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Phylogeny of Oweniidae (Polychaeta) based on morphological data and taxonomic revision of Australian fauna

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The family Oweniidae Rioja, 1917 is a small group of broadly distributed polychaetes whose relationships and position in the annelid tree are still poorly understood. A comprehensive revision of the group with reconsideration of character homologies and terminology under a phylogenetic framework was needed. We investigated the relationships of members of Oweniidae and other polychaetes by performing maximum parsimony analyses of 18 oweniid species of the five recognized genera to date and members of the families Siboglinidae, Sabellidae, Spionidae, Magelonidae, and Chaetopteridae. Phylogenetic hypotheses confirmed the monophyly of Oweniidae and suggested sister-group relationships with Magelonidae, although weakly supported. Analyses also recovered *Owenia* and *Myriowenia* as monophyletic and allowed recognition of *Myrioglobula* as a junior synonym of *Myriochele* based on the presence of acicular chaetae and the shape of the head. Implied weighting analyses supported these findings and recovered *Galathowenia australis* as sister group of *Myriochele*. The presence of acicular chaetae justifies the consideration of this species as belonging to *Myriochele*. Nomenclatural changes are proposed for those species previously considered as members of *Myrioglobula*, and these are: *Myriochele antarctica* **comb. nov.**, *Myriochele japonica* **comb. nov.**, *Myriochele islandica* **comb. nov.**, *Myriochele malmgreni* **comb. nov.**, and *Myriochele australis* **comb. nov.** After analyses and definition of generic diagnostic features, other new combinations include *Galathowenia eurystoma* **comb. nov.** and *Galathowenia haplosoma* **comb. nov.**, previously considered as members of *Myriochele*. Taxonomic revision of Australian collections revealed the presence of *Myriochele heruensis* Gibbs, 1971, which is herein redescribed, and allowed the description of four new species: ***Galathowenia annae* sp. nov.**, ***Galathowenia arafurensis* sp. nov.**, ***Galathowenia quelis* sp. nov.**, and ***Myriochele australiensis* sp. nov.**, mostly from the east coast of Australia, in addition to the three recently well-documented species of *Owenia*. Australian species have been described, illustrated, and compared in detail with similar taxa. Distribution patterns and ecological notes have also been given. Keys to oweniid genera and Australian species are provided.

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ADDITIONAL KEY WORDS: Annelida – Australia – family and genera emendation – genus synonymization – systematics – taxonomy – terminology.

INTRODUCTION

Oweniidae is a small group of polychaetes that comprises five genera and 55 species (Villalobos-Guerrero, 2009) with relatively simple external morphology. They are common in soft bottoms of continental shelves, but not exclusive to these environments. Monophyly of Oweniidae has been substantiated by some uncommon features amongst annelids: presence of monociliated epidermal cells, a characteristic structure of the body wall, lack of cuticle (Gardiner, 1978; Gardiner & Rieger, 1980; Westheide, 1997; Hausen, 2005a), presence of neuropodial patches of hooks or

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*Corresponding author. E-mail: capa.maria@gmail.com uncini (Nilsen & Holthe, 1985; Meyer & Bartolomaeus, 1996), presence of mitraria larvae (Wilson, 1932; Thorson, 1946; Smith, Ruppert & Gardiner, 1987; Smart & Dassow, 2009), presence of specialized parapodial glands, and reduction of the nephridia except for a single pair in the sixth segment (Liwanow & Porfirjewa, 1967; Meyer & Bartolomaeus, 1996).

The position of the oweniids in the annelid tree remains unresolved. Based on morphological features, they were traditionally considered as members of 'Sedentaria' (e.g. Hartman, 1966, 1969) and later were placed amongst the basal polychaetes (Bubko, 1973; Rieger, 1976, 1988; Minichev & Bubko, 1992) or related to Siboglinidae (Liwanow & Porfirjewa, 1967; Rouse & Fauchald, 1997). Molecular techniques, integration of different sources of data, and the application of phylogenetic methodologies have still not resolved the sister-group relationships and position of Oweniidae within the annelids. Some hypotheses still suggest a close relationship of Oweniidae and Siboglinidae as derived annelids (e.g. Eeckhaut *et al.*, 2000; Rousset *et al.*, 2004; Struck *et al.*, 2007; Capa *et al.*, 2011) whereas others point to a basal position amongst Annelida (Struck *et al.*, 2008; Zrzavý *et al.*, 2009).

The phylogenetic relationships within Oweniidae have been addressed recently (Sene-Silva, 2002), based on morphological data. Three of the five existing genera were recovered as monophyletic (*Owenia* Delle Chiaje, 1844, *Myrioglobula* Hartman, 1967, and *Myriowenia* Hartman, 1960) whereas *Myriochele* Malmgren, 1867 and *Galathowenia* Kirkegaard, 1959, were retrieved as paraphyletic. These results needed to be reviewed and updated in light of the additional morphological information presented herein and synonymies that should have been considered.

Several species have been recorded as cosmopolitan or widely distributed because of morphological resemblance of specimens from several geographically distant localities and bathymetric ranges (Dauvin & Thiébaut, 1994). Various techniques have been used in resolving some of these taxonomic issues and biogeographical patterns (e.g. Blake, 2000; Koh & Bhaud, 2001, 2003; Koh, Bhaud & Jirkov, 2003; Parapar, 2003a; Ford & Hutchings, 2005; Martín *et al.*, 2006), although mostly concentrating on the genus *Owenia*. Taxonomic revisions of certain species and complexes of species were also required, some of which are dealt with in this study.

In Australia, prior to the present study only the genus *Owenia* had been reviewed, resulting in the description of three new species (Ford & Hutchings, 2005) previously referred to as *Owenia fusiformis* (Dauvin & Thiébaut, 1994). Records of other genera in the Australian coasts had been cited (Hutchings, 2000) but a revision of the material, identification, and description of the species was needed.

For the present study, a taxonomic revision of the Oweniidae was carried out, after the study of material housed in Australian institutions. Detailed examination of morphological structures led us to interpretations of characters and states different from previous interpretations (Sene-Silva, 2002). We included the type species of the currently accepted genera, the Australian species, and comparative non-Australian species, in order to incorporate the maximum phenotypic variability within each group. This data set was used to assess the monophyly, relationships, and composition of the Oweniidae genera and track the evolution of the main morphological features.

MATERIAL AND METHODS

MATERIAL EXAMINED

For the revision of the Australian oweniid fauna more than 2100 specimens deposited in the main Australian museum collections were examined and identified to species (Appendix 1). Type material was deposited in the Australian Museum, Sydney (AM), Museum and Art Galleries of the Northern Territory, Darwin (NTM), and Museum Victoria, Melbourne (MV). As comparative material and in order to prepare Tables 2–6, several specimens belonging to the type series of species previously described in other geographical areas (Iceland and Antarctica) and deposited in the Museo Nacional de Ciencias Naturales, Madrid (MNCN) were also revised (Appendix 1). Publications on Oweniidae from the Indo-Pacific were used for comparison with the Australian material (e.g. Caullery, 1944; Gibbs, 1971, 1972; Tan & Chou, 1993; Al-Hakim & Glasby, 2004). An attempt was made to review the oweniid specimens described by Caullery (1944) from the Siboga expedition (Bleeker & van der Spoel, 1992), but the material was not available.

After the study of specimens under a stereomicroscope, some parapodia (typically from the mid region) were removed and mounted with glycerine on slides in order to study the uncini. Light microscopy photographs were taken with a Leica MZ16 microscope and Spot flex 15.2 camera attached. Some specimens were dehydrated in ethanol, critical point dried, and covered with 20 nm of gold and examined under a Leo 435VP scanning electron microscope (SEM) in the AM, using an Everhart-Thornley secondary electron detector. The use of scanning electron microscopy has been shown to be an essential tool for oweniid taxonomic purposes since the pioneering work of Thomassin & Picard (1972). Certain features, such as the relative position of uncinal teeth, the presence and relative number of acicular and capillary chaetae, the ultrastructure of chaetae, and the ciliary longitudinal grooves, are only adequately visible under SEM.

For the cladistic analyses type species were included, plus the Australian species and other representatives exhibiting the morphological variation found within each of the five oweniid genera, totalling 18 oweniid species (Appendix 1). The matrix (Table 1) was scored in NEXUS DATA EDITOR (Page, 2001) based on direct examination of the specimens and the original descriptions and illustrations. The outgroup was formed by several members of the families Siboglinidae, Sabellidae, Spionidae, Magelonidae, and Chaetopteridae, representing those groups previously considered to be related to Oweniidae (e.g. Liwanow & Porfirjewa, 1967; Bubko, 1973; Minichev & Bubko, 1992; Rouse & Fauchald, 1997; Eeckhaut *et al*., 2000; Rousset *et al*., 2004; Struck *et al*., 2007, 2008; Zrzavý *et al*., 2009).

TERMINOLOGY AND CHARACTERS USED IN THE DESCRIPTIONS AND ANALYSES

The terminology and character description of members of Oweniidae is inconsistent in the literature. Some studies (e.g. Nilsen & Holthe, 1985; Imajima & Morita, 1987; Blake, 2000; Parapar, 2001, 2003a, b, c, 2006) have made an effort to establish a terminology but uniformity of nomenclature and homology grounds between structures within oweniids and between oweniids and other polychaete groups has not always been followed. We have revised the terminology and described the general taxonomic features in oweniids. These have been incorporated into the data matrix for phylogenetic analyses (Appendix 2). A total of 35 morphological characters considered as being diagnostic (e.g. Hartman, 1960, 1967; Blake, 1984, 2000; Nilsen & Holthe, 1985; Parapar, 2001, 2003a, b, c, 2006), as well as others thought to be phylogenetically informative, were considered for analyses. Absence/presence and multistate coding methods were used. The 'C-method' proposed by Pleijel (1995) was used for character scoring. Missing data were scored with '?' and inapplicable data with a hyphen. The score given for each state implies nothing about polarity or order.

