived from the Latin noun hasta, meaning spear, the specific epithet makes reference to the unusually stiff, spear-like setal element IIIv of the fourth antennular segment.

Diagnosis. Third antennular segment bearing stiff seta IIIv, fourth segment with two nipple-like protuberances. Terminal antennular segment modified, with inner rounded expansion and elongate distal half, latter sabre-like and representing $58 \%$ of length of segment; inner expansion of this segment ornamented with four spinules. One free postgenital somite; preanal and anal somites apparently fused with no trace of intersegmental suture. Genital complex of type II (defined below), with mammiliform distal tips of lappets. Spinous hyaline fringe posteriorly on dorsal surface of fused preanal+anal somites and free postgenital somite.

Remarks. This male specimen is easily assignable to the genus Monstrillopsis by its possession of a distinctively modified fifth antennular segment, with an inner rounded protuberance and an attenuated, sabre-like distal half (see Huys \& Boxshall 1991; Suárez-Morales et al. 2006). The position of the oral papilla far anteriorly on the cephalothorax, the fully developed eyes, and the presence of four setal elements on the caudal rami are also regarded as diagnostic of this genus (Sars 1921; Suárez-Morales et al. 2006). This specimen has a reduced number of free postgenital somites compared to its congeners, one instead of two: as mentioned in the descriptive section, the preanal and anal somites appear to be completely fused, without traces of an intersomite suture. This condition is usually found in males of Cymbasoma and has not been known to occur in Monstrillopsis except for incomplete fusion marked by a ventral suture and lateral constrictions in M. chathamensis Suárez-Morales \& MoralesRamírez, 2009 (Suárez-Morales \& Morales-Ramírez 2009) and also in Monstrillopsis boonwurrungorum, described in the present work. In other species of the genus in which the division of the preanal and anal somites is fully expressed, as in Mon. sarsi (Isaac, 1974), Mon. chilensis Suárez-Morales, Ramírez \& Derisio, 2008 (SuárezMorales et al. 2008), and Mon. cahuitae Suárez-Morales \& Carrillo, 2013 (Suárez-Morales et al. 2013), the anal somite is short.

Among the males of Monstrilla and Monstrillopsis there are two main types of genital complex, one of which is represented by a long, cylindrical apparatus with paired distal globose processes (type I). This kind of genital structure has been recorded mainly in species of Monstrilla (Suárez-Morales et al. 2013), but also in Monstrillopsis fosshageni (Suárez-Morales \& Dias 2001) and its congener Mon. cahuitae (Suárez-Morales et al. 2013). The type II apparatus is similar to that present in our specimen, with a short shaft and relatively long, basally separated lappets. This kind of genital complex was earlier reported in two other species of Monstrillopsis, Mon. chilensis Suárez-Morales, Bello-Smith and Palma, 2006 from the Beagle Channel (Suárez-Morales et al. 2008) and Mon. chathamensis from the Eastern Tropical Pacific (Suárez-Morales \& Morales-Ramírez 2009). The present new species has a type II genital complex but differs from its above-mentioned congeners in having mammiliform, not rounded, lappet tips. The new species also differs in characters of the antennule structure; it has a longer terminal sabre-like process of the fifth segment than in Mon. chilensis and Mon. chathamensis and it also has a set of 4-5 spinules on the proximal rounded process of the segment, whereas this process is naked in Mon. chathamensis and in two of the four Australian species described herein. This process is ornamented with a patch of minute spinules
in Mon. chilensis (Suárez-Morales et al. 2008). A set of spiniform elements is present in another Australian species described herein, Mon. nanus sp. nov., but the genital lappets have a different structure.


FIGURE 1. Monstrillopsis hastata sp. nov., adult male. A) habitus, lateral view; B) habitus, dorsal view; C) left antennule, dorsal view; D) detail of paired processes on medial inner margin of fourth antennular segment. Scale bars: A, B $=200 \mu \mathrm{~m}, \mathrm{C}=100 \mu \mathrm{~m}$, $\mathrm{D}=10 \mu \mathrm{~m}$.


FIGURE 2. Monstrillopsis hastata sp. nov., adult male. A) cephalic area, ventral view; B) same, dorsal view; C) urosome and caudal rami, dorsal view; D) urosome showing genital complex, ventral view; E) urosome, lateral view, showing fifth legs and features of genital complex. Scale bars: A-E $=100 \mu \mathrm{~m}$.


FIGURE 3. Monstrillopsis hastata sp. nov., adult male. A) first swimming leg showing intercoxal sclerite; B) third swimming leg; C) fourth swimming leg. Scale bars: A-C $=100 \mu \mathrm{~m}$.

The present new species can be distinguished from all other species of Monstrillopsis on the basis of: 1) the stiff seta IIIv, which is usually flexible, not so rigid or spiniform as here, in both Monstrillopsis and other known monstrilloids; 2) the presence of two nipple-like protuberances on the fourth antennular segment (Fig. 1D), a feature not hitherto reported in any monstrilloid; 3) the mammiliform distal tips of the genital lappets; and 4) the spinous hyaline fringes on the dorsal surface of the free postgenital (preanal) and anal somites. A similar fringe was described in both Mon. chathamensis and Mon. chilensis, but only on the anal somite and at a more posterior position (Suárez-Morales \& Morales-Ramírez 2009; Suárez-Morales et al. 2008).

## Monstrillopsis boonwurrungorum sp. nov.

(Figs 4-5)
Material examined: Holotype: adult male from Port Phillip Bay, (Station C of Kimmerer \& McKinnon 1985), Victoria, Australia ( $38^{\circ} 2.583^{\circ} \mathrm{S}$; $144^{\circ} 57.08^{\prime} \mathrm{E}$ ), partially dissected, slide-mounted in glycerine, sealed with Entellan®. Date of collection: 5 January 1984. Slide deposited in MTQ, Australia (cat. MTQW24269).

Description. Male: Total body length of adult holotype: 0.91 mm . Cephalothorax 0.45 mm long, representing almost $50 \%$ of total body length. Antennule 0.42 mm long, about as long as cephalothorax (Fig. 4A, B) and representing almost $50 \%$ total body length. Oral papilla small, located anteriorly, about $26 \%$ of way back along ventral surface of cephalothorax (Fig. 4C, D). Pair of relatively large ocelli present, pigment cups moderately developed, separated by less than half eye diameter, weakly pigmented; ventral cup slightly larger than lateral cups. Forehead rounded, moderately protuberant, with no observable cuticular ornamentation. Ventral surface of cephalic area bearing low, rounded process between bases of antennules (arrowed in Fig. 4C). One pair of weakly developed nipple-like cuticular processes on anterior ventral surface between antennule bases and oral papilla (arrowed in Fig. 4D). Otherwise, cephalic ventral surface smooth except for faint preoral horizontal striations (Fig. 4C, D).

As usual in male monstrilloids, antennules five-segmented, geniculate (Fig. 4A, 5E). In terms of pattern described by Grygier and Ohtsuka (1995), element 1 present on first segment, elements $2 \mathrm{~d}_{1}, 2 \mathrm{~d}_{2}, 2 \mathrm{v}_{1}, 2 \mathrm{v}_{2}, 2 \mathrm{v}_{3}$, and IId present on second segment. Third segment with elements 3, IIId, and IIIv. Segment four bearing elements $4 d_{1,2}$ and $4 \mathrm{v}_{1-3}$ as well as IVd (Fig. 5E). Following Huys et al.'s (2007) nomenclature, armature of terminal segment including elements 1 and 4-7 as well as unbranched elements $\mathrm{A}-\mathrm{D}$ (latter on posterior margin). As usual in male Monstrillopsis, terminal antennular segment modified: inner expansion on proximal half bearing rounded process (arrowed in Fig. 5E), with no special ornamentation; distal half forming remarkably long, distally curved, sabrelike structure representing $64 \%$ of length of segment (Fig. 5E).

First pedigerous somite incorporated into cephalothorax; this and succeeding three free pedigerous somites each bearing pair of biramous swimming legs. Pedigerous somites 2-4 together accounting for $29 \%$ of total body length in dorsal view. Intercoxal sclerites of legs 1-4 sub-rectangular, without ornamentation on surface or along distal margin. Basis of legs articulating with rectangular coxa along diagonal line. Basis with thin, naked lateral seta on legs 1,2 , and 4 ; on leg 3 , this seta thicker and 2.5 times longer than in other legs, reaching beyond distal margin of first exopodal segment, and lightly setulate from distal $2 / 3$ (arrow in Fig. 5A). Endopodites and exopodites of swimming legs $1-4$ triarticulate (Fig. 5A). Ramus setae all lightly and biserially plumose except for spiniform outer seta on exopodal segments 1 and 3 and inner seta of first exopodal segment, these all being short and slender. Outer apical exopodal seta of swimming legs 1-4 with outer margin spinulose, inner margin lightly setulate (Fig. 5B).

Armature formula of swimming legs as in Monstrillopsis hastata.
Fifth legs absent. Urosome consisting of five somites: fifth pedigerous somite, genital somite with genital apparatus, two free postgenital somites (second of which referred to as preanal somite), and anal somite. Preanal and anal somites partially fused, with suture visible in ventral view (arrow in Fig. 4E) and bilateral intersomite constriction. Ventral surface of genital somite forming enlarged base of cylindrical shaft with elongate distal genital lappets. Genital complex of type II. Lappets represented by pair of posteriorly directed, divergent, arm-like processes with rounded tips. Lappets reaching to midlength of anal somite (Fig. 5C, D). Caudal rami subrectangular, weakly divergent, approximately 1.5 times longer than wide, each ramus bearing four setae.

Female: unknown.
Type locality. Port Phillip Bay, Victoria, Australia ( $38^{\circ} 2.583^{\prime} \mathrm{S}$; $144^{\circ} 57.08^{\prime} \mathrm{E}$ ).


FIGURE 4. Monstrillopsis boonwurrungorum sp. nov., adult male from Australia. A) habitus, dorsal view; B) habitus, lateral view; C) cephalic area showing medioventral protuberance (arrow), lateral view ; D) cephalic area showing faint nipple-like ventral processes (arrow), ventral view; E) urosome showing genital complex, ventral view. Scale bars: A, B=200 $\mu \mathrm{m}, \mathrm{C}-\mathrm{E}=$ $100 \mu \mathrm{~m}$.

B




FIGURE 5. Monstrillopsis boonwurrungorum sp. nov., adult male. A) second swimming leg with outer basipodal seta of third swimming leg (arrow); B) detail of ornamentation of outer apical spiniform seta of third exopodal segment of second swimming leg; C) urosome showing genital complex, dorsal view; D) same, lateral view; E) right antennule, dorsal view. Scale bars: $\mathrm{A}, \mathrm{C}-\mathrm{E}=100 \mu \mathrm{~m}, \mathrm{~B}=25 \mu \mathrm{~m}$.