The terms 'thoracic' and 'abdominal' were avoided and, in order to facilitate the description of morphological features of the anterior region of the specimens, the terminology proposed by Nilsen & Holthe (1985) was followed with some modifications. Instead of 'relative length of thoracic chaetigers' (RLTC), we used 'relative length of uniramous segments' (RLUS) and 'relative length of first biramous segments' (RLFBS). In some cases we also refer to 'relative length of anterior segments' (RLAS). Similarly, the term 'thoracic formula' (TF) proposed by Parapar (2003c) to refer to the nature of the parapodia of anterior segments (TF = No1 : Ne1–No2 : Ne2–No3 : Ne3, where No means 'notopod' and Ne 'neuropod', and the sub-index denotes the position of each chaetiger in the thorax. The presence of chaetae or hooks are denoted by '1' and their absence by '0', for example 1:0–1:0–1:1) was modified, using instead 'U' when these are uniramous, and 'B' when they are biramous (e.g. TF = U : U : B).

PHYLOGENETIC ANALYSES

Maximum parsimony heuristic searches used 10 000 replicates of random taxon addition and tree bisection-reconnection (TBR) branch swapping algorithm, saving ten trees per replicate using TNT 1.1 (Goloboff, Farris & Nixon, 2008a). All characters were given equal weight and multistate characters were considered non-additive. Nodal support was estimated by 1000 jackknife replicates using TBR in TNT 1.1 (Goloboff *et al*., 2008a). New technology searches, such as ratchet, drift, and tree fusing were implemented, both separately and in combination using TNT 1.1 (Goloboff *et al*., 2008a). One thousand repetitions were performed and the most parsimonious trees were hit 100 times. Tree metrics are abbreviated as follows: tree length (TL), consistency index excluding parsimony non-informative characters in the data matrix (CI), and retention index (RI). Support values are given on the trees. Implied weighting (as in Goloboff, 1993, 1995, Goloboff *et al*., 2008b) was implemented, varying the concavity values from 3 to 20 and the results compared.

RESULTS

PHYLOGENETIC ANALYSES

Maximum parsimony analysis of equally weighted characters yielded 185 most parsimonious trees (TL: 86, CI: 0.56, RI: 0.76). Oweniidae was recovered as monophyletic in all of them although the support value for this clade was weak (jackknife value, JK: 62, Fig. 1A). The synapomorphies for this clade are the presence of dorsolateral ciliary folds (a feature that is not observed in all the terminals) and the presence of neuropodial uncini from segment 4 (displayed from segments 2 or 3 in some oweniids as a secondary arrangement) (Fig. 1B). Other homoplastic features supporting this clade are the presence of an intraepidermal cord (shared with Siboglinidae) and unequal length of segments 4–6 (shared by most oweniids terminals) (Fig. 1B).

Magelonidae is suggested as the sister group to Oweniidae although support is weak (JK: < 50). Oweniids and magelonids share a prostomium fused to the peristomium, the absence of nuchal organs, and

Figure 1. A, strict consensus of 185 most parsimonious cladograms with equal weighting for species of Oweniidae with jackknife support values > 50 below nodes. B, first most parsimonious tree (tree length: 86 steps, consistency index: 0.56; retention index: 0.76); solid circles represent unique transformations and open circles multiple transformations. C, strict consensus of seven most parsimonious trees with implied weighting (*k*, concavity constant = 3–4). D, most parsimonious tree with implied weighting (*k* = 20). The generic names used in this figure correspond to the classification of the species previous to the present study.

the presence of a ventral buccal organ (Fig. 1B). If Magelonidae is omitted from the analyses, Siboglinidae is recovered as a sister group of Oweniidae.

Within Oweniidae, only two of the traditional genera are recovered as monophyletic. A basal *Myriowenia* clade is supported (JK: 89) by the presence of a breakage groove between the head and the first segment and also by a straight oesophageal commissure (this last feature shared with *Myriochele* and *Myrioglobula*), amongst other features also shared with outgroups (Fig. 1B). *Owenia* (JK: 93) is supported by the presence of a tentacular crown, a large number (often more than 20) of rows of uncini in neuropodial tori, and other homoplastic features such as the presence of a collar between the head and the first segment, having anterior segments similar in length, and the presence of uncinal teeth arranged side by side (Fig. 1B). *Myriochele* and *Myrioglobula* are found scattered within a derived clade (JK: 50). This clade is supported by the presence of longitudinal grooves on both sides of the body and other homoplastic characters such as the presence of dorsal longitudinal ciliated grooves, presence of acicular chaetae in the notopodial, and presence of straight oesophageal commissures (Fig. 1B). As *Myriochele* is an older name than *Myrioglobula*, the latter is proposed as a junior synonym of *Myriochele*. Monophyly of *Galathowenia* is not resolved and most relationships within this group and between *Myrioglobula* and the *Myriochele–Myrioglobula* clade are not resolved in the consensus topology (Fig. 1A).

Implied weighting yielded different results depending on the values of the concavity constant (*k* ranging from 3 to 20) but all of them shared some similarities with respect to the nonweighted data set: *Myriowenia* was recovered at the base of the oweniid tree, the *Myriochele* and *Myrioglobula* terminals were retrieved scattered in a single clade, and the monophyly of *Galathowenia* is not resolved because of the position of *Galathowenia australis* outside of the clade. Implied weighting with *k*-values of 3 and 4 yielded seven most parsimonious trees (consensus topology shown in Fig. 1C). The main differences with respect to the nonweighted data set are the position of *Owenia*, now sister to *Galathowenia*, and the more resolved relationships within the *Myriochele–Myrioglobula* clade. Analyses with *k*-values between 5 and 19 resulted in two most parsimonious trees leaving the relationships amongst four clades (*Owenia*, the *Myriochele–Myrioglobula*, *Galathowenia australis*, and a clade including the remaining *Galathowenia* species) unresolved. Implied weighting with *k*-values of 20 yielded a unique tree (Fig. 1D), distinguished from previous results in the placement of *G. australis*, at the base of the *Myriochele–Myrioglobula* clade. This result suggests a reclassification of this group, defined by the presence of acicular chaetae and the shape of the mouth opening.

TAXONOMY

FAMILY OWENIIDAE RIOJA, 1917, EMENDED

Ammocharidea Kinberg, 1866.
Ammocharidae Malmgren, 1867.
Oweniidae Rioja, 1917; Fauchald, 1977; Nilsen & Holthe, 1985; Blake, 2000.

Emended diagnosis: Body cylindrical. Prostomium and peristomium fused forming the head. Nuchal organs absent. Mouth terminal or shifted ventrally. Segments of unequal length present. Anterior region with one to three short, contiguous or not, uniramous segments, following segments biramous. Notopodial chaetae emerging from body wall, capillaries with characteristic structure of the cortex, resembling small imbricate scales and, on occasions, smooth acicular chaetae. Neuropodia as low tori with irregular rows of bidentate uncini. Parapodial branchiae or cirri absent. Tube as a thin secreted layer encrusted with foreign objects. Distinct mitraria larvae. Intraepidermal nerve cord present.

Remarks: Previous diagnoses or descriptions of the family (e.g. Rioja, 1917; Fauchald, 1977; Nilsen & Holthe, 1985; Blake, 2000) did not include some of the features that were revealed as synapomorphies after our analyses and therefore these features have been incorporated in the emended diagnosis of the family. Nevertheless, the definition of Oweniidae consists of a unique combination of homoplastic characters. The presence of the collar or anterior head appendages (tentacular crown, palps, and lobes) and the shape of the pygidium have been excluded from the diagnosis because of high variation within the group. According to the present study, the family is composed of four genera: *Owenia*, *Myriochele*, *Galathowenia*, and *Myriowenia*, with about 55 species (Villalobos-Guerrero, 2009).

GENUS *GALATHOWENIA* KIRKEGAARD, 1959, EMENDED

Galathowenia Kirkegaard, 1959; Fauchald, 1977; Blake, 1984, 2000.
Clymenia Ørsted, 1844 [not Münster (Ammonoidea)].
Psammocollus Grube, 1866.

Emended diagnosis: Head cylindrical, anteriorly truncated, terminal mouth extending midventrally as an elongated slit and with ventral pharyngeal organ. Breakage groove between first and second chaetiger. Oesophageal commissure Y-shaped. First three segments generally uniramous, with capillaries on notopodia. Following segments biramous, notopodia with capillary chaetae only and neuropodial uncini with two teeth generally obliquely arranged.

Type species: Galathowenia africana Kirkegaard, 1959, by original designation.

Remarks: The presence of a breakage groove between the first and second chaetiger has been identified in several species of the genus (Blake, 1984; Parapar, 2001, 2003a), including the type material of the type species (as drawn by Kirkegaard, 1959 and studied by J. P.), as a line of autotomy. Although it has not been described in several other *Galathowenia* species it could have been overlooked and represents a potential synapomorphy for the genus (Fig. 1B). Other main features characterizing *Galathowenia* are the presence of a cylindrical head with a truncated anterior end, an attribute shared with *Owenia* but differing from this genus in lacking a tentacular crown, and the presence of a ventral slit with prominent lateral lips. An exception to this head shape, with the ventral slit not well developed, is *G. australis* (Grube, 1866), which has been shown here not to belong to this group (Fig. 1C, D), contrary to earlier studies (Parapar, 2003b).

GALATHOWENIA ANNAE SP. NOV.

FIGURES 2A–D, 3, TABLES 1, 2

Holotype: New South Wales, Botany Bay, east end of runway 34R, AM W37222, 33°58′S, 151°12′E, sandy mud, 16 m, 15.ix.2004.

Paratypes: New South Wales, Botany Bay, east end of runway 34R, AM W37223, same sample [five specimens (specs)]; AM W37208, same sample (one spec. on SEM pin); AM W37224, 33°58′31″S, 151°11′49″E, mud, 16 m, 1.xii.2004 (four specs) and AM. W37064, same sample (one spec. on SEM pin); AM W37225, 33°57′37″S, 151°11′15″E, mud, 7.4 m, 1.xii.2004 (15 specs); AM W37226, 33°58′38″S, 151°11′45″E, mud, 18.6 m, 1.xii.2004 (one spec.); AM W37227, 33°57′43″S, 151°11′18″E, mud, 7.6 m, 1.xii.2004 (four specs); AM W37228, 33°58′40″S, 151°11′49″E, sandy mud, 18.2 m, 15.ix.2004 (two specs).