Etymology. The specific epithet, a genitive noun, makes reference to the Boonwurrung people, a Kulin nation of aboriginal Australians who are the traditional owners of the coast and land along the northern, eastern, and southern shorelines of Port Phillip Bay. The name was Latinized using the masculine plural form.

Diagnosis. Terminal antennular segment strongly modified, with smooth inner rounded expansion and elongate distal half, latter sabre-like and representing more than $60 \%$ of length of segment. Cephalothorax with anterior ventral protuberance on cephalic part, widely separated from oral papilla. Two free postgenital somites present before anal somite, with preanal and anal somites partially fused but well distinguishable. Genital complex of type I, its lappets with rounded tips. Caudal rami with four setae.

Remarks. This new species shares several important characters with its Australian congener Mon. hastata sp. nov., including the position of the oral papilla, the body proportions, the presence of four caudal setae, the remarkably elongate sabre-like antennular process, and the general structure of the genital complex (type II). Monstrillopsis boonwurrungorum differs from Mon. hastata in several ways, including 1) the presence of an antero-ventral cephalic protuberance, which is absent in Mon. hastata; 2) the presence of a ventral suture and lateral constriction dividing the preanal and anal somites, vs. fused somites in Mon. hastata; 3) a relatively longer distal sabre-like process of the fifth antennular segment ( $58 \%$ of that segment's length in Mon. hastata vs. $64 \%$ in the present species); 4) the lack of ornamentation on the same segment's proximal rounded process, which has a row of four spiniform elements in Mon. hastata; 5) the subquadrate intercoxal plates, vs. rectangular plates in Mon. hastata; and 6) the distally rounded lappets of the genital complex vs. distally attenuated lappets with nipple-like tips in Mon. hastata. In addition, the perioral cuticular ornamentation and the development of the post-antennular nipple-like processes are clearly weaker in Mon. boonwurrungorum (see Fig. 4D) than in Mon. hastata (Fig. 2A).

This male specimen differs from all its known congeners in having a very long sabre-like distal part of the fifth antennular segment, comprising more than $60 \%$ the length of the segment, and a smooth proximal inner rounded protuberance on that segment. An anteroventral cephalic protuberance between the antennular bases has been observed previously only in two other species of the genus, Mon. cahuitae (Suárez-Morales et al. 2013) from Costa Rica and Mon. fosshageni Suárez-Morales \& Dias, 2001 from off Brazil. In these two species the process arises very close to the oral papilla (Suárez-Morales et al. 2013 fig. 4D; Suárez-Morales \& Dias 2001 fig. 36), not widely separated from it as in Mon. boonwurrungorum (see Fig. 4C). Also, the genital complex is of type I in both of these species but type II in Mon. boonwurrungorum, and the distal sabre-like antennular process of the fifth antennular segment is clearly shorter in Mon. cahuitae ( $32 \%$ of segment length) and Mon. fosshageni (43\%) than in Mon. boonwurrungorum (64\%). In addition, Mon. boonwurrungi has only four caudal setae vs. six in Mon. cahuitae (Suárez-Morales et al. 2013); the number of setal elements is unknown in Mon. fosshageni.

## Monstrillopsis nanus sp. nov.

(Figs 6-8)

Material examined: Holotype: adult male from Giralia Bay, Exmouth Gulf, Western Australia ( $22^{\circ} 28^{\prime}$ 'S; $114^{\circ} 20.75^{\prime}$ E; McKinnon \& Ayukai 1996), undissected, ethanol-preserved, slide mounted in glycerine, sealed with Entellan®. Date of collection: 25 September, 1994. Slide deposited in WAMC, Australia (cat. WAMC55071).

Description. Male: Total body length of adult holotype 0.50 mm . Cephalothorax 0.25 mm long, representing $50 \%$ of total body length. Antennule 0.23 mm , relatively long, 1.15 times as long as cephalothorax and representing $48 \%$ of total body length (Fig. 6A, B). Oral papilla small, located anteriorly, about $35 \%$ of way back along ventral surface of cephalothorax (Fig. 6A). Pair of relatively small ocelli present, pigment cups moderately developed, separated by less than half eye diameter, weakly pigmented on outer rim; ventral cup slightly larger than lateral cups. Forehead nubbly, with medial rounded protrusion (Fig. 7C, D). Ventral surface of cephalic area with single pair of nipple-like cuticular processes and adjacent field of transverse cuticular striations between antennule bases and oral papilla (Fig. 7D).

As usual in male monstrilloids, antennules five-segmented, geniculate (Fig. 7A). In terms of pattern described by Grygier and Ohtsuka (1995), element 1 present on first segment; elements $2 \mathrm{~d}_{1}, 2 \mathrm{~d}_{2}, 2 \mathrm{v}_{1}, 2 \mathrm{v}_{2}, 2 \mathrm{v}_{3}$, and IId present on second segment. Third segment with elements 3, IIId, and IIIv. Segment four bearing elements $4 d_{1,2}$ and $4 \mathrm{v}_{1,2}$ (Fig. 7B) (element $4 \mathrm{v}_{3}$ not observed), as well as elements IVd and IVv. A spiniform setal element observed between elements IVd and IVv, not identifiable by position following Grygier and Ohtsuka (1995),thus provisionally


FIGURE 6. Monstrillopsis nanus sp. nov., adult male. A) habitus, lateral view; B) habitus, dorsal view; C) urosome, dorsal view; D) same, ventral view. Scale bars: A, B=100 $\mu \mathrm{m}, \mathrm{C}, \mathrm{D}=50 \mu \mathrm{~m}$.


FIGURE 7. Monstrillopsis nanus sp. nov., adult male. A) right antennule, dorsal view; B) detail of arrangement of setal elements 4 v and 4 d on fourth segment; C) cephalic area showing rugose forehead surface, dorsal view; D) same, ventral view. Scale bars: A, C, D $=50 \mu \mathrm{~m}, \mathrm{~B}=10 \mu \mathrm{~m}$.
designated as element $4 \mathrm{v}_{1}$ (Fig. 7A). Following Huys et al.'s (2007) nomenclature, armature of terminal segment including elements $1,2,5$, and 6 , plus unbranched elements $\mathrm{A}-\mathrm{D}$ on posterior margin. Terminal antennular segment modified, inner rounded expansion ornamented with row of five short, spiniform elements; elongate distal half sabre-like, curved distally, comprising $50 \%$ of segment length.

First pedigerous somite incorporated into cephalothorax; this and succeeding three free pedigerous somites each bearing pair of biramous swimming legs. Pedigerous somites $2-4$ together accounting for $33 \%$ of total body length in dorsal view. Intercoxal sclerites of legs 1-4 sub-rectangular, without ornamentation on surface or along distal margin. Basis of legs articulating with rectangular coxa along diagonal line. Basis with thin, naked outer basipodal seta on legs 1,2 , and 4 ; on leg 3 , this seta thicker, lightly setulate, and 3.5 times longer than that on leg

1, 2 times longer than those on legs 2 and 4, reaching well beyond distal margin of second exopodal segment (Fig. 8B). Endopodites and exopodites of swimming legs 1-4 triarticulate (Fig. 8A-C). Ramus setae all lightly and biserially plumose except for spiniform outer seta on exopodal segments 1 and 3 and inner seta of first exopodal segment, these all being short and slender. Outer apical exopodal seta of swimming legs $1-4$ with outer margin smooth, inner margin lightly setulate.

Armature formula of swimming legs as in Monstrillopsis hastata sp. nov.


FIGURE 8. Monstrillopsis nanus sp. nov., adult male. A) first swimming leg; B) third swimming leg showing intercoxal sclerite; C) fourth swimming leg. Scale bars: A-C= $100 \mu \mathrm{~m}$.

Fifth legs absent. Urosome consisting of four somites: fifth pedigerous somite, genital somite with genital apparatus, one free postgenital somite, and large anal somite possibly incorporating fused preanal somite as described above in Mon. hastata. Anal somite comprising $35 \%$ of length of urosome. Dorsal surface of genital somite with row of hyaline papillae along distal margin. Ventral surface of genital somite forming enlarged base of short, cylindrical shaft with distal genital lappets. Genital complex of type II. Lappets represented by pair of short, posteriorly directed but moderately divergent bulbous processes (Fig. $6 \mathrm{C}, \mathrm{D}$ ); lappets reaching to about midlength of anal somite. Caudal rami subrectangular, weakly divergent, approximately 1.8 times longer than wide, each ramus bearing five setae.

Female: unknown.
Type locality. Giralia Bay in Exmouth Gulf, Western Australia ( $22^{\circ} 28^{\prime} \mathrm{S}$; $114^{\circ} 20.75^{\prime} \mathrm{E}$ ).
Etymology. The specific epithet, a noun in apposition, is from the Latin noun nanus, meaning dwarf, to emphasize the size of this species, the smallest among its known congeners. The noun is used in masculine gender to match that of the specimen examined.

Diagnosis. Remarkably small species, total body length 0.50 mm . Terminal sabre-like process of fifth antennule relatively short, representing $50 \%$ of segment length. Genital complex of type II, with short shaft and globose terminal lappets. Anteriormost section of prosome, between antennules, with distinctive nubbly surface. Oral papilla situated at $35 \%$ of length of cephalothorax. Caudal rami with five caudal setae.

Remarks. With a total body length of 0.50 mm , Mon. nanus sp. nov. is the smallest Monstrillopsis known, followed by Mon. cahuitae from Central America (Suárez-Morales et al. 2013) that measures 0.55 mm . Among the

Monstrilloida, only Monstrilla pygmaea Suárez-Morales, 2000 ( 0.43 mm ) and Mon. minuta Isaac, 1975 ( 0.49 mm ) are smaller. In addition, the proximal rounded process of the fifth antennular somite is clearly weaker than in the other three Australian congeners and the terminal sabre-like process is relatively shorter than in the other Australian species ( $50 \%$ vs. $58-64 \%$ of fifth segment length). The genital apparatus of Mon. nanus, with a short shaft and globose terminal lappets, also differs from that found in its Australian congeners. This combination of characters has not been found in any other species of Monstrillopsis.

## Genus Australomonstrillopsis Suárez-Morales \& McKinnon gen. nov.

Diagnosis for males. Cephalothorax with paired perioral sac-like protrusions on ventral surface and folds on dorsal surface. Antennules geniculate, five-segmented; terminal antennular segment bearing two inner rounded expansions; apical element 2 modified into short, curved sabre-like structure, element 1 subequally long. Cephalothorax with anteroventral perioral sac-like protuberances and dorsal cuticular folds. Legs $1-4$ with usual segmentation and armature of monstrilloids except for absence of inner seta on first exopodal segment. Fifth legs absent. Urosome 5 -segmented. Genital complex poorly developed, with extremely short shaft and minute, rounded lappets. Postgenital somite with ventral rounded process. Caudal rami with 5 setae, rami symmetrical but strongly modified, massively developed, with several protuberances armed with one or two setae each. Females unknown.

Etymology. Combined name referring to Australia, the country from which it was first collected and Monstrillopsis, the genus to which it has the closest morphological affinity.

Type species. Australomonstrillopsis crassicaudata sp. nov.
Remarks. The new genus is erected to accommodate a male specimen with a remarkable combination of important genus level characters not present in any other genus of the Monstrilloida. It has a 5 -segmented geniculate antennule that resembles that of Monstrillopsis in its general structure and armature, particularly in the presence of an inner protuberance of the last segment and the structure of the apical elements. Setal element 2 (sensu Huys et al. 2007) forms a distinctive sabre-like structure in males of Monstrillopsis (Huys \& Boxshall 1991; Suárez-Morales et al. 2006) and element 1 is relatively short, as in Mon. fosshageni, Mon. chathamensis, and Mon. cahuitae (Suárez-Morales \& Dias 2001; Suárez-Morales \& Morales-Ramírez 2009; Suárez-Morales et al. 2013). In the new genus element 2 is short, curved and only slightly longer than element 1 . This character is not present in males of Monstrillopsis. Another unique character present in the new genus is the peculiar cuticular processes of the cephalothorax, forming sac-like protuberances on the anteroventral surface but also dorsal folds. An important apomorphy found in this genus is the absence of an inner seta on the first segment of the exopods of legs 1-4. The absence of such a seta is shared only with Maemonstrilla (Grygier \& Ohtsuka 2008).

As in males of Monstrillopsis and Cymbasoma, but also in species of Monstrilla, the fifth legs are absent, but the extremely reduced genital complex diverges not only from those found in Monstrillopsis but from all other known monstrilloids for which males have been described (Suárez-Morales \& Dias 2001; Suárez-Morales et al. 2006; Suárez-Morales \& Morales-Ramírez 2009; Suárez-Morales et al. 2013). This genital complex has some resemblance with that depicted for Monstrilla cf. helgolandica Scott, 1909 (Huys \& Boxshall 1991). The presence of a ventral process on the first post-genital somite is also a unique character; the ventral surface of all postgenital somites is always smooth. This kind of structure has not been described in any other monstrilloid; its function and/ or homology are intriguing. The urosome segmentation is similar to that found among males of Monstrillopsis, but the remarkably odd structure of the caudal rami with a massive size and bearing armed lobes is probably the most striking character of this genus; it strongly diverges from the usual pattern found among the Monstrilloida. The number of caudal setae, which is 5 in the new genus, falls within the range known in males of Monstrillopsis (4-6). The new genus is monotypic.

## Australomonstrillopsis crassicaudata sp. nov.

(Figs 9-10)
Material examined. Adult male from Davies Reef, Queensland, Australia ( $19^{\circ} 7.34^{\prime} \mathrm{S} ; 146^{\circ} 53.024^{\prime} \mathrm{E}$ ), undissected, ethanol-preserved, slide-mounted in glycerine, sealed with Entellan®. Date of collection: 5 October, 1985. Slide deposited in MTQ, Australia (cat. MTQW34270).


FIGURE 9. Australomonstrillopsis crassicaudata gen. et sp. nov., adult male A) left antennule, dorsal view; B) habitus showing bulging perioral processes (arrows), ventral view; C) urosome and caudal rami showing suture-like constrictions (arrows), ventral view; D) cephalic area showing oral papilla (arrow) and adjacent protuberances. Scale bars: A, C, D = $50 \mu \mathrm{~m}$, $B=100 \mu \mathrm{~m}$.


FIGURE 10. Australomonstrillopsis crassicaudata gen. et sp. nov., adult male. A) first swimming leg; B) fourth swimming leg; C) outer basipodal seta of third swimming leg; D) urosome and modified caudal rami, dorsal view; E) same with caudal setae cut short, lateral view; F) habitus, lateral view (swimming setae omitted). Scale bars: A-E=50 $\mu \mathrm{m}, \mathrm{F}=100 \mu \mathrm{~m}$.

Description. Male: Total body length of adult holotype 0.54 mm . Cephalothorax 0.25 mm long, representing $47 \%$ of total body length. Antennule 0.22 mm long, representing $81 \%$ of cephalothorax length (Fig. 9B, 10F). Oral papilla small, located anteriorly, about $25 \%$ of way back along ventral surface of cephalothorax (arrowed in Fig. 9B). Pair of ocelli present, pigment cups moderately developed, separated by half eye diameter, weakly pigmented; ventral cup about as large as lateral cups. Forehead rounded. Ventral surface of perioral area with three sac-like protrusions (Fig. 9B, D), one between usual nipple-like processes and surrounded by field of transverse cuticular striae, additional pair of larger processes flanking oral papilla (arrowed in Figs 9B, 10F). Cephalothorax with irregular pattern of coarse cuticular folds and protuberances visible in lateral and ventral views (Figs 9B, 10F).

Antennules five-segmented, geniculate (Fig. 9A). In terms of pattern described by Grygier and Ohtsuka (1995), element 1 present on first segment, biserially setulate; elements $2 \mathrm{~d}_{1}, 2 \mathrm{~d}_{2}, 2 \mathrm{v}_{1}, 2 \mathrm{v}_{2}, 2 \mathrm{v}_{3}$, and IId present on second segment. Third segment with elements 3, IIId, and IIIv; element 3 remarkably long, reaching to midlength of fourth segment. Segment four bearing elements $4 d_{1}$ and $4 v_{1-3}$ as well as IVv and IVd. In terms of Huys et al.'s (2007) nomenclature, terminal segment with reduced armature, only elements 1,2 , and 5 and unbranched elements A-D being present on both antennules. Terminal antennular segment with low inner rounded expansion and secondary rounded protuberance on proximal half, and distal half modified as short, distally curved, sabre-like structure (Fig. 10A).

First pedigerous somite incorporated into cephalothorax; this and succeeding three free pedigerous somites each bearing pair of biramous swimming legs. Pedigerous somites $2-4$ together accounting for $27 \%$ of total body length in dorsal view. Intercoxal sclerites of legs 1-4 sub-quadrate (legs 1 and 2) to sub-rectangular (legs 3 and 4), without ornamentation on surface or along distal margin. Basis of legs articulating with rectangular coxa along diagonal line. Basis with thin, naked lateral seta on legs 1,2 , and 4 ; on leg 3 , this seta thicker, lightly setulate from base, and 3.5-4 times longer than in other legs, reaching well beyond distal margin of exopodal ramus (Fig. 10C). Endopodites and exopodites of swimming legs 1-4 triarticulate (Fig. 10A, B). Ramus setae all lightly and biserially plumose except for spiniform outer seta on exopodal segments 1 and 3 and inner seta of first exopodal segment, these all being short and slender. Outer apical exopodal seta of swimming legs $1-4$ with outer margin smooth, inner margin lightly spinulose. There is no inner seta on first exopodal segment of legs 1-4 (Fig. 10A, B).

Armature formula of swimming legs:

|  | basis | endopodite | exopodite |
| :--- | :--- | :--- | :--- |
| leg 1 | $1-0$ | $0-1 ; 0-1 ; 1,2,2$ | $\mathrm{I}-0 ; 0-1 ; \mathrm{I}, 2,2$ |
| legs $2-4$ | $1-0$ | $0-1 ; 0-1 ; 1,2,2$ | $\mathrm{I}-0 ; 0-1 ; \mathrm{I}, 1,2,2$ |

Fifth legs absent. Urosome consisting of five somites: fifth pedigerous somite, genital somite with genital apparatus, two free postgenital somites, and anal somite, longer than second free postgenital somite. Ventral surface of genital somite forming protuberant base of very short shaft with distal genital lappets. Lappets represented by pair of rounded, poorly developed, posteriorly directed processes separated by shallow medial notch (Fig. 9C). Postgenital somite bearing ventral rounded process (arrowed in Fig. 10E). Caudal rami each with five setae, but rami of remarkably unusual form: massively developed, almost as long as anal and preanal somites combined, with transverse suture resembling intersegmental division (Fig. 10D). Each ramus with several processes, each being armed distally with one seta. Innermost process longest, cylindrical, with outer basal secondary process, each process armed with single terminal seta. Other processes including medial one armed with single seta and outer one, with two setae (Fig. 9C).

Female: unknown.
Type locality. Davies Reef, Queensland, Australia ( $19^{\circ} 7.34{ }^{\prime}$ S; $146^{\circ} 53.024^{\prime} \mathrm{E}$ ).
Etymology. The specific epithet, an adjective, is a combination of two Latin terms, crassus meaning bulky, and cauda meaning tail or posterior appendage. It refers to the unusual development and size of the caudal rami.

Remarks. This male specimen is similar to those of the genus Monstrillopsis in the possession of a modified fifth antennular segment with inner rounded protuberances and an attenuated distal half resembling a short, curved, sabre. Also, the oral papilla is far anterior on the cephalothorax (Sars 1921; Suárez-Morales et al. 2006). As described and discussed in the genus comparisons, this species has a combination of characters not found in any other known monstrilloid, such as the reduced genital complex, the sac-like protuberances in the perioral area of the cephalothorax, the absence of an inner seta on the first exopodal segment of legs $1-4$, the presence of a process
on the ventral surface of the postgenital somite, and the remarkable, highly modified structure of the caudal rami, with a development and size which are unique among all known monstrilloids. The female of this species is unknown but it is expected that it could be easily recognizable by the presence of these unique characters, particularly the modified caudal rami and the lack of an inner seta on the first exopodal segment of legs 1-4.

## Genus Maemonstrilla Grygier and Ohtsuka, 2008

## Maemonstrilla ohtsukai sp. nov.

(Figs 11-13)

Material examined. Adult female holotype from Western Port Bay, Victoria, ( $38^{\circ} 35.344$ 'S; $144^{\circ} 59.687^{\prime} \mathrm{E}$; Station G of Kimmerer \& McKinnon 1985) slides mounted in glycerine, sealed with Entellan®, undissected, collected 5 January 1984 (cat. MTQW34271). Additional locality: Hamelin Pool Channel, Shark Bay, Western Australia ( $25^{\circ} 37.973^{\prime}$ 'S; $113^{\circ} 43.846^{\prime}$ E; Kimmerer et al., 1985). Date of collection: 16 June 1983. Note: Figures are based on a paratype specimen from Hamelin Pool Channel, that is now lost.