Other material examined (Appendix 1): New South Wales, Botany Bay (34 specs), Pittwater (one spec.).

Description of holotype: Slender, thread-like body, cylindrical in cross section, 10.2 mm long, 0.1 mm wide, with 17 chaetigers. Head elongated with anterior end truncated; terminal ciliated mouth opening, extending midventrally as elongated slit (Figs 2A, B, 3A–D), with a pair of ventrolateral brownish eyespots (Fig. 2A, B). Division of head and first segment inconspicuous, no groove or variation in width apparent. Anterior three segments with uniramous parapodia, each with notochaetae only (Fig. 3A, B). Second segment twice as long as first and third; RLUS = 1:2:1 (Fig. 3B). Deep groove between first and second chaetigers, on ventral and lateral sides (Fig. 3B, D). Oesophageal commissures evident as a white ventral longitudinal band with a Y shape in anterior segments. Fourteen biramous chaetigers. Anterior biramous chaetigers five to more than ten times longer than wide (e.g. Fig. 3A), becoming shorter and compacted in far posterior segments. Chaetiger 6 longest. Capillaries decreasing in size ventrally on notopodia with proximal part smooth or slightly striated and mid and distal end covered with scales (Fig. 3E). Posterior chaetigers with fewer but longer chaetae. Neurochaetae present from chaetiger 4, in long and broad ventral tori; tori of posterior segments much shorter. Acicular chaetae absent. Uncini arranged in about four irregular transverse rows in anterior segments (Fig. 3F); each uncinus provided with two convex teeth arranged in an oblique row (Fig. 3G, H). Anus terminal with three prominent digitiform lobes, dorsal one slightly smaller than lateral ones (Fig. 3I, J). Tube three to four times longer than animal, with thin secreted layer encrusted with sand grains (Fig. 2D). Colour in alcohol brownish or pale yellow, head with short brownish red pigmented areas (Fig. 2B) and some slightly pigmented bands in anterior four segments.

Variation: All specimens examined are cylindrical in shape and very thin, not exceeding 0.1 mm in width. Length and number of segments vary between 5–11 mm and from 14 to 17 segments. Most specimens were incomplete or difficult to extract from their tubes so variation could be greater than reported herein. The colour pattern varies amongst the material examined. Some specimens have a fully pigmented brownish head and first segments whereas in others the body is almost colourless or presents only few scattered brownish pigments spots. Eyespots have faded in some specimens, probably because of the length of time in alcohol. In most specimens pygidial lobes are of similar size, but the dorsal lobe has been found to vary from being shorter or longer than lateral ones.

Ecological notes: Galathowenia annae sp. nov. lives in estuaries of the Sydney region (Fig. 14), inhabiting muddy and sandy sediments between 13 and 18 m in depth.

Etymology: This species is dedicated to Anna Murray (AM, Sydney) for providing valuable preliminary notes on the identification of Australian oweniids.

Remarks: Species of *Galathowenia* are characterized by a combination of only a few relevant features, a reason why some specimens collected around the

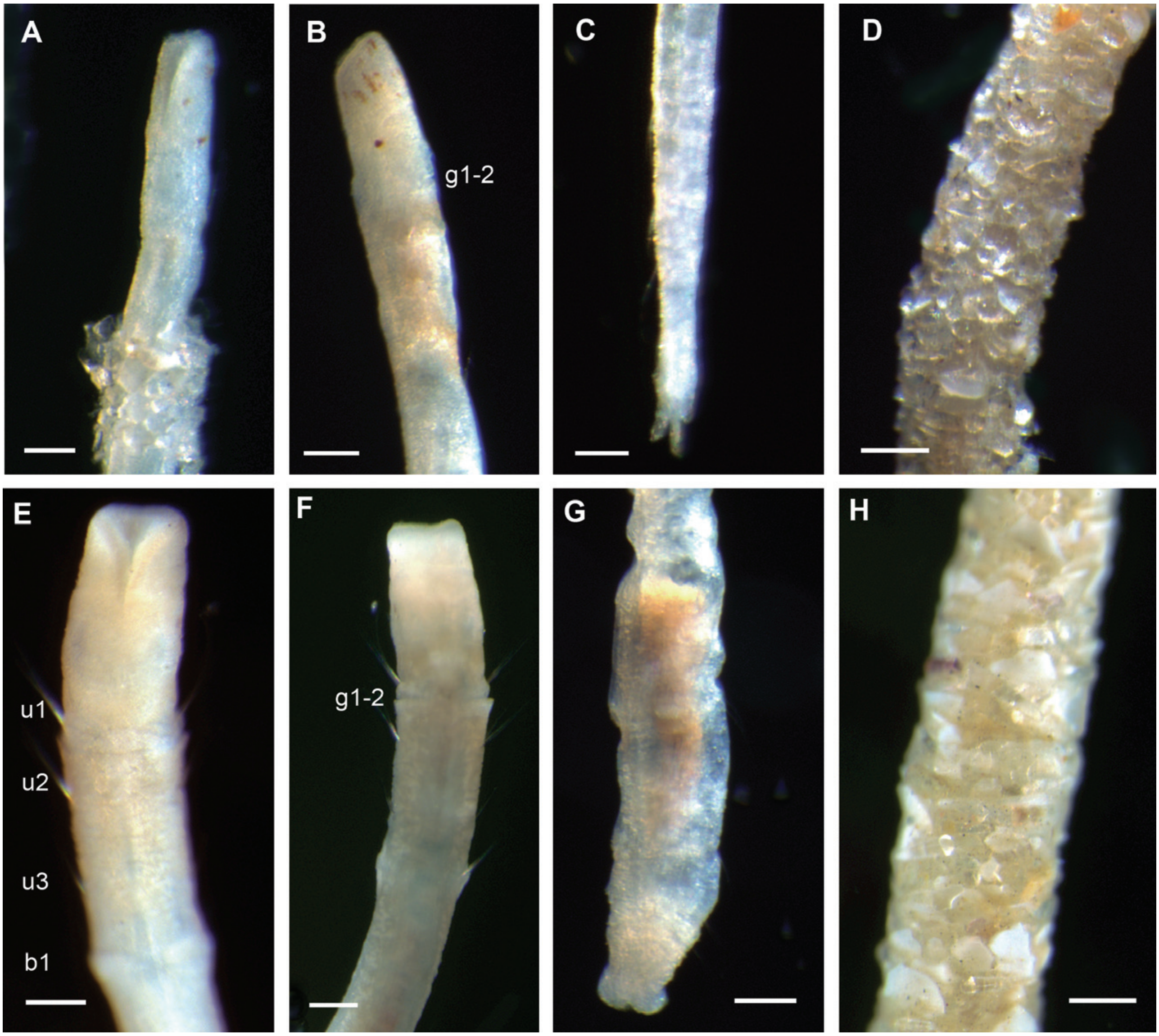

Figure 2. A–D, ***Galathowenia annae* sp. nov.** Paratype, AM W37233. A, anterior end, ventrolateral view. B, anterior end, lateral view. C, posterior end, ventral view. D, tube. E–H, ***Galathowenia quelis* sp. nov.** AM W37821-37822. E, anterior end, ventral view. F, anterior end, dorsal view. G, posterior end, ventral view. H, tube. Abbreviations: b1, biramous segment; g1-2, groove between segment 1 and 2; u1-u3, uniramous segments 1 to 3. Scale bars: A–D = 50 μm; E–H = 75 μm.

globe have been attributed to a few 'cosmopolitan species'. This is the case for *Galathowenia oculata* (Zachs, 1923), originally described from the White Sea (Zachs, 1923) and reported in several localities from boreal to American Pacific regions, and depths ranging from 12 to 2500 m (e.g. Nilsen & Holthe, 1985; Imajima & Morita, 1987; Blake, 2000; Parapar, 2003a). Some of the diagnostic features present in *G. oculata*, such as the presence of eyespots, short anterior uniramous segments, long biramous segments (particularly the fifth), and pygidium provided with two or three blunt lobes are commonly present in specimens across the broad range of its geographical distribution. However, specimens from different biogeographical areas show several differences that some authors have recognized as interpopulation variation, but that could be also interpreted as specific differences. Accordingly, we interpret *G. oculata* as a species complex to which *G. annae* sp. nov., belongs, but can be distinguished based on a range of characters (Table 2). *Galathowenia annae* sp. nov. is characterized by its thread-like body, being one of the