Description. Female: Mean total body length of specimens in type series 0.62 mm , range $0.49-0.82 \mathrm{~mm}(\mathrm{n}=4)$, holotype 0.62 mm . Cephalothorax representing up to $64 \%$ of total body length (Fig. 11A, C), robust, not bulbous, $0.35-0.52 \mathrm{~mm}$ long $(\mathrm{n}=4)$, holotype 0.39 mm . Cephalothorax with reticulate pattern of low ridges on dorsal and ventral surfaces, reticulation reaching pedigerous somites $2-4$ and observed also on antennular segments. High reticular ridges only on "forehead" region (Fig. $11 \mathrm{~B}, \mathrm{D}$ ). Antennules relatively long, $0.12-0.18 \mathrm{~mm}$ (holotype 0.16 mm ), representing $42 \%$ of cephalothorax length (Fig. 11A, C). Oral papilla relatively small, located anteriorly, about $20 \%$ of way back along ventral surface of cephalothorax (Fig. 11C). Pair of relatively large ocelli present, pigment cups weakly developed, separated by less than half eye diameter, unpigmented; ventral cup slightly larger than lateral cups. Three pairs of nipple-like cuticular processes on anterior ventral surface between antennule bases and oral papilla (arrowed in Fig. 11 B, C).

Antennule four-segmented, with weak division between segments 3 and 4 (Fig. 13F). In terms of pattern described by Grygier and Ohtsuka (1995), element 1 present on first segment, biserially setulate; elements $2 \mathrm{~d}_{1}, 2 \mathrm{~d}_{2}$, $2 \mathrm{v}_{1}, 2 \mathrm{v}_{2}, 2 \mathrm{v}_{3}$, and IId present on second segment, element IIv broken off, socket observable. Third segment with elements 3, IIId, and IIIv. Segment four bearing elements $4 \mathrm{~d}_{1,2}$ and $4 \mathrm{v}_{1-3}$ as well as IVd, IVv, Vd, Vm, and 5 . Elements of groups 2 v and 3 longer than those of groups 4 d and 4 v . Outer distal $\mathrm{b}_{1-3}$ and also $\mathrm{b}_{4-5}$ setae unbranched. Apically, only element $\sigma_{2}$ together with aesthetasc 6 aes present, element $6_{1}$ absent in all specimens examined.

First pedigerous somite incorporated into cephalothorax; this and succeeding three free pedigerous somites each bearing pair of biramous swimming legs. Pedigerous somites $2-4$ together accounting for $38 \%$ of total body length in dorsal view. Dorsal surface of fourth pedigerous somite with row of four short pit setae (sensu Grygier \& Ohtsuka, 2008) near posterior margin. Intercoxal sclerites of legs 1-4 sub-rectangular, without ornamentation on surface or along distal margin. Basis of legs articulating with rectangular coxa along diagonal line. Basis with thin, naked lateral seta on legs 1,2 , and 4 ; on leg 3 , this seta thicker, biserially setulate, and 3.5 times longer than on other legs, reaching well beyond distal margin of exopodal ramus (Fig. 13C). Endopodites and exopodites of swimming legs $1-4$ triarticulate (Fig. 13A-D). Ramus setae all lightly and biserially plumose except for spiniform outer setae on exopodal segments 1 and 3, that on third exopodal segment with both margins smooth. Outer margin of third exopodal segment of legs $1-4$ with patch of minute spinules (arrowed in Fig. 13B-D). Outer apical exopodal seta of swimming legs $1-4$ with outer margin spinulose, inner margin lightly setulate (Fig. 13E). No inner seta on first exopodal segment of legs $1-4$.

Armature formula of swimming legs:

|  | basis | endopodite | exopodite |
| :--- | :--- | :--- | :--- |
| leg 1 | $1-0$ | $0-0 ; 0-1 ; 1,2,2$ | $\mathrm{I}-0 ; 0-1 ; \mathrm{I}, 2,2$ |
| legs $2-4$ | $1-0$ | $0-0 ; 0-1 ; 1,2,2$ | $\mathrm{I}-0 ; 0-1 ; \mathrm{I}, 1,2,2$ |



FIGURE 11. Maemonstrilla ohtsukai sp. nov., adult female. A) habitus, dorsal view; B) cephalic area of holotype showing cuticular reticulation, ventral view; C) habitus, lateral view; D) cephalic area of paratype specimen, ventral view. Scale bars: A, $\mathrm{C}=100 \mu \mathrm{~m}, \mathrm{~B}, \mathrm{D}=50 \mu \mathrm{~m}$.


FIGURE 12. Maemonstrilla ohtsukai sp. nov., adult female. A) urosome showing fifth legs, ovigerous spines, and weak posteroventral protuberance of genital compound somite (arrow), lateral view; B) urosome, ventral view; C) urosome showing ovigerous spines and position of genital pore (arrow), ventral view; D) same, another specimen, showing caudal rami with arrowed seta VII and fifth legs. Scale bars: A-D $=50 \mu \mathrm{~m}$.


FIGURE 13. Maemonstrilla ohtsukai sp. nov., adult female. A) first swimming leg with coxal sclerite; B) second swimming leg with coxal sclerite; C) third swimming leg with coxal sclerite; D) fourth swimming leg; E) ornamentation of outer apical spiniform seta of third exopodal segment of second leg; F) right antennule, dorsal view. Scale bars: A, C-E $=100 \mu \mathrm{~m}, \mathrm{~B}=25$ $\mu \mathrm{m}$.

Fifth legs paired, rod-like, with two setae, one distal, one subdistal (Fig. 12D); legs reaching to posterior margin of preanal somite. Urosome consisting of four somites: fifth pedigerous somite, compound genital somite with transverse suture at midlength, and two free postgenital somites, i.e. the preanal and anal somites (Fig. $12 \mathrm{~A}-$ D). Ventral surface of genital somite bearing ovigerous spines arising from low conical projection of anterior half of compound somite. Posterior half of genital compound somite with weakly developed ventral protuberance (arrowed in Fig. 12A). Copulatory opening located on ventral surface at posterior base of ovigerous spine cone (arrowed in Fig. 12C). Tips of ovigerous spines reaching to between legs 2 and posterior margin of cephalothorax. Spines cylindrical, smooth, and straight in proximal two-thirds; distal one-third either with moderately swollen bulbous process or tapering and curving distally (Fig. 12A, C, D). Caudal rami subrectangular, weakly divergent, approximately 1.8 times longer than wide, each ramus bearing six setae. Inner dorsal seta thinnest (seta VII of Huys \& Boxshall 1991; arrowed in Fig. 12D).

Etymology. This species is dedicated to Dr. Susumu Ohtsuka, Hiroshima University, Japan, for his remarkable contributions to the knowledge of the taxonomy and ecology of the marine Copepoda, including the description of the genus Maemonstrilla.

Diagnosis. Small species, of less than 1 mm in total body length. Cuticular ridges present on cephalothorax, antennules, and pedigerous somites. Reticulation absent from urosomites and caudal rami. Oral papilla small, with no particular features. Pigmented spots absent from body. Inner seta absent on first exopodal segment of legs 1-4; outer margin of coxa of legs $1-4$ smooth. Posteroventral protrusion of genital compound somite weakly developed. Fifth leg uniramous, rod-like, armed with two distal setae.

Remarks. This species is assignable to the Maemonstrilla hyottoko species group as defined by Grygier and Ohtsuka (2008) mainly by its having a reticulate pattern of cuticular ridges on the cephalothorax, antennules, and pedigerous somites, no inner seta on the first exopodal segment of legs $1-4$, and unbranched, rod-like fifth legs with two distal or subdistal setae.

By reference to Grygier and Ohtsuka's (2008) key to the species of this species-group, this species is distinguished by its possession of a unique combination of features: 1) cuticular reticulation present on the cephalothorax, antennules, and pedigerous somites, but absent from the urosomites and caudal rami; 2) a small, ventrally directed oral papilla, not particularly long as in Mae. spinicoxa Grygier \& Ohtsuka, 2008 or Mae. polka Grygier \& Ohtsuka, 2008, nor flanked with "puffed cheeks" as found in Mae. okame Grygier \& Ohtsuka, 2008, or bent as in some specimens of Mae. polka; 3) lacking pigmented spots throughout the body, thus being distinguished from Mae. polka (cf. Grygier \& Ohtsuka 2008); 4) a weakly developed posteroventral protrusion of the genital compound somite, not spur-like or well-developed as in other Maemonstrilla of this group (Grygier \& Ohtsuka 2008); 5) a smooth outer margin of the coxa in legs $1-4$, thus contrasting with the distinct coxal ornamentation patterns described for Mae. hyottoko, Mae. polka, and Mae. spinicoxa (Grygier \& Ohtsuka 2008); and 6) a body length of less than $1 \mathrm{~mm}(0.49-0.82 \mathrm{~mm})$, thus differing from Mae. hyottoko (1.15-1.60 mm), Mae. polka (2.562.66 mm ), Mae. spinicoxa (1.48-1.70 mm), Mae. okame (1.20-1.67), Mae. simplex (1.80-1.98 mm), and Mae. turgida (A. Scott, 1909) (1.38-2.21 mm) (Grygier \& Ohtsuka 2008).

## Maemonstrilla hoi sp. nov.

(Figs 14-17)
Material examined. Adult female holotype from Port Phillip Bay, Victoria, Australia ( $38^{\circ} 16.085^{\prime}$ 'S; $144^{\circ} 40.0815^{\prime} \mathrm{E}$; Kimmerer \& McKinnon 1985), partially dissected, ethanol-preserved, three slides mounted in glycerine, sealed with Entellan $\circledR$, cephalothorax damaged in mounting medium. Date of collection: 15 October 1984. Slides deposited in collection of MTQ, Australia (cat. MTQW34272).

Description. Female: Total body length of holotype 1.3 mm . Body robust. Cephalothorax short, robust, representing up to $56 \%$ of total body length (Figs. 14A, 17A, B), reticulate on dorsal and ventral surfaces. Reticulation not reaching pedigerous somites 2-4 but present on antennular segments (Fig. 15B). High reticular ridges only on second and proximal part of third antennular segments, appearing as marginal keel-like structures (arrowed in Fig. 15B). Antennule short, robust, 0.19 mm long, representing $18 \%$ of cephalothorax length (Fig. 14A). Oral papilla conical, nearly straight, protruding ventrally, located anteriorly, about $19 \%$ of way back along ventral surface of cephalothorax (Fig. 14B). Pair of relatively large ocelli present, pigment cups separated by less


FIGURE 14. Maemonstrilla hoi sp. nov., adult female. A) habitus, dorsal view; B) cephalic area of holotype showing cuticular reticulation and oral papilla, lateral view; C) urosome showing fifth leg and tongue-like posteroventral process of genital compound somite (arrow), lateral view; D) detail of insertion of distal setae of fifth leg. Scale bars: $A=500 \mu \mathrm{~m}, \mathrm{~B}, \mathrm{C}=100 \mu \mathrm{~m}$, $\mathrm{D}=50 \mu \mathrm{~m}$.