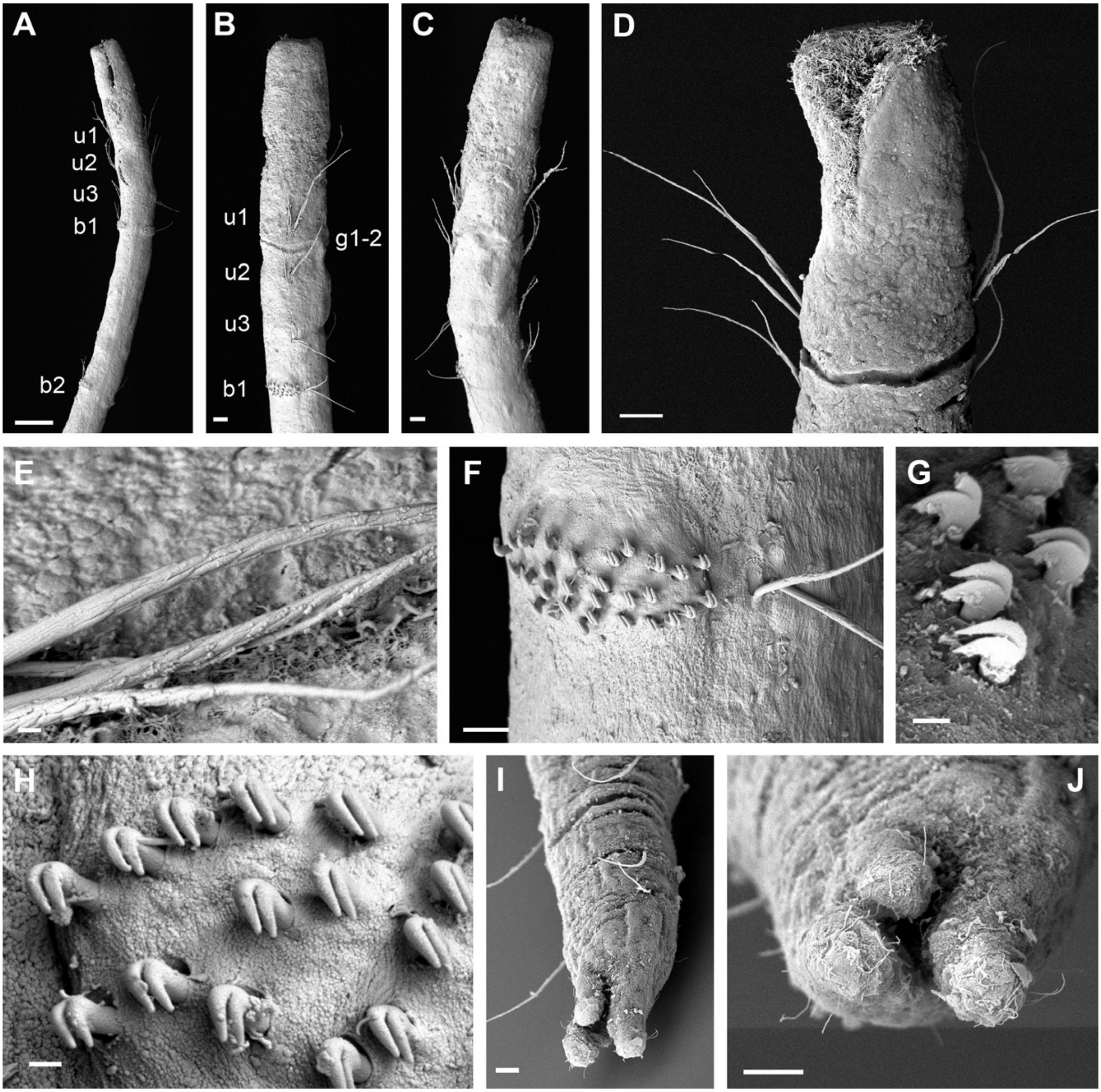

Figure 3. ***Galathowenia annae* sp. nov.** A, anterior end, ventral view. B, anterior end, lateral view. C, anterior end, dorsal view. D, head and first segments, ventral view. E, capillary chaetae, segment 6. F, uncinal patch in first biramous segment. G, uncini, segment 6, side view. H, uncini, segment 4, top view. I, posterior end, lateral view. J, pygidium and anus, posterior view Abbreviations: b1-2, biramous segment 1 to 2; g1-2, groove between segment 1 and 2; u1-u3, uniramous segments 1 to 3. Registration numbers: A–C, E, H, AM W37064; D, G, I, J, AM W37190; F, AM W37208. Scale bars: A = 100 μm; B–D = 20 μm; E, G = 2 μm; F, H = 3 μm; I, J = 10 μm.

thinnest species described in *Galathowenia*, and the presence of a pygidium with three prominent digitiform lobes, two of which are ventrolateral and the third dorsal. These lobes have only been described in *G. oculata* from the western Mediterranean (Martín, 1989), which could represent another undescribed species based on this and other features (Blake, 2000; Parapar, 2003a). After the examination of two specimens from the Mediterranean we verified the similarities between these and *G. annae* sp. nov. They share the presence of eyes, the pigmentation in the anterior end, the relative size of the three first

Table 1. Character matrix of morphological features for resolving oweniid relationships

	1–5	6–10	11–15	16–20	21–25	26–30	31–35
Chaetopteridae	1?1–0	0110–	?A100	04000	–0001	0–010	000?0
Magelonidae	?2001	01011	00000	04000	–0010	10000	00011
Sabellidae	0?1–0	0000–	0A100	01000	–031A	1A010	000–0
Spionidae	121–1	01120	?1100	04000	–0310	10100	000?0
Siboglinidae	1?1––	0000–	00000	01010	–A300	10000	001?0
*Galathowenia africana**	11012	00011	?1000	13110	–2100	11000	001?1
Galathowenia annae **sp. nov.**	10012	00010	?1000	13110	–2100	11000	00111
Galathowenia arafurensis **sp. nov.**	10012	00010	?0000	13110	–2100	11000	131?1
Galathowenia australis	10012	00010	?0000	13110	–2100	11000	03111
Galathowenia fragilis	10012	00010	?1000	13110	–?100	11000	02111
Galathowenia quelis **sp. nov.**	11012	00011	?1010	13110	–2100	11000	03111
Galathowenia scotiae	10012	00010	?0000	03111	22100	11000	00111
Myriochele australiensis **sp. nov.**	00001	0001?	?0000	01011	12000	11011	10101
*Myriochele heeri**	00001	00011	10000	02111	21000	11011	10101
Myriochele heruensis	00001	00011	10000	03111	31000	11011	10101
Myriochele olgae	00001	00011	10000	01111	02000	11011	10101
Myriochele robusta	00001	00010	11000	03111	22100	11011	01101
*Myrioglobula antarctica**	00001	0001?	?0000	01111	??200	110??	?1101
Myrioglobula islandica	01001	0001?	?1000	01011	31000	11011	?0101
*Myriowenia californiensis**	12000	01111	10001	03110	–1001	10000	0?101
Myriowenia sp.	11000	01111	10001	03110	–1001	10000	00101
Owenia australis	00010	10011	1101?	03010	–3200	11000	00111
*Owenia fusiformis**	00010	10011	1101?	03010	–3200	11000	00111

*, type species of each genus.
Multistate characters: A = 0 + 1.
The generic names used in this table correspond to the classification of the species previous to the present study.

Table 2. Comparison of three Australian species of *Galathowenia* and *Galathowenia oculata* from different geographical areas

	G. oculata sensu Nilsen & Holthe, 1985	*G. oculata sensu* Imajima & Morita, 1987	*G. oculata sensu* Martín, 1989	*G. oculata sensu* Blake, 2000	***Galathowenia annae* sp. nov.**	***Galathowenia quelis* sp. nov.**	*Galathowenia* sp.
Locality	Norway	Japan	Spain, Mediterranean	California, USA	Australia	Australia	Australia
Length (mm)	30	23	20	4–35*	5–11	11–20	7
Width (mm)	0.6	0.8	0.3†	0.25–1.25	0.05–0.1	0.2	0.1
Uniramous segments	3	3	3	3	3	3	3
Biramous segments	21–31	23–30	17–27	10–22	11–14	12–20	14
Eyespots	In some populations	Present	Present	Present or absent	Present	Present (or faded)	Present
RLUS	1:1:1	1:1:0.5	1:1:1	1:1:1‡	1:2:1	1:2:1	1:2:1
Longest segment	5	nd	5†	5	6	5	6
Acicular notopodial chaetae	Absent	Absent	Absent	Absent	Absent	Absent	Absent
Unicinal teeth	Oblique	Oblique	Oblique	Oblique	Oblique	Oblique	Almost vertical
Pygidium	Two short lobes, sometimes three	Two short lobes	Two lateral and one dorsal lobe	Two short, blunted lobes	Two lateral and one dorsal lobe	Low rim	Low rim
Tube	Sand grains	Sand grains and sponge spicules	Sand grains and shell fragments	Sand grains	Sand grains	Sand grains	Sand grains
Pigmented prostomium	In some populations	Present	Present†	Absent§	Present	Absent	Absent
Anterior regeneration	Present¶	Absent	Absent	Absent	Absent	Absent	Absent
Transversal groove (between segments)	Absent	Present (head-1–2)†	Present (1–2)‡	Present (head-first)†	Present (1–2)	Present (1–2)	Present (head-1–2)

*Smaller specimens are probably juveniles.
†From the study of two specimens.
‡Feature not described, information obtained from drawings of photographs.
§From Blake & Dean (1973).
¶In Icelandic populations (Parapar, 2003a).
nd, no data available; RLUS, relative length of uniramous segments.

segments (RLUS = 1:2:1), and the presence of three pygidial cirri, one arranged dorsally and the other two lateroventrally. However, in the Mediterranean specimens of *G. oculata* the pygidial cirri are similar in size, the deep groove between first and second chaetiger is absent, and the longest segment is the fifth instead of the sixth (see Table 2). These differences, if confirmed in a greater number of specimens from the Mediterranean, could establish the limits between these two species and the rest of the *G. oculata* complex. Nilsen & Holthe (1985) described some populations of *G. oculata* as presenting a small dorsal lobe in the pygidium but according to the drawings (Nilsen & Holthe, 1985: fig. 7C), it is very small compared to the one found in *G. annae* sp. nov. Some populations of *G. oculata* from northern Europe were also described with a dorsal pigmented band on the head (Nilsen & Holthe, 1985), different from the irregular and inconstant pattern observed in the specimens of *G. annae* sp. nov. studied herein. The specimens of *G. oculata* described from Japan (Imajima & Morita, 1987) share the colour pattern with *G. annae* sp. nov., but they are distinguished by the shape of the pygidium, with two lobes in the Japanese specimens and three in the Australian ones. *Galathowenia annae* sp. nov. presents a deep groove between the first and the second chaetiger in the specimens examined and this could be related to regeneration processes, as indicated by Parapar (2003a) for *Galathowenia fragilis* (Nilsen & Holthe, 1985). This feature has not been described in any of the hitherto-published descriptions of *G. oculata* (see Parapar, 2003a), although one groove between the head and the first segment was illustrated for this species based on specimens from California, USA (Blake, 2000: fig. 5.1A) and two grooves indicated in specimens from Japan (Imajima & Morita, 1987: fig. 6A–C). One of the specimens collected on Makassar, Sulawesi (Indonesia) by Caullery (1944: fig. 42C) and considered as a variety of *Myriochele eurystoma* Caullery, 1944, resembles *G. annae* sp. nov., in the shape of the head and in the colour pattern. Unfortunately, the description of this specimen is not complete and the material was not available for a detailed comparison.