FIGURE 15. Maemonstrilla hoi sp. nov., adult female. A) urosome showing fifth legs, ovigerous spines, posteroventral protuberance of genital compound somite, genital pore (arrow), and caudal seta VII (arrow), ventral view; B) left antennule, dorsal view. Scale bars: A, B $=100 \mu \mathrm{~m}$.


FIGURE 16. Maemonstrilla hoi sp. nov., adult female. A) first swimming leg; B) second swimming leg; C) third swimming leg with coxal sclerite; D) fourth swimming leg; E) ornamentation of outermost spine of third exopodal segment of second leg. Scale bars: A-D $=100 \mu \mathrm{~m}, \mathrm{E}=25 \mu \mathrm{~m}$.


FIGURE 17. Maemonstrilla hoi sp. nov., adult female. Microphotograph. A) lateral view of holotype specimen showing egg mass; B) dorsal view of same specimen. Scale bars: A, B $=500 \mu \mathrm{~m}$.
than half eye diameter, unpigmented; ventral cup slightly smaller than lateral cups. Forehead with wide medial rounded protrusion. Three pairs of nipple-like cuticular processes on anterior ventral surface posterior to antennule bases, with adjacent pattern of transverse cuticular striae on preoral surface (Fig. 14B).

Antennule four-segmented, with weak division between segments 3 and 4, third segment represented by inner lobe partially fused with succeeding fourth segment (Fig. 15B). Antennules unusually inserted $15 \%$ of way back along cephalothorax, at same level as ocelli. In terms of pattern described by Grygier and Ohtsuka (1995), element 1 present on first segment, relatively long and slender, reaching to beyond midlength of second antennular segment. Elements $2 \mathrm{~d}_{1-2}, 2 \mathrm{v}_{1-3}$, and IId present on second segment; among 2 v and 2 d groups, elements 2 v 1 and 2 v 3 longest, elements $2 \mathrm{~d}_{1-2}$ and $2 \mathrm{v}_{2-3}$ clustered at distal margin of segment. Third segment with elements 3 , IIId, and IIIv; element 3 long and slender, reaching to midlength of fourth segment. Segment four bearing elements $4 \mathrm{~d}_{1,2}$ and $4 \mathrm{v}_{1-3}$ as well as IVd, $\mathrm{IVv}, \mathrm{Vd}, \mathrm{Vv}, \mathrm{Vm}$, and 5 . Elements of groups 2 v and 3 longer than those of groups 4 v and 4 d . Outer distal $b_{1-3}$ branched, but seta $b_{4}$ unbranched. Apically, only element $6_{2}$ present on antennules, element $6_{1}$ possibly broken off, sockets observed on both antennules.

First pedigerous somite incorporated into cephalothorax; this and succeeding three free pedigerous somites each bearing pair of biramous swimming legs. Pedigerous somites $2-4$ together accounting for $30 \%$ of total body length in dorsal view, third somite being the largest, alone representing $38 \%$ of their combined length. Intercoxal sclerites of legs 1-4 low and wide with dorsally produced corners, surface of sclerites naked. Coxae with smooth outer margins. Basis of legs articulating with rectangular coxa along diagonal line. Basis with thin, naked lateral seta on legs 1,2 , and 4 ; on leg 3, this seta thicker, biserially setulate, about 6 times longer than that on leg 1 and 3 times longer than those on legs 2 and 4, reaching well beyond distal margin of exopodal ramus (Fig. 16C). Endopodites and exopodites of swimming legs 1-4 triarticulate (Fig. 16A-D). Ramus setae all lightly and biserially plumose except for spiniform outer setae on exopodal segments 1 and 3, latter seta with outer margin smooth, inner margin spinulose (Fig. 16E). Outer apical exopodal seta of swimming legs $1-4$ with outer margin spinulose, inner margin naked (Fig. 13E). No inner seta on first exopodal segment of legs $1-4$; seta represented by cuticular notch or socket-like structure.

Armature formula of swimming legs as in Maemonstrilla ohtsukai sp. nov.
Fifth legs paired, rod-like, with two lightly setulate setae, one distal, one subdistal (Figs. 14D, 15A). Fifth legs longer than in Mae. ohtsukai, reaching posterior margin of anal somite (Figs. 14C, 15A). Urosome consisting of four somites: fifth pedigerous somite, compound genital somite with incomplete transverse suture, and two free postgenital somites, i.e. the preanal and anal somites (Fig. 15A). Ventral surface of genital somite bearing ovigerous spines arising from low, conical projection of anterior half. Posterior half of genital compound somite with tongue-like ventral protuberance (arrowed in Fig. 14C). Copulatory opening on ventral surface at posterior base of ovigerous spine cone (arrowed in Fig. 15A). Tips of ovigerous spines reaching to between legs 2 and posterior margin of cephalothorax. Spines cylindrical, smooth, and straight in proximal three-fourths; distal one-
fourth moderately swollen and tapering distally (Fig. 15A). Specimen with large mass of eggs on ventral surface (Fig. 17A, B). Caudal rami subrectangular, weakly divergent, approximately 1.6 times longer than wide, each ramus bearing six setae. Inner dorsal seta thinnest (seta VII of Huys and Boxshall 1991; arrowed in Fig. 15A).

Male: unknown.
Etymology. The species is named after Dr. Ju-shey Ho, California State University, Long Beach, for his abundant and valuable contributions to the knowledge of the symbiotic Copepoda.

Diagnosis. Cuticular ridges limited to cephalothorax and antennules, with high ridges along outer margins of antennular segments 2 and 3 . Antennule relatively short, representing about $18 \%$ of cephalothorax length. Oral papilla conical, straight, not particularly long. Pigmented spots absent from body. Inner seta absent from first exopodal segment of legs $1-4$; outer margin of coxa smooth. Posteroventral protrusion of genital compound somite developed into short, tongue-like process. Fifth leg uniramous, rod-like, relatively long, reaching posterior margin of anal somite, armed with two distal setae.

Remarks. For the same reasons as Mae. ohtsukai sp. nov., this new species is assignable to the Maemonstrilla hyottoko species group (Grygier \& Ohtsuka 2008). It displays cuticular reticulation only on the cephalothorax and antennules, in contrast to the extensive reticulation on the cephalothorax, lateral sides of the trunk, dorsum of the urosomites, and caudal rami shown by most other members of this species group (Grygier \& Ohtsuka 2008). A similar, reduced reticulation is present in Mae. simplex, in which only the cephalothorax is reticulate. In addition, Mae. simplex shares some other features with Mae. hoi sp. nov., including a conical, ventrally projecting oral papilla, long fifth legs, and general body shape and proportions; nonetheless, there are important differences between these two species. In Mae. hoi, the ventral protuberance of the genital compound somite is moderately developed, forming a small, tongue-like process, whereas this structure is very large and conspicuous in Mae. simplex (Grygier \& Ohtsuka 2008, fig. 22E). In Mae. hoi, the antennule is very short, about $18 \%$ of the cephalothorax length, but it is clearly longer ( $47 \%$ of the cephalothorax length) in Mae. simplex. The high cuticular ridges present along the outer margins of antennular segments 2-3 in Mae. hoi are absent in Mae. simplex, in which these margins are smooth. Some additional details of the antennule structure and armature are useful to separate these two species. Element 1 is longer in Mae. hoi, reaching to about midlength of the second segment, whereas it is quite short in Mae. simplex, barely reaching beyond the distal margin of the first segment (Grygier \& Ohtsuka 2008, fig. 18C). The distal part consisting of segments 3 and 4 is noticeably elongated in Mae simplex, representing $62 \%$ of the total length of the antennule, whereas the same two segments represent only $43 \%$ of the antennule length in Mae. hoi. The third segment is clearly aligned with the longitudinal axis of the antennule in Mae. simplex (see Grygier \& Ohtsuka 2008, fig. 18C), but in Mae. hoi, this segment appears reduced, forming a well-defined lobe protruding along the inner margin of the antennule (Fig. 15B). Finally, in M. simplex, antennular elements $2 \mathrm{~d}_{1-2}$ are distinctively smaller than elements $2 \mathrm{v}_{1-3}$ (Grygier \& Ohtsuka 2008, fig. 18C) whereas in Mae. hoi, all elements of both groups are represented by subequally long, slender setae (Fig. 15B).

## Maemonstrilla protuberans sp. nov.

(Figs 18-20)
Material examined. Adult female holotype from Davies Reef, Queensland, Australia ( $19^{\circ} 7.34^{\prime} \mathrm{S} ; 146^{\circ} 53.024^{\prime} \mathrm{E}$ ), partially dissected, ethanol-preserved, slide mounted in glycerine, sealed with Entellan®. Date of collection: 5 October, 1985. Slide deposited in collection of MTQ, Australia (cat. MTQW34273).

Description. Female: Total body length of holotype 0.57 mm . Cephalothorax robust in dorsal view, representing up to $58 \%$ of total body length (Fig. 18A, B). Cephalothorax covered with pattern of minute spinules mixed with light reticulation. Reticulation observed only on anterior dorsal and ventral surfaces of cephalothorax and on some antennular segments (Figs. 18A, B, 19C). Antennule relatively long, 0.22 mm , representing $35 \%$ of total body length and $61 \%$ of cephalothorax length (Fig. 18A). Oral papilla conical, ventrally projecting, relatively large, located anteriorly, about $20 \%$ of way back along ventral surface of cephalothorax (Fig. 18C). Pair of relatively large ocelli present, pigment cups weakly developed, separated by about half eye diameter, unpigmented; ventral cup slightly smaller than lateral cups. Forehead rounded, protruding medially. Preoral surface with ventral rounded protuberance (arrowed in Fig. 18C) and two pairs of nipple-like cuticular processes with adjacent pattern of striae (Fig. 18C, D).

Antennule four-segmented, with weak divisions between segments 2-3 and 3-4 only marked by constrictions (Fig. 19C). High reticular ridges on outer margin of segments 3 and 4 (arrowed in Fig. 19C). Element 1 present on first segment, reaching to proximal one-third of second antennular segment. Elements $2 \mathrm{~d}_{1}, 2 \mathrm{~d}_{2}, 2 \mathrm{v}_{1}, 2 \mathrm{v}_{2}, 2 \mathrm{v}_{3}$, and IId present on second segment. Third segment with elements 3, IIId, and IIIv; element 3 strongly developed. Segment four bearing aesthetasc 4 aes and elements $4 d_{1,2}$ and $4 \mathrm{v}_{1,2}$, with $4 \mathrm{v}_{1}$ being remarkably long; elements IVd, IVv, Vd, $\mathrm{Vv}, \mathrm{Vm}$, and 5 also present. Most elements of groups $2 \mathrm{v}, 2 \mathrm{~d}$ and 3 longer than those of group 4 , but element $4 \mathrm{v}_{1}$ only slightly longer than most elements of $2 \mathrm{v}, \mathrm{d}$ groups and shorter than element 3 . Outer distal $\mathrm{b}_{1-3}$ branched, elements $b_{5-6}$ unbranched. Apically, only $6_{2}$ present, but socket of element $6_{1}$ observed on both antennules.


FIGURE 18. Maemonstrilla protuberans sp. nov., adult female. A) habitus showing preoral protuberance (arrow), lateral view; B) habitus, ventral view; C) cephalic area showing cuticular reticulation, preoral ventral protuberance (arrow), and oral papilla, lateral view; D) same, ventral view. Scale bars: A, B $=100 \mu \mathrm{~m}, \mathrm{C}, \mathrm{D}=50 \mu \mathrm{~m}$.


FIGURE 19. Maemonstrilla protuberans sp. nov., adult female. A) urosome showing fifth legs, ovigerous spines, genital pore (arrow), and caudal seta VII (arrows), ventral view; B) same, lateral view; C) left antennule showing high reticulation ridges on outer margin (arrows), dorsal view. Scale bars: A-C $=50 \mu \mathrm{~m}$.


FIGURE 20. Maemonstrilla protuberans sp. nov., adult female. A) first swimming leg showing intercoxal sclerite; B) second swimming leg showing intercoxal sclerite; C) third swimming leg; D) fourth swimming leg. Coxal sclerites cut short. Scale bars: $\mathrm{A}-\mathrm{D}=100 \mu \mathrm{~m}$.

First pedigerous somite incorporated into cephalothorax; this and succeeding three free pedigerous somites each bearing pair of biramous swimming legs. Pedigerous somites $2-4$ relatively short, together accounting for only $22 \%$ of total body length. Intercoxal sclerites of legs 1-4 low, wide, without ornamentation on surface or along distal margin. Basis of legs articulating with coxa along diagonal line. Basis with thin lateral seta on legs $1-$ 4 ; on leg 3 , this seta thicker, biserially setulate and 4 times longer than in legs 1 and 4, 2.5-3 times longer than in leg 2, reaching distal margin of second segment of exopodite (Fig. 20C). Endopodites and exopodites of swimming legs 1-4 triarticulate (Fig. 20A-D). Ramus setae all lightly and biserially plumose except spiniform outer seta on exopodal segments 1 and 3 and inner seta of first exopodal segment, these all being short and slender. Outer apical exopodal seta of swimming legs 1-4 with outer margin spinulose, inner margin naked (Fig. 20A-D). Inner seta on first exopodal segment of legs 1-4 absent, no remnant being observed.

Armature formula of swimming legs as in Maemonstrilla ohtsukai.
Fifth legs paired, rod-like, with two setae, one distal, one subdistal (Fig. 19A, B). These legs short, not reaching posterior margin of genital compound somite (Fig. 19A). Urosome consisting of four somites: fifth pedigerous somite, compound genital somite with incomplete transverse suture, and two free postgenital somites, i.e. the preanal and anal somites (Fig. 19A, B). Ventral surface of genital double somite bearing ovigerous spines arising from conical projection of ventrally protuberant anterior half. Posterior half of genital compound somite straight, without ventral process. Copulatory opening located on ventral surface at posterior base of ovigerous spine cone (arrowed in Fig. 19A). Ovigerous spines relatively short, reaching to between legs 2 and 3, partially concealed by relatively small egg mass (Fig. 18B). Spines cylindrical, smooth, and straight, tapering and diverging distally, not swollen or bulbous distally (Fig. 19A). Caudal rami subquadrate, weakly divergent, approximately 1.3 times longer than wide, each ramus bearing six setae. Inner dorsal seta (seta VII of Huys \& Boxshall 1991) thinnest (arrowed in Fig. 19A).

Male: unknown.
Etymology. The specific epithet makes reference to the ventral preoral protuberance, a feature not previously described in any species of Maemonstrilla.

Diagnosis. Cuticular reticulation limited in extent, as in Mae. spinicoxa. Antennule relatively long, representing more than $60 \%$ of cephalothorax length. Oral papilla conical, straight, long. Ventral rounded preoral protuberance present. Pigmented spots absent from body. Inner seta on first exopodal segment of legs 1-4 absent; outer margin of coxa of these legs smooth. Posteroventral margin of genital compound somite straight, with no process.

Remarks. Maemonstrilla protuberans is assignable to the Maemonstrilla hyottoko species group as defined by Grygier and Ohtsuka (2008) mainly by its possession of a lightly reticulate cephalothorax and antennules mixed with a dense spinulose pattern, the absence of an inner seta on the first exopodal segment of legs $1-4$, and unbranched, rod-like fifth legs with two setae. The ornamentation pattern observed in this species has some resemblance with that described for Mae. spinicoxa, but it is more complex in Mae. spinicoxa (Grygier \& Ohtsuka 2008, fig. 14A). Both species share a similar shape of the antennules, including the constrictions marking the divisions between segments 2-3 and 3-4 and the high reticulation ridges on the outer margins of segments 3 and 4, but in Mae. spinicoxa the antennule is only $37 \%$ of the cephalothorax length and Mae. protuberans lacks the large denticles on the proximal outer coxal lobes that are distinctive of Mae. spinicoxa. The ventral preoral protuberance of Mae. protuberans has not been reported in any other species of this genus, all of which have a straight or smooth preoral area (Grygier \& Ohtsuka 2008). The length of the antennule, representing more than $60 \%$ of the cephalothorax length, distinguishes this species from all other Maemonstrilla, in which the antennule length ranges between $29 \%$ and $51 \%$ of the cephalothorax length (Grygier \& Ohtsuka 2008). In contrast to the other species of the Maemonstrilla hyottoko group, this new species has a straight, unmodified posteroventral margin of the compound genital somite. This has been considered a defining character of the M. turgida group (Grygier \& Ohtsuka 2008), although the posteroventral protrusion of M. ohtsukai sp. nov. is only weakly developed. Maemonstrilla protuberans has a moderately developed, ventrally directed oral papilla, not long as in Mae. spinicoxa and Mae. polka nor either flanked with "puffed cheeks" as in Mae. okame or bent anteriorly at midlength as in some specimens of Mae. polka. Its body length $(0.57 \mathrm{~mm})$ is similar to that of Mae. ohtsukai $(0.55-0.82 \mathrm{~mm})$, thus distinctly smaller than most of the other known species of the genus, which are all well over 1 mm long (Grygier \& Ohtsuka 2008). These two species are the smallest members of Maemonstrilla currently known.

## Maemonstrilla crenulata sp. nov.

(Figs 21-23)

Material examined. Adult female holotype from Scott Reef, Western Australia ( $14^{\circ} 2.3^{\prime} \mathrm{S}$; $121^{\circ} 53.3^{\prime} \mathrm{E}$; Station CH of McKinnon et al. 2013), partially dissected, slide-mounted in glycerine, sealed with Entellan $\circledR$. Date of collection: 30 November 2009. Slide deposited in collection of WAMC, Australia (cat. WAMC55072).

Description. Female: Total body length of holotype 1.75 mm . Cephalothorax elongate, robust, 1.03 mm long, representing up to $60 \%$ of total body length (Fig. 21A), with faint reticulate pattern limited to small areas of ventral and dorsal surfaces of cephalic area (Figs. 21A, 22A). Pair of spine-like scales present on dorsal posterior margin of third pedigerous somite. Antennule relatively short, 0.34 mm , representing $18 \%$ of total body length and $31 \%$ of cephalothorax length (Fig. 21A). Oral papilla well developed, thick, with wide base, located anteriorly, about 19\% of way back along ventral surface of cephalothorax (Fig. 22A). Pair of relatively large ocelli present, pigment cups separated by more than eye diameter, weakly pigmented; ventral cup slightly smaller than lateral cups. Forehead with moderate-sized medial rounded protrusion and two sensilla. Two pairs of nipple-like cuticular processes on anterior ventral surface between antennule bases and oral papilla, this area showing transverse striation pattern (Fig. 22A).

Antennule four-segmented, with weak division between segments 3 and 4 (Fig. 22B). In terms of pattern described by Grygier and Ohtsuka (1995), element 1 present on first segment, biserially setulate; elements $2 \mathrm{~d}_{1}, 2 \mathrm{~d}_{2}$, $2 \mathrm{v}_{1}, 2 \mathrm{v}_{2}, 2 \mathrm{v}_{3}$, and IId present on second segment, element $2 \mathrm{~d}_{2}$ being the longest. Third segment with elements 3 , IIId, and IIIv. Segment four bearing elements $4 d_{1,2}$ and $4 \mathrm{v}_{1-3}$ as well as IVd, IVv, Vd, Vm, and 5. Element $4 \mathrm{v}_{1}$ longest among those of groups 4 v and 4 d . Elements of group 2 v moderately longer than those of groups 4 v and 4 d . Outer distal setae $b_{1-3}$ dichotomously branched, $b_{4,5}$ unbranched. Apically, elements $6_{1,2}$ present together with aesthetasc 6aes.

First pedigerous somite incorporated into cephalothorax; this and succeeding three free pedigerous somites each bearing pair of biramous swimming legs. Pedigerous somites $2-4$ together accounting for $26 \%$ of total body length in dorsal view. Second pedigerous somite largest of somites $2-4$, representing almost $43 \%$ of this somite group. Third pedigerous somite with dorsal pair of spine-like scales in middle of posterior margin. Dorsal surface of fourth pedigerous somite with row of three pit setae near posterior margin (Figs. 21A, 22C). Intercoxal sclerites of legs 1-4 wide, slender, without ornamentation on surface or along distal margin. Basis of legs articulating with rectangular coxa along diagonal line. Coxa of legs $1-4$ with patches of minute spinules plus crenulation-like transverse indentations along outer margin. Basis with thin lateral seta on legs 1,2 , and 4 ; on leg 3 , this seta thicker, biserially setulate and $3-5$ times longer than in other legs, reaching distal margin of exopodal ramus (Fig. 23C). Endopodites and exopodites of swimming legs 1-4 triarticulate (Fig. 23A-C); outer margin of first endopodal segment of legs 2 and 3 with notch (arrowed in Fig. 23B, C). Outer margin of first exopodal segment of legs 2-4 with spiniform processes; similar processes also present on outer margin of third exopodal segment of leg 1 (arrowed in Fig. 23A). Ramus setae all lightly and biserially plumose except for spiniform outer setae on exopodal segments 1 and 3. Outer apical exopodal seta of swimming legs $1-4$ with outer margin spinulose, inner margin naked (Fig. 23A-C).