GALATHOWENIA QUELIS SP. NOV.

FIGURES 2E–H, 4, TABLES 1, 2

Holotype: New South Wales, Pittwater, AM W37821, west of Sand Point, 33°35′44″S, 151°18′20″E, sandy mud, 15.6 m, 2.xii.2004.

Paratypes: New South Wales, Pittwater, AM W37822, same sample (six specs); Botany Bay, AM W37823, east end of runway 34R, 33°58′33″S, 151°11′42″E, sandy mud, 16.5 m, 15.ix.2004 (eight specs), AM W37824, 800–1000 m off Port Botany, 33°58′45″S, 151°11′1″E, 7 m, 28.vii.1992 (one spec.), AM W37825, 800–1000 m off Port Botany, 33°58′45″S, 151°11′1″E, 7 m, 28.vii.1992 (one spec.), AM W37826, 33°58′16″S, 151°11′58″E, 7 m, 27.vii.1992 (one spec.).

Other material examined (Appendix 1): New South Wales (256 specs): Botany Bay, Malabar, Port Jackson, Pittwater; Queensland (12 specs): Shoalwater Bay; Northern Territory (two specs): Arafura Sea.

Description of holotype: Slender, thread-like body, measuring 13.0 mm long, 0.15 mm wide, with 20 chaetigers; cylindrical in cross section (Figs 2E–G, 4A–C). Head elongated, cylindrical, of same width as anterior segments; anterior end truncated, with terminal ciliated mouth opening (Figs 2E, F, 4A, B, D, E), extending midventrally as an elongated slit. Head smooth, with no folds or grooves, continuing to first segment with no apparent external division, with a pair of ventrolateral brownish eyespots. Anterior region with three short uniramous segments, each with notochaetae only. Second segment twice as long as first and third; RLUS = 1:2:1 (Figs 2E, F, 4B, C). Deep groove encircling the body, between first and second chaetiger, except for a short dorsal portion (Fig. 4A–C). Oesophageal commissures with Y shape in anterior segments. Biramous chaetigers six to ten times longer than wide, becoming shorter and compact in last three posterior segments; chaetiger 6 longest. Notochaetae of all segments similar, capillaries, decreasing in length ventrally within each fascicle, with proximal part smooth or slightly striated and mid and distal end with sculpture resembling scales (Fig. 4F, G). Acicular chaetae absent. Posterior chaetigers with fewer but longer chaetae than anterior segments (Fig. 4 K, L). Neurochaetae, as uncini, present from chaetiger 4 in long and broad lateroventral tori, decreasing posteriorly in size and number of uncini. Anterior uncinal fields with around six to eight transverse rows of uncini (Fig. 4H); tori of posterior part much shorter. Each uncinus bifid, provided with two nearly equally convex teeth, one offset slightly higher than the other and arranged in an oblique row (Fig. 4I, J). Anus terminal surrounded by a ciliated rim (Fig. 4 K–M), with two low blunted lobes on each side (Fig. 2G). Tube three to four times longer than animal, with thin secreted layer encrusted with sand grains (Fig. 2H). Colour in alcohol pale yellow, with no pigment pattern (Fig. 2E–G).

Variation: The specimens examined vary between 15 to 20 segments and 6–16 mm in length. Some paratypes and additional material show the anterior

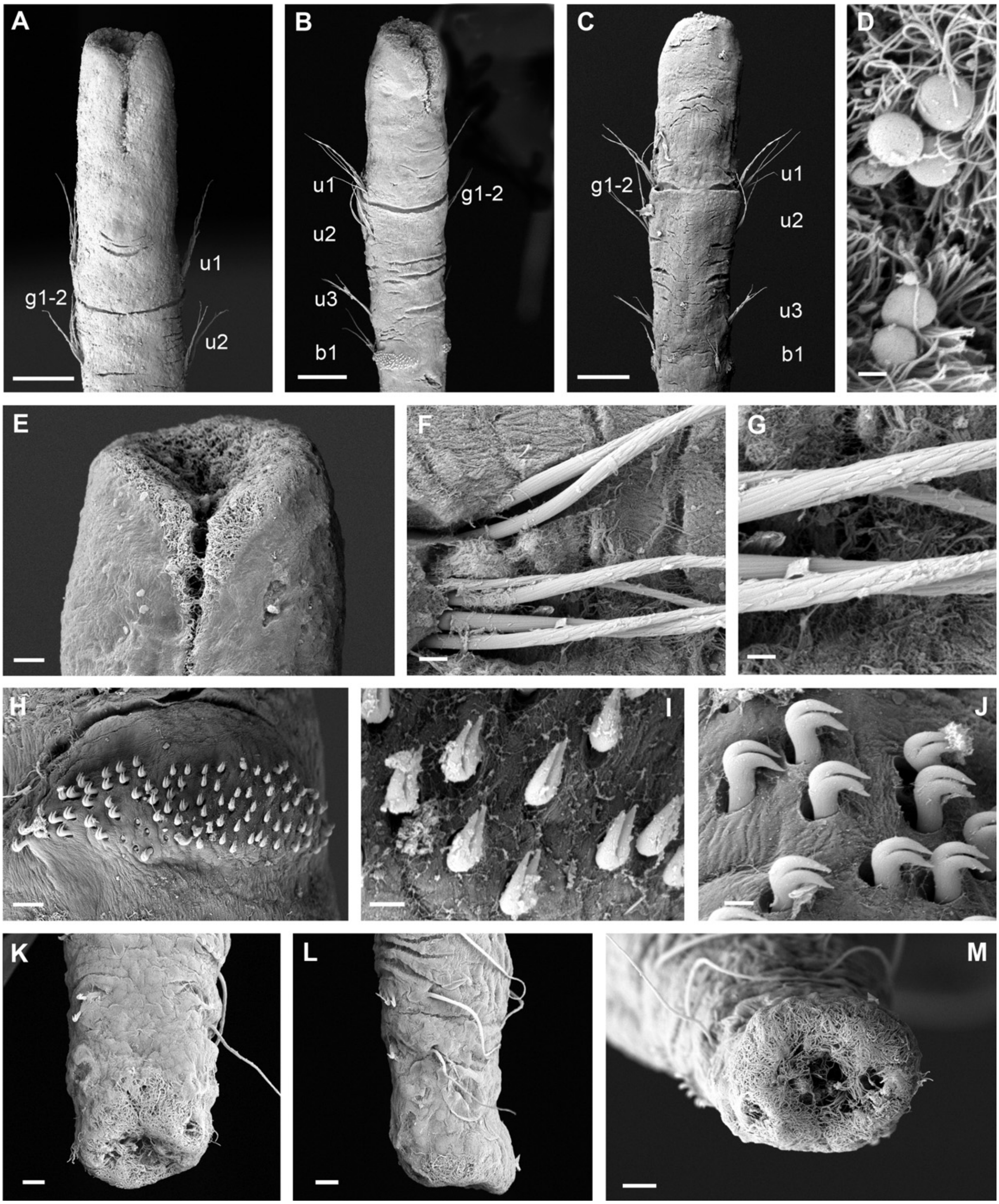

Figure 4. ***Galathowenia quelis*** **sp. nov.** A, anterior end, ventral view. B, anterior end, ventrolateral view. C, anterior end, dorsal view. D, detail of small spheres (diatoms?) located between the buccal ciliature. E, mouth and ventral slit, ventral view. F, anterior capillary chaetae, proximal end. G, detail of scale covering in capillary chaetae, segment 3. H, neuropodial uncinal field, segment 4 (first biramous chaetiger). I, uncini, same segment, top view. J, uncini, same segment, side view. K, posterior end, ventral view. L, posterior end, lateral view. M, anus, posterior view. Abbreviations: b1, biramous segment 1; g1-2, groove between segment 1 and 2; u1-u3, uniramous segments 1 to 3. Registration numbers: A, AM W37195; B–D, F–J, W37191; E, AM W37192; K–M, AM W37193. Scale bars: A–C = 100 μm; D, G, I, J = 2 μm; E, H, K–M = 10 μm; F = 4 μm.

end weakly rounded instead of truncated. Eyespots have faded in some specimens, probably related to the time of storage in alcohol. Shape of pygidium varies slightly amongst specimens and probably as a result of methods of fixation and/or manipulation for observation; specimens studied under the dissecting microscope showed a well-marked bilobed pygidium (Fig. 2G) whereas in specimens observed under SEM, the pygidium resembled a short rim with a slightly enlarged dorsal border (Fig. 4 K–M). We believe that this difference may be because of the critical point drying method. Some specimens are slightly brownish after preservation but none of the material examined exhibited any distinguishable colour pattern.

Ecological notes: This species has been found mostly in estuaries and sheltered bays in muddy and sandy sediments between 1 and 60 m in depth, but some specimens were also found in deeper exposed environments along the temperate and tropical coast of eastern Australia (Fig. 14). *Galathowenia quelis* sp. nov. cohabits with *G. annae* sp. nov. in some New South Wales estuaries. The holotype and other specimens were found with one parasitic copepod living inside the tube and attached to the worm body by its anterior end.

Etymology: This species is dedicated to Ángeles Iglesias-Díaz (nickname Quelis), who was supportive of the project.

Remarks: Galathowenia quelis sp. nov. could be another example of a species belonging to what we have named the *G. oculata* complex, as it shares with this species the general combination of features mentioned above. However, *G. quelis* sp. nov. differs from previous descriptions of *G. oculata* in some features (see Table 2). The RLUS (= 1:2:1), differs from the European, west Greenland, and Californian specimens (1:1:1, Nilsen & Holthe, 1985; as per Blake & Dean, 1973 and Blake, 2000: fig. 5.1a) and those from Japan (1:1:0.5, Imajima & Morita, 1987). *Galathowenia haplosoma* (Gibbs, 1972) was described from the Cook Islands as a *Myriochele* species. Owing to the shape of the head and the lacking references to the acicular chaetae, we consider that it should be moved to *Galathowenia*. Members of this species are small (4.0 to 7.5 mm length) and share with *G. quelis* sp. nov. the presence of eyes and a pygidium divided by a small cleft (Gibbs, 1972: fig. 8a–c), but differ in the relative length of uniramous segments (1:1:0.5 in *G. haplosoma* vs. 1:2:1 in *G. quelis* sp. nov.).