Armature formula of swimming legs:

|  | basis | endopodite | exopodite |
| :--- | :--- | :--- | :--- |
| leg 1 | $1-0$ | $0-1 ; 0-1 ; 1,2,2$ | $\mathrm{I}-1 ; 0-1 ; \mathrm{I}, 2,2$ |
| legs $2-4$ | $1-0$ | $0-1 ; 0-1 ; 1,2,2$ | $\mathrm{I}-1 ; 0-1 ; \mathrm{I}, 1,2,2$ |

Fifth legs paired, rod-like, distally bilobed, inner lobe with one seta, outer lobe with one distal and two subdistal setae (Fig. 21C). These legs relatively short, reaching to midlength of compound genital somite. Urosome consisting of four somites: fifth pedigerous somite, compound genital somite with incomplete transverse suture on dorsal surface, and two free postgenital somites, i.e. the preanal and anal somites (Fig. 21B). Ventral surface of genital somite bearing ovigerous spines arising from low conical projection of anterior half ; this area also with anteroventral rounded protuberance (arrowed in Fig. 22D). Posterior half of genital compound somite with ventral margin straight, unmodified (Fig. 21B). Copulatory opening located on ventral surface at posterior base of ovigerous spine cone (arrowed in Fig. 21C). Tips of ovigerous spines reaching to between legs 2 and posterior
margin of cephalothorax. Spines cylindrical, straight, rugose in distal one-third and tapering distally (Fig. 21 D). Caudal rami short, quadrate, each bearing five setae.


FIGURE 21. Maemonstrilla crenulata, adult female. A) habitus showing partial faint reticulation of anterior part of cephalothorax, dorsal view; B) urosome showing fifth legs and proximal section of ovigerous spines, lateral view; C) same, ventral view; D) detail of terminal part of ovigerous spines. Scale bars: A $=500 \mu \mathrm{~m}, \mathrm{~B}-\mathrm{D}=100 \mu \mathrm{~m}$.


FIGURE 22. Maemonstrilla crenulata, adult female. A) cephalic area showing oral papilla, faint reticulation and cuticular striation, lateral view; B) left antennule, dorsal view; C) urosome, dorsal view; D) urosome showing anteroventral rounded process of genital compound somite (arrow), fifth legs omitted. Scale bars: A-D $=100 \mu \mathrm{~m}$.


FIGURE 23. Maemonstrilla crenulata, adult female. A) first swimming leg showing ridges on outer margin of third exopodal segment (arrow); B) second swimming leg showing notch on outer margin of first endopodal segment (arrow); C) third swimming leg showing notch on outer margin of first endopodal segment (arrow). Scale bars: A-C $=100 \mu \mathrm{~m}$.


FIGURE 24. The occurrence of the monstrilloid copepod genera Monstrillopsis, Maemonstrilla and Australomonstrillopsis in Australia.

Male: unknown.
Etymology. The specific epithet, an adjective, makes reference to the unique crenulated margin of the coxa of legs 1-4.

Diagnosis. Maemonstrilla with cephalothorax mostly non-reticulated, reticulation limited, faint. Cephalothorax representing $60 \%$ of total body length. Antennule relatively short, representing $31 \%$ of cephalothorax length. Oral papilla thick, with wide base. Inner seta present on first exopodal segment of legs $1-4$. Outer margin of coxa of these legs crenulate. First endopodal segment of legs 2 and 3 with outer notch. Third pedigerous somite with two dorsal spine-like scales on posterior margin. Anteroventral process of compound genital somite rounded, with secondary apical protrusion. Fifth leg biramous, exopodal lobe with three setae, endopodal lobe with one distal seta.

Remarks. Among the Australian species, only Mae. crenulata sp. nov. is assignable to the Maemonstrilla turgida species group as defined by Grygier and Ohtsuka (2008) mainly by the lack of reticulation on most of the cephalothorax, as well as the antennules and pedigerous somites, the presence of a pair of spiniform processes on the dorsal posterior margin of the third pedigerous somite, the presence of an inner seta on the first exopodal segment of legs $1-4$, the bilobed fifth leg with one endopodal and three exopodal setae, and the unmodified posteroventral margin of the genital compound somite. Additional characters shared with Mae. turgida include the body length (within the range of Mae. turgida as described by Grygier and Ohtsuka 2008), widely separated eye cups, the relatively large, ventrally projecting oral papilla, the short, subquadrate caudal rami, and the fifth legs reaching only to about midlength of the compound genital somite.

This is the largest species of Australian Maemonstrilla recorded. The new species has several important
differences from the closely related Mae. turgida: 1) the cephalothorax is relatively shorter in Mae. turgida (49.4$54.8 \%$ of total body length) (Grygier \& Ohtsuka 2008) than in Mae. crenulata sp. nov. (60\%); 2) the antennule length is $41.6-51.3 \%$ that of the cephalothorax in Mae. turgida (Grygier \& Ohtsuka 2008) vs. $31 \%$ in Mae. crenulata; 3) the anteroventral process of the compound genital somite is merely rounded in Mae. turgida (Grygier \& Ohtsuka 2008, fig. 27 H ) but has a secondary apical protrusion in Mae. crenulata; 4) in the new species, the coxae of legs 1-4 have a series of deep indentations and patches of minute spinules along the outer margin, but in Mae. turgida, the indentations are absent and the coxal margins of legs 1-4 have only patches of very small spinules (Grygier \& Ohtsuka 2008, fig. 25F); 5) in the new species, the third exopodal segment of leg 1 and the first exopodal segment of legs $2-4$ bear an outer row of spiniform processes that are absent in Mae. turgida (Grygier \& Ohtsuka 2008, fig. 27); 6) in Mae. crenulata, the first endopodal segment of legs 2 and 3 has an outer notch that is absent in Mae. turgida (Grygier \& Ohtsuka 2008, fig. 27); 7) in the antennule armature of Mae. turgida, the elements of groups 2 v and 2d are equally long (Grygier \& Ohtsuka 2008, fig. 24B), but in Mae. crenulata, element $2 \mathrm{~d}_{2}$ is clearly longer and element $2 \mathrm{~d}_{1}$ is shorter than the other elements in these groups. It is notable that in these species, both belonging to the Mae. turgida group, elements $4 \mathrm{v}_{1,2}$ are longer than those in group 4 d , thus diverging with the pattern observed in the known species of the hyottoko group, in which both groups of elements are equally long; 8) leg 5 is longer and more slender (length/width ratio $=6.0$ ) in the new species than in Mae. turgida (3.0). Also, in the new species the inner lobe does not reach the distal margin of the outer lobe (Fig. 21C), whereas in Mae. turgida the inner lobe is longer than the outer one (Grygier \& Ohtsuka 2008, fig. 27 G ).

## Discussion

In their revision of the genus Monstrillopsis, Suárez-Morales et al. (2006) recognized the following nominal species: Mon. dubia (Scott, 1904) from Scotland ( $60^{\circ} \mathrm{N}$ ), Mon. zernowi from the Black Sea ( $43^{\circ} \mathrm{N}$ ), Mon. sarsi Isaac, 1974 from England ( $54^{\circ} \mathrm{N}$ ), Mon. fosshageni from Brazil ( $20^{\circ}$ S), Mon. dubioides Suárez-Morales, 2004 from Norway $\left(62^{\circ} \mathrm{N}\right)$, Mon. ferrarii Suárez-Morales and Ivanenko from the White Sea in the Arctic Ocean $\left(66^{\circ} \mathrm{N}\right)$, Mon. chilensis from off Chile $\left(33^{\circ} \mathrm{S}\right)$, and Mon. igniterra from the Southern Ocean $\left(55^{\circ} \mathrm{S}\right)$. Subsequently, Suárez-Morales and Morales-Ramírez (2009) added Mon. chathamensis from the Eastern Pacific and Suárez-Morales et al. (2013) described Mon. cahuitae Suárez-Morales \& Carrillo, 2013 from Costa Rica. With the addition of the three new species described herein, the number of species in the genus has increased to 13 species. As mentioned by Suárez-Morales et al. (2006) and also by Grygier and Ohtsuka (2008), there are some species in the genus that are still in doubt, such as the intriguing Mon. zernowi Dolgopol'skaya, 1948 from the Black Sea (Dolgopol'skaya 1948). Our description of four new species from Australia increases the known diversity of this genus in the Southern Hemisphere (from 3 to 6 species) to a level equal to that known in the Northern Hemisphere.

The absence of female Monstrillopsis in this collection is characteristic of the genus. Of the 13 species now contained in Monstrillopsis, 3 are known only from females and 7 from males; in only 3 species are both genders known, though doubts remain in these cases. It is potentially possible to match males to females of monstrilloid species (Suárez-Morales \& Escamilla 1997; Grygier \& Ohtsuka 2008; Suárez-Morales 2011) by using distinctive morphological features shared between the sexes. All the males recorded from Australia have distinctive characters not connected to sexually-related modifications (i.e. the genital complex or the modified fifth antennular segment) that are likely to be expressed in the corresponding females. Hence, aside from the fact that these male specimens represent undescribed, clearly distinguishable species and an advance in the knowledge of the Australian monstrilloid fauna, we expect that their description will ease the task of detecting and matching the respective females from future sampling efforts in the region. The opposite situation is the case for Maemonstrilla, a genus in which all species are known from females; male monstrilloids have been collected in reef areas of Japan but none of these were actually identified as belonging to this genus (Grygier \& Ohtsuka 2008).

When the genus Maemonstrilla was erected by Grygier \& Ohtsuka (2008), they recognized five new species, Mae. hyottoko, Mae. polka, Mae. spinicoxa, Mae. okame, and Mae. simplex and also incorporated two species originally described under the genus Monstrilla, Mae. longipes (A. Scott, 1909) and Mae. turgida. With the addition of the four new species from Australia, Maemonstrilla is now represented by eleven species.