Galathowenia quelis sp. nov. also resembles *G. annae* sp. nov. described above, as both have anterolateral eyespots, a groove between the first and second segments, a similar number and relative length of anterior segments (RLUS), and the same type of sediment attached to the tube. Moreover, these two species are sympatric in New South Wales (even being found in the same samples). However, they are easily distinguished by conspicuous pigmentation on the head (an attribute of *G. annae* sp. nov.) and by the pygidium (as a low rim or bilobed in *G. quelis* sp. nov. against three digitiform lobes in *G. annae* sp. nov.).

GALATHOWENIA ARAFURENSIS **SP. NOV.**

FIGURES 5, 6, TABLES 1, 3

Holotype: Northern Territory, Arafura Sea, NTM W21072, 9°23′6″S, 134°10.37″E, 88 m.

Paratypes: Northern Territory, Arafura Sea, NTM W21073, 9°50′118″S, 134°17′762″E, 83 m (one spec.); AM W34017, 9°47′59″S, 135°22′00″E, in foraminifera and dead mollusc shells bottom, 92 m, 1.v.2005 (one spec. on a SEM pin); AM W34019, 9°22′52″S, 133°39′53″E, bioturbated soft bottom with detritus, 112 m, 13.v.2005 (one spec.); AM W34020, 9°01′50″S, 133°15′01″E, bioturbated soft bottom with detritus, 233 m, 20.v.2005 (one spec.).

Description of holotype: Body cylindrical, 28 mm long, 0.6 mm wide, with 31 segments. Head elongated, truncated anteriorly (Figs 5A–D, 6A–D), with terminal mouth extending midventrally as a short slit (Figs 5D, 6B) and a pair of ventrolateral brownish eyespots (Fig. 5C, D). Ventral pharyngeal organ observed (Fig. 6E). A groove present between first and second segments except for a short dorsal portion (Figs 5C, D, 6B–D). Anterior three segments uniramous, each with notochaetae only and second slightly longer than first and third (RLUS = 1:1.5:1). Oesophageal commissures evident as a white ventral longitudinal band with Y shape in anterior segments (Fig. 5D). Anterior biramous segments five to six times longer than wide. Second biramous chaetiger (segment 5) about 1.5 times longer than first biramous (segment 4); segment 8 the longest, being about four times longer than segment 4. Capillary notochaetae of each fascicle decreasing in length ventrally (Fig. 6F), with proximal third smooth and distal end ornamented with scales. Acicular chaetae absent. Neurochaetae present from chaetiger 4, arranged on long and broad ventral tori (Fig. 6G) with uncini arranged in 12–16 irregular transverse rows; each uncinus provided with two curved teeth nearly equal in size, arranged in a slight oblique row (Fig. 6H). Pygidium with seven short digitiform lobes (Fig. 5E–G) surrounding two papillae, located at both sides of the anus opening in the middle of the

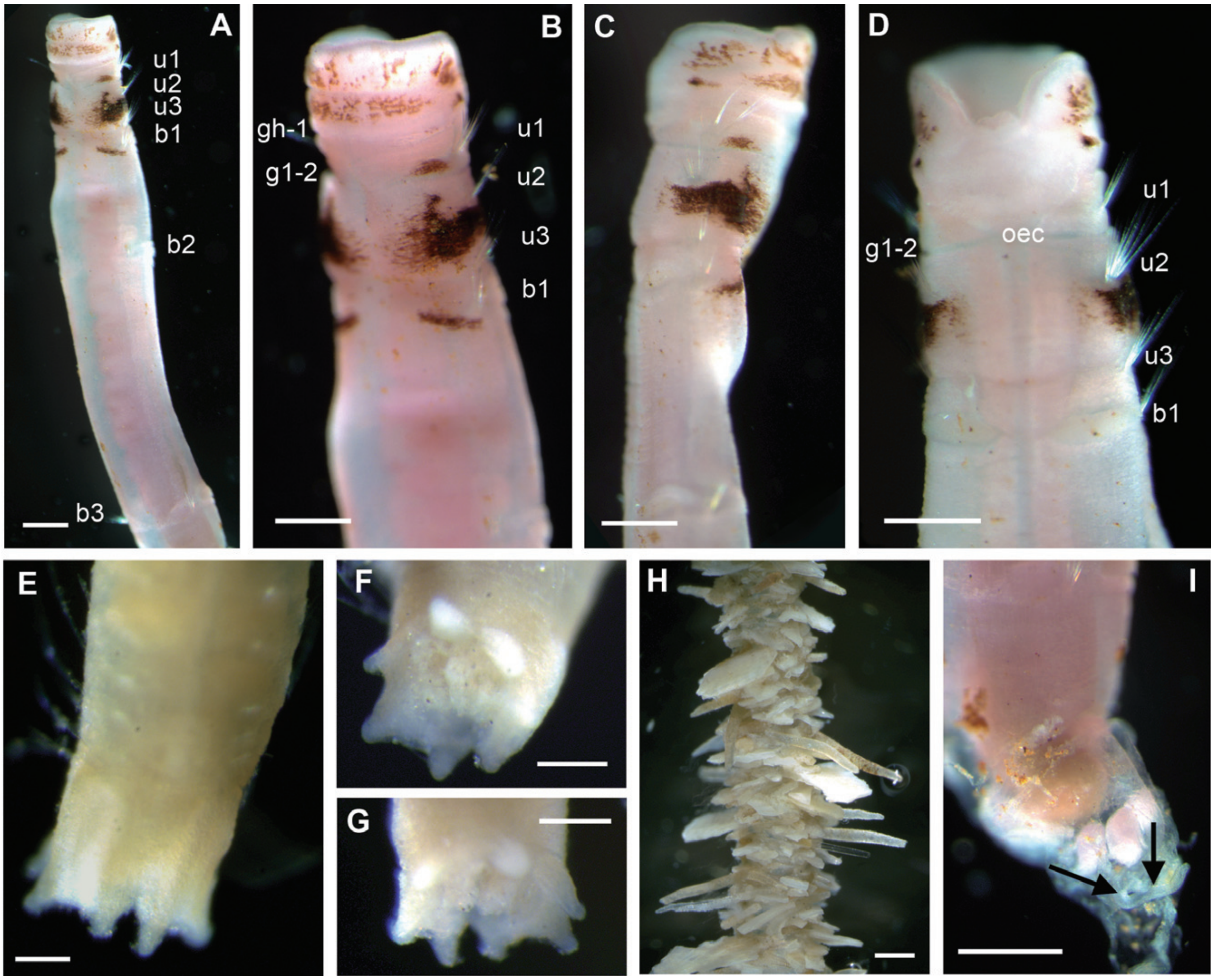

Figure 5. ***Galathowenia arafurensis* sp. nov.** AM W34017. A, anterior end, dorsal view. B, detail of head and anterior end, dorsal view. C, anterior end, lateral view. D, anterior end, ventral view. E, posterior end, ventral view. F, posterior end, showing anus and multilobed pygidium. G, posterior end, dorsal view. H, tube. I, posterior end of a fragment in regeneration, side view. Abbreviations: b1-b3, biramous segment 1 to 3; gh-1, groove between head and segment 1; g1-2, groove between segment 1 and 2; oec, oesophageal commissures; u1-u3, uniramous segments 1 to 3; arrows: regeneration appendices. Scale bars: A–D, H, I = 200 μm; E–G = 100 μm.

pygidium (Fig. 5F, G). Tube made out of shell fragments and sponge spicules overlapping like roof tiles (Fig. 5H). Colour in alcohol brownish or pale yellow, anterior body region with brown-red pigmented areas (Fig. 5A–D).

Variation: Only the holotype and one paratype (NTM W21073) are complete. Remaining specimens of similar width (0.6–0.8 mm) and pigmentation pattern. Some slight variation was observed on the relative length of the uniramous segments (Figs 5B vs. 6B). The pygidium of the paratype is also provided with seven digitiform lobes but this number could vary within the species as it does in other *Galathowenia* species (see below and Table 3). Incomplete specimens show filamentous prolongations of the tegument associated with the broken posterior ends (Fig. 5I). We interpreted them as 'regeneration processes' and they have also been found in other oweniids (see also for *Myriowenia* sp. below).

Ecological notes: The specimens were found only in the Arafura Sea (Fig. 14), in soft bottoms composed of foraminifera, dead molluscs, and detritus at depths between 92–233 m.

Etymology: This species is named after the Arafura Sea where the type specimens were collected.

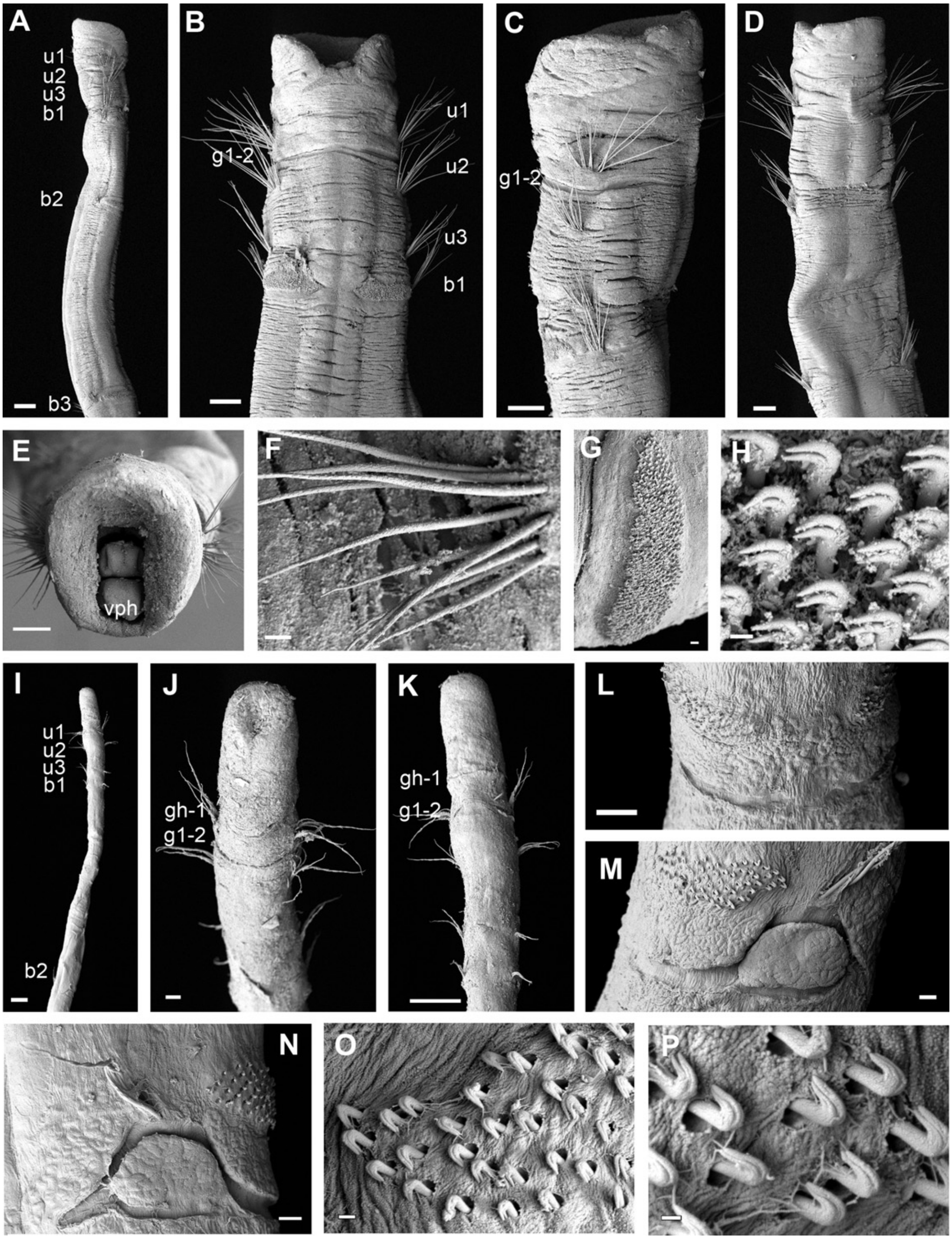

Figure 6. A–H, ***Galathowenia arafurensis* sp. nov.** A, anterior segments, lateral view. B, anterior end, ventral view. C, anterior end, lateral view. D, anterior end, dorsal view. E, mouth. F, anterior capillary chaetae. G, neuropodial uncini field, segment 5. H, uncini, same segment, oblique view. I–P, *Galathowenia* sp. I, anterior segments, dorsal view. J, anterior end, ventral view. K, anterior end, dorsal view. L, detail of groove between segment 1 and 2, ventral view. M, detail of lateral flap, segment 5. N, detail of lateral flap, segment 6. O, neuropodial uncinal field, segment 6. P, uncini, segment 6, oblique view. Abbreviations: b1-b3, biramous segment 1 to 3; gh-1, groove between head and segment 1; g1-2, groove between segment 1 and 2; u1-u3, uniramous segments 1 to 3; vph, ventral pharyngeal organ. Registration numbers: A–H, AM W34017: I–P, AM W37065. Scale bars: A = 200 μm, B–E = 100 μm; F, G, N = 10 μm; H = 2 μm; I, K = 100 μm, J, L, M = 20 μm; O = 2 μm; P = 1 μm.

Table 3. Comparison of ***Galathowenia arafurensis* sp. nov.** and other species of this genus with more than four pygidial lobes from different geographical areas

	Galathowenia pygidialis (Hartman, 1960)	*Galathowenia fragilis* (Nilsen & Holthe 1985)	*Galathowenia joinvillensis* (Hartmann-Schröder & Rosenfeldt, 1989)	*Galathowenia scotiae* (Hartman, 1978)	***G. arafurensis* sp. nov.**
Locality	California, USA and Mexico	Norwegian Sea	Joinville Island, Antarctica	Antarctica	Northern Territory, Australia
Length (mm)	57–90	30	36	32–64	28
Width (mm)	0.6–1	0.8	1.2	1–1.5	0.6
Uniramous segments	3	3	2*	3	3
Biramous segments	39–40	22	28	22–25	28
Eyespots	Absent	Absent	Absent	Absent	Present
RLUS	1.5:1:1	1:2:1	1:1*	1:2:1	1:1.5:1
Longest segment	6–7	5–6	3*	4†	8
Acicular notopodial chaetae	Absent	Absent	Absent	Absent	Absent
Unicinal teeth	Side by side	Oblique	Oblique	Oblique	Oblique
Pygidium	Seven to nine lobes	Five to six lobes	Around ten short lobes and one large dorsal	Five to 11 lobes‡	Seven lobes
Tube	Sand grains	Sand grains, foraminiferans, and sponge spicules	Sand grains	Sand grains	Shell fragments and sponge spicules
Pigmented prostomium	Absent	Absent	Absent§	Absent	Present
Transversal groove (between segments)	Present (1–2)	Present (1–2)	Absent	Present (1–2)	Present (1–2)

*Even though no type material was studied, it is probable that this species was described from incomplete specimens lacking the head and first segment (see also note† for evidence in other species) and therefore the longest segment is not the third but the fourth (second biramous).

†Although in the original description it was reported that the third segment is the longest, it has been demonstrated that specimens described were incomplete (Parapar, 2001: 408) and that it corresponds to segment 4.

‡According to Parapar (2001).

§The author mentions a darker anterior region but does not indicate any particular pigment pattern.

RLUS, relative length of uniramous segments.

Remarks: Galathowenia arafurensis sp. nov. shares with some other species of *Galathowenia* the presence of a pygidium provided with multiple lobes. These species are *Galathowenia pygidialis* (Hartman, 1960) from the Eastern Tropical Pacific, *Galathowenia scotiae* (Hartman, 1978) from Antarctica, *Galathowenia fragilis* Nilsen & Holthe, 1985 with boreal distribution, and *Galathowenia joinvillensis* (Hartmann-Schröder & Rosenfeldt, 1989), also from Antarctica. *Galathowenia arafurensis* sp. nov. differs from *G. pygidialis* in the arrangement of uncinal teeth, as *G. pygidialis* is the only species of the genus that has a side by side arrangement whereas in the rest of the species, including the one described herein, they are oblique. *Galathowenia joinvillensis* differs from the new species and others in the genus in the presence of only two uniramous segments instead of three. In addition, *G. arafurensis* sp. nov. is distinguished from this species and *G. fragilis* and *G. scotiae* by the presence of eyes, a pigmented anterior end and the presence of an unusual elongated segment 8, measuring around 20 times the length of the uniramous ones, three features absent in the three previously described species. The differences between *G. arafurensis* sp. nov. and other Australian species of *Galathowenia* described in the present study include the body size (more robust and broader in *G. arafurensis*), shape of the pygidium, the relative length of the anterior segments (RLUS), and pigment pattern of the anterior end. A species described from Indonesia, *Myriochele eurystoma* Caullery, 1944, that clearly belongs to the genus *Galathowenia* because of the shape of the prostomium, presence of ventral slit, and a groove between the head and the first segment and also between the first and the second one (Caullery, 1944: fig. 42A–D; Gibbs, 1971: fig. 15A), seems to share some features with *G. arafurensis* sp. nov. Nevertheless, the animals described were incomplete, lacking the pygidium, and the description is too poor for a complete comparison with the Australian material. This material was unavailable for study but a future comparison between the two species would be of interest.

GALATHOWENIA SP.

FIGURE 6I–P, TABLES 1,2

Material examined (Appendix 1): Queensland, Halifax Bay, north of Townsville, around 19°10′S, 146°37′E (44 specs from seven samples).

Description: Thin and fragile specimens, most broken and incomplete. Body cylindrical (Fig. 6I–K), around 7 mm long, 0.1 mm wide, with 18 chaetigers. Head elongated, truncated anteriorly, with terminal ciliated mouth extending midventrally as an elongated slit (Fig. 6J). A pair of ventrolateral brownish eyespots in prostomium. Two transverse grooves present, between head and first segment and first and second segments (Fig. 6J, K). Anterior three segments uniramous, each with notochaetae only. Second segment twice the length of first and third (RLUS = 1:2:1). Oesophageal commissures as white ventral longitudinal band with Y shape in anterior segments. First biramous segment similar in length to uniramous (Fig. 6I–K). Second biramous chaetiger (segment 5) longest, around eight times longer than wide. Only capillary notochaetae observed, with proximal third smooth and distal end ornamented with scales, with few chaetae in each fascicle (Fig. 6J, K). Neurochaetae present from chaetiger 4 in long and narrow ventral tori (Fig. 6L–N). Uncini arranged in five to seven transverse rows; each uncinus provided with two nearly equal curved teeth, slightly obliquely arranged, almost vertical and almost fused to each other (Fig. 6O, P). Anterior biramous segments with a lateral flap behind chaetae (Fig. 6M, N), connected ventrally by a ventral groove (Fig. 6L). Pygidium as a rim around anus, appearing as two low lobes under dissection microscope. Tube with thin secreted layer encrusted with small sand particles. Colour in alcohol brownish or pale yellow.

Ecological notes: Species only found in Halifax Bay (Fig. 14), in soft bottoms.

Remarks: Most specimens examined are small, incomplete, or damaged. Some of the relevant diagnostic features, like the presence of the parapodial flaps in the anterior biramous segments have been verified only in two specimens under SEM and are not seen under optical microscopy. The designation of these specimens to an already-described species or their description as a new one is not possible with the limited data available and the poor condition of the material.

GENUS *MYRIOCHELE* MALMGREN, 1867, EMENDED

Myriochele Malmgren, 1867; Blake, 2000; Parapar, 2006.

Myrioglobula Hartman, 1967.

Emended diagnosis: Body short and thick, tapering at both ends (cigar-like). Head lacking appendages, with anterior end rounded. Mouth terminal or slightly elongated ventrally but without a ventral slit and developed lips on the sides. Anterior one to three segments uniramous, subsequent ones biramous. Notopodia with capillary and acicular chaetae (latter type often absent in anterior-most chaetigers). Neuropodial tori with uncini bearing two similar-sized teeth generally vertically arranged, but obliquely in some species.