Ecological comments. Species of Monstrillopsis have been recorded from different latitudes including the

Arctic, Sub-Antarctic, temperate, tropical, and subtropical zones (Suárez-Morales \& Ivanenko 2004; SuárezMorales et al. 2006; Suárez-Morales et al. 2008), but the genus seems to be most diverse in temperate and cold latitudes ( 7 of 10 previously known species). Maemonstrilla has only been recorded from the Indo-West Pacific, with species known from Japan, Indonesia, India, Singapore, the South China Sea, the Red Sea, and Australia (Grygier \& Ohtsuka 2008; present data).

The present collections of Monstrillopsis, Maemonstrilla, and Australomonstrillopsis, come from both temperate and tropical regions of Australia (Fig. 24). The habitats sampled span coastal embayments with rich seagrass communities (Western Port Bay, Shark Bay, and Exmouth Gulf), a large temperate bay (Port Phillip Bay), a platform reef within the Great Barrier Reef (Davies Reef), and an isolated Indian Ocean coral reef off the Western Australian shelf (Scott Reef). Details of the collection sites and their plankton communities can be found in the original literature cited in the Material Examined sections, although two species (the possibly endemic Australomonstrillopsis crassicaudata and Maemonstrilla protuberans) were recovered from an ad hoc collection made at Davies Reef in October 1985-details of the plankton community at this location can be found in McKinnon (1991). With the exception of Maemonstrilla ohtsukai, all the new species are described on the basis of single individuals occurring in plankton collections. The two genera co-occurred at four of the six locations. Maemonstrilla ohtsukai occurred both in Western Australia (Exmouth Gulf and Shark Bay) and Victoria (Western Port Bay), indicating that this species is probably widely distributed. Although the paucity of specimens compromises any conclusion regarding the distribution of the other species, the fact that in no case did congeneric species co-occur, contrary to the case in the Ryukyu Islands (Grygier \& Ohtsuka 2008), hints that there may be a rich species diversity yet to be discovered within the Australian Monstrilloida.

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## References

Boxshall, G.A. \& Halsey, S.H. (2004) An Introduction to Copepod Diversity. The Ray Society, London, 966 pp.
Davis, C.C. (1949) A preliminary revision of the Monstrilloida, with descriptions of two new species. Transactions of the American Microscopical Society, 68, 245-255.
Dolgopol'skaya, M.A. (1948) K faune Monstrillidae Chernogo morya. Trudy Zoologicheskogo Instituta Akademii Nauk SSSR, 7, 177-183. [in Russian]
Grygier, M.J. (1995) Annotated chronological bibliography of Monstrilloida (Crustacea: Copepoda). Galaxea, 12, 1-82.
Grygier, M.J. \& Ohtsuka, S. (1995) SEM observation of the nauplius of Monstrilla hamatapex, new species, from Japan and an example of upgraded descriptive standards for monstrilloid copepods. Journal of Crustacean Biology, 15, 703-719. http://dx.doi.org/10.2307/1548820
Grygier, M.J. \& Ohtsuka, S. (2008) A new genus of monstrilloid copepods (Crustacea) with anteriorly pointing ovigerous spines and related adaptations for subthoracic brooding. Zoological Journal of the Linnean Society, 152, 459-506. http://dx.doi.org/10.1111/j.1096-3642.2007.00381.x
Huys, R. \& Boxshall, G.A. (1991) Copepod Evolution. The Ray Society, London, 468 pp.
Huys, R., Llewellyn-Hughes, J., Conroy-Dalton, S., Olson, P.D. Spinks, J.N. \& Johnston, D.A. (2007) Extraordinary host switching in siphonostomatoid copepods and the demise of the Monstrilloida: Integrating molecular data, ontogeny and antennulary morphology. Molecular Phylogenetics and Evolution, 43, 368-378. http://dx.doi.org/10.1016/j.ympev.2007.02.004
Isaac, M.J. (1974) Copepoda Monstrilloida from south-west Britain including six new species. Journal of the Marine Biological Association of the United Kingdom, 54, 127-140. http://dx.doi.org/10.1017/s0025315400022116
Isaac, M.J. (1975) Copepoda, Suborder: Monstrilloida. Fiches d'Identification du Zooplancton, 144/145, 1-10.
Kimmerer, W.J. \& McKinnon, A.D. (1985) A comparison of the zooplankton in two adjacent embayments, Port Phillip and Westernport Bays, Australia. Estuarine, Coastal and Shelf Science, 21, 145-159. http://dx.doi.org/10.1016/0272-7714(85)90094-0
Kimmerer, W.J., McKinnon, A.D., Atkinson, M.J. \& Kessell, J.A. (1985) Spatial distributions of plankton in Shark Bay, Western

Australia. Australian Journal of Marine and Freshwater Research, 36, 421-432.
http://dx.doi.org/10.1071/mf9850421
McKinnon, A.D. (1991) Community composition of reef-associated copepods in the lagoon of Davies Reef, Great Barrier Reef, Australia. Proc. Fourth Int. Conference on Copepoda; Bulletin of the Plankton Society of Japan, Special Volume (1991), 467-478.

McKinnon, A.D. \& Ayukai, T. (1996) Copepod egg production and food resources in Exmouth Gulf, Western Australia. Marine and Freshwater Research, 47, 595-603.
http://dx.doi.org/10.1071/mf9960595
McKinnon, A.D., Duggan, S., Böttger-Schnack, R., Gusmão, L.F.M. \& O'Leary, R.A. (2013) Depth structuring of pelagic copepod biodiversity in waters adjacent to an Eastern Indian Ocean coral reef. Journal of Natural History, 47, 639-665.
http://dx.doi.org/10.1080/00222933.2012.673645
Nicholls, A.G. (1944) Littoral Copepoda from South Australia (II) Calanoida, Cyclopoida, Notodelphyoida, Monstrilloida and Caligoida. Records of the South Australian Museum, 8, 1-62.
Razouls, C. (1981) Répertoire Mondiale Taxinomique et Bibliographique Provisoire des Copépodes Planctoniques Marins et des Eaux Saumâtres. Divers Systèmes de Classification. Laboratoire Arago, Banyuls-sur-Mer, 359 pp.
Razouls, C. (1996) Diversité et répartition géographique chez les Copépodes pélagiques. 2. - Platycopioida, Misophrioida, Mormonilloida, Cyclopoida, Poecilostomatoida, Siphonostomatoida, Harpacticoida, Monstrilloida. Annales de l' Institut Océanographique Nouvelle Série, 72, 5-142.
Razouls, C., de Bovée, F., Kouwenberg, J. \& Desreumaux, N. (2005-2013) Diversity and geographic distribution of marine planktonic copepods (sensu lato) (from 1883 to 2011/2012) Calanoida, Platycopioida, Misophrioida, Mormonilloida, Cyclopoida (gnathostomes and poecilostomes), Siphonostomatoida, Harpacticoida, Monstrilloida. Available from: http:// copepodes.obs-banyuls.fr/en (accessed 18 February 2014)
Sale, P.F., McWilliams, P.S. \& Anderson, D.T. (1976) Composition of the near-reef zooplankton at Heron Reef, Great Barrier Reef. Marine Biology, 34, 59-66.
http://dx.doi.org/10.1007/bf00390788
Sale, P.F., McWilliams, P.S. \& Anderson, D.T. (1978) Faunal relationships among the near-reef zooplankton at three locations on Heron Island, Great Barrier Reef, and seasonal changes in this fauna. Marine Biology, 49, 133-145. http://dx.doi.org/10.1007/bf00387113
Sars, G.O. (1921) An account of the Crustacea of Norway with short descriptions and figures of all the species. Vol. VIII. Copepoda Monstrilloida and Notodelphyoida. The Bergen Museum, Bergen, 91 pp. + XXXVII pls.
Suárez-Morales, E. (2001) An aggregation of monstrilloid copepods in a western Caribbean reef area: ecological and conceptual implications. Crustaceana, 74, 689-696. http://dx.doi.org/10.1163/156854001750377966
Suárez-Morales, E. (2011) Diversity of the Monstrilloida (Crustacea: Copepoda). PLoS ONE, 6 (8), e22915. http://dx.doi.org/10.1371/journal.pone. 0022915
Suárez-Morales, E. \& Dias, C. (2001) Taxonomic report of some monstrilloids (Copepoda: Monstrilloida) from Brazil with description of four new species. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie, 71, 65-81.
Suárez-Morales, E. \& Escamilla, J.B. (1997) An undescribed monstrilloid copepod (Copepoda: Monstrilloida) from the northern Yucatán Peninsula, Mexico. Bulletin of Marine Science, 61, 539-547.
Suárez-Morales, E. \& Ivanenko, V.N. (2004) Two new species of Monstrillopsis Sars (Crustacea: Copepoda: Monstrilloida) from the White Sea and Norway, with comments on M. dubia Scott. Arctic, 57, 37-46.
Suárez-Morales, E. \& Morales-Ramírez, A. (2009) New species of Monstrilloida (Crustacea: Copepoda) from the Eastern Tropical Pacific. Journal of Natural History, 43, 1257-1271. http://dx.doi.org/10.1080/00222930902894419
Suárez-Morales, E., Bello-Smith, A. \& Palma, S. (2006) A revision of the genus Monstrillopsis Sars (Crustacea: Copepoda: Monstrilloida) with description of a new species from Chile. Zoologischer Anzeiger, 245, 95-107.
http://dx.doi.org/10.1016/j.jcz.2006.05.002
Suárez-Morales, E., Carrillo, A. \& Morales-Ramírez, A. (2013) Report on some monstrilloids (Crustacea: Copepoda) from a reef area off the Caribbean coast of Costa Rica, Central America with description of two new species. Journal of Natural History, 47, 619-638. http://dx.doi.org/10.1080/00222933.2012.742933
Suárez-Morales, E., Paiva Scardua, M. \& Da Silva, P.M. (2010) Occurrence and histo-pathological effects of Monstrilla sp. (Copepoda: Monstrilloida) and other parasites in the brown mussel Perna perna from Brazil. Journal of the Marine Biological Association of the United Kingdom, 90, 953-958.
http://dx.doi.org/10.1017/s0025315409991391
Suárez-Morales, E., Ramírez, F.C. \& Derisio, C. (2008) Monstrilloida (Crustacea: Copepoda) from the Beagle Channel, South America. Contributions to Zoology, 77, 217-226.
Suárez-Morales, E., Harris, L.H., Ferrari, F.D. \& Gasca, R. (2014) Late postnaupliar development of Monstrilla sp. (Copepoda: Monstrilloida), a protelean endoparasite of benthic polychaetes. Invertebrate Reproduction and Development, 58, 60-73. http://dx.doi.org/10.1080/07924259.2013.816787