Type species: Myriochele heeri Malmgren, 1867, by original designation.

Remarks: Our phylogenetic analyses recover *Myrioglobula* species scattered within those traditionally assigned to *Myriochele* (Fig. 1A–D, unlike Sene-Silva, 2002). Although the support value for this clade is not strong (Fig. 1A), the morphological features maintaining the two genera cannot be justified. Differences between *Myriochele* and *Myrioglobula* were traditionally based on the number of uniramous segments (Hartman, 1967), with *Myrioglobula* characterized by having one (TF = U : B : B) and *Myriochele* two or three (TF = U : U : B and U : U : U). However, this feature has been demonstrated not to be informative because it varies within *Myriochele* (two or three segments), and there are species, such as *Myriochele robusta* Parapar, 2003c, which show a different pattern with a biramous second segment between the uniramous first and third (TF = 1:0–1:1–1:0 *sensu* Parapar, 2003c and U : B : U in this study). Features shared by the two groups are the shape of the body and head, presence of acicular chaetae, and arrangement of uncinal teeth; strong enough, according to the phylogenetic hypothesis presented here, to consider *Myrioglobula* as a junior synonym of *Myriochele*. We also propose here to include *G. australis* within the genus *Myriochele*, a species with acicular chaetae on parapodium and a poorly defined anteriorly truncated head and ventral slit (Parapar, 2003b; see Fig. 1D), regardless of the possible variation of the arrangement of uncinal teeth in the genus *Galathowenia*. *Myriochele* is the most morphologically diverse genus in the family Oweniidae with over 21 species known (Villalobos-Guerrero, 2009).

MYRIOCHELE HERUENSIS GIBBS, 1971
FIGURES 7, 8, 9A–D, TABLES 1, 4

Myriochele heruensis Gibbs, 1971: 190–191, figure 15B–G.

Material examined (Appendix 1): Victoria, Port Phillip Bay (828 specs); New South Wales (264 specs): Malabar, Pittwater, between 1 and 60 m, in sand and muddy sand.

Description of Australian specimens: Body long, cylindrical, narrowing at posterior end, measuring 4–20 mm long, 0.2–0.5 mm wide, consisting of 12–18 segments. Epithelium wrinkled. Head similar in width to rest of body and swollen dorsally resembling a ‘humpback’ and divided from the segmented region by a deep groove, oblique from side view (Figs 7A, B, 8A–C). Anterior shape of prostomium varies amongst specimens, appearing as rounded or truncated depending on the shape of the mouth opening and the development of the ‘humpback’, whose size changes between individuals. Pair of lateral red eyespots located on ventrolateral side, just below groove

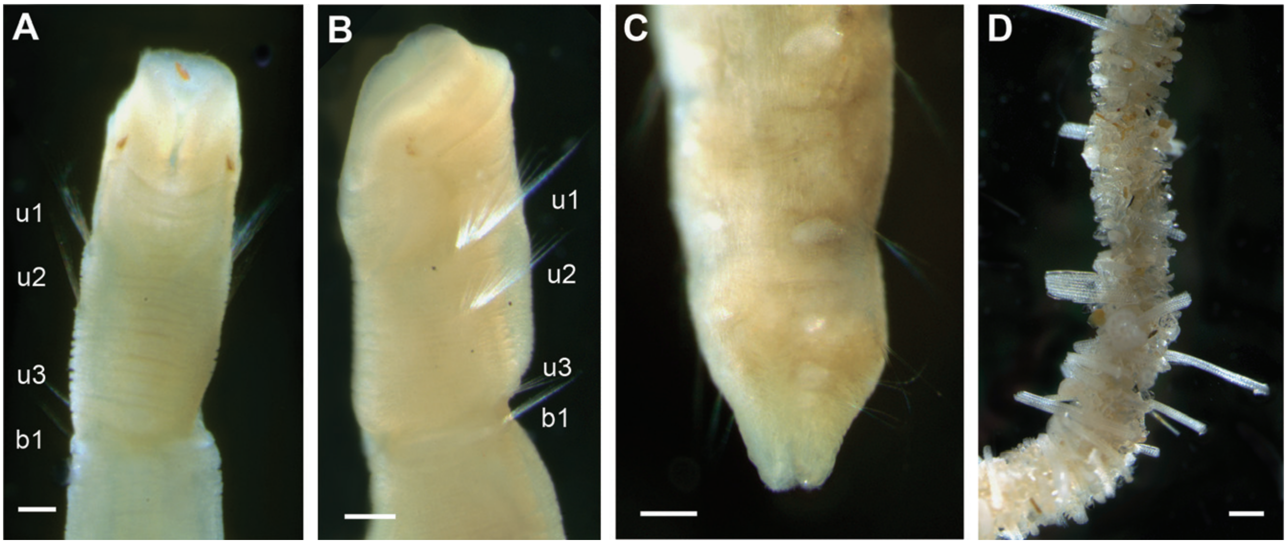

Figure 7. *Myriochele heruensis* AM W16316. A, anterior end, ventral view. B, anterior end, lateral view. C, posterior end, ventral view. D, tube. Abbreviations: b1, biramous segment 1; u1-u3, uniramous segments 1 to 3. Scale bars: A–C = 100 μm; D = 200 μm.

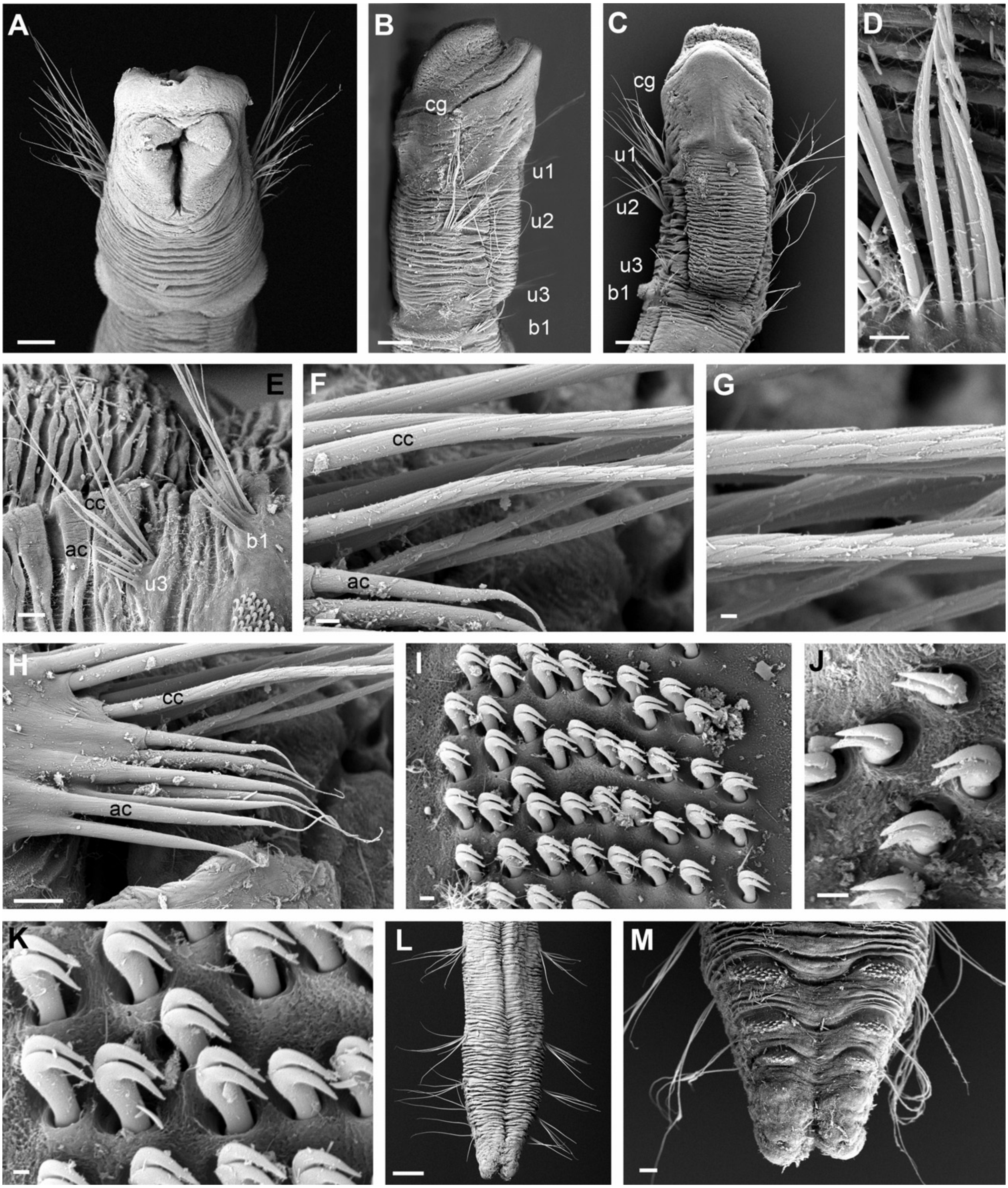

Figure 8. *Myriochele heruensis.* A, anterior end, frontal view. B, anterior end, lateral view. C, anterior end, dorsal view. D, capillary notochaetae, segment 2. E, notopodia segment 2 and 3. F, notochaetae segment 3. G, detail of scales covering capillary chaetae. H, acicular chaetae, segment 3. I, neuropodial uncini field (part), segment 3. J, detail of uncini, top view. K, detail of uncini, side view. L, posterior end, dorsal view. M, posterior end, ventral view. Abbreviations: ac, acicular chaetae; b1, biramous segment 1; cc, capillary chaetae; cg, cephalic groove; u1-u3, uniramous segments 1 to 3. Registration numbers: A, J, AM W37178; B–E, M, AM W37181; F–I, K, AM W37179. Scale bars: A–C, L = 100 μm; D, H = 10 μm; E, M = 20 μm; F = 3 μm; G, K = 1 μm; I, J = 2 μm.

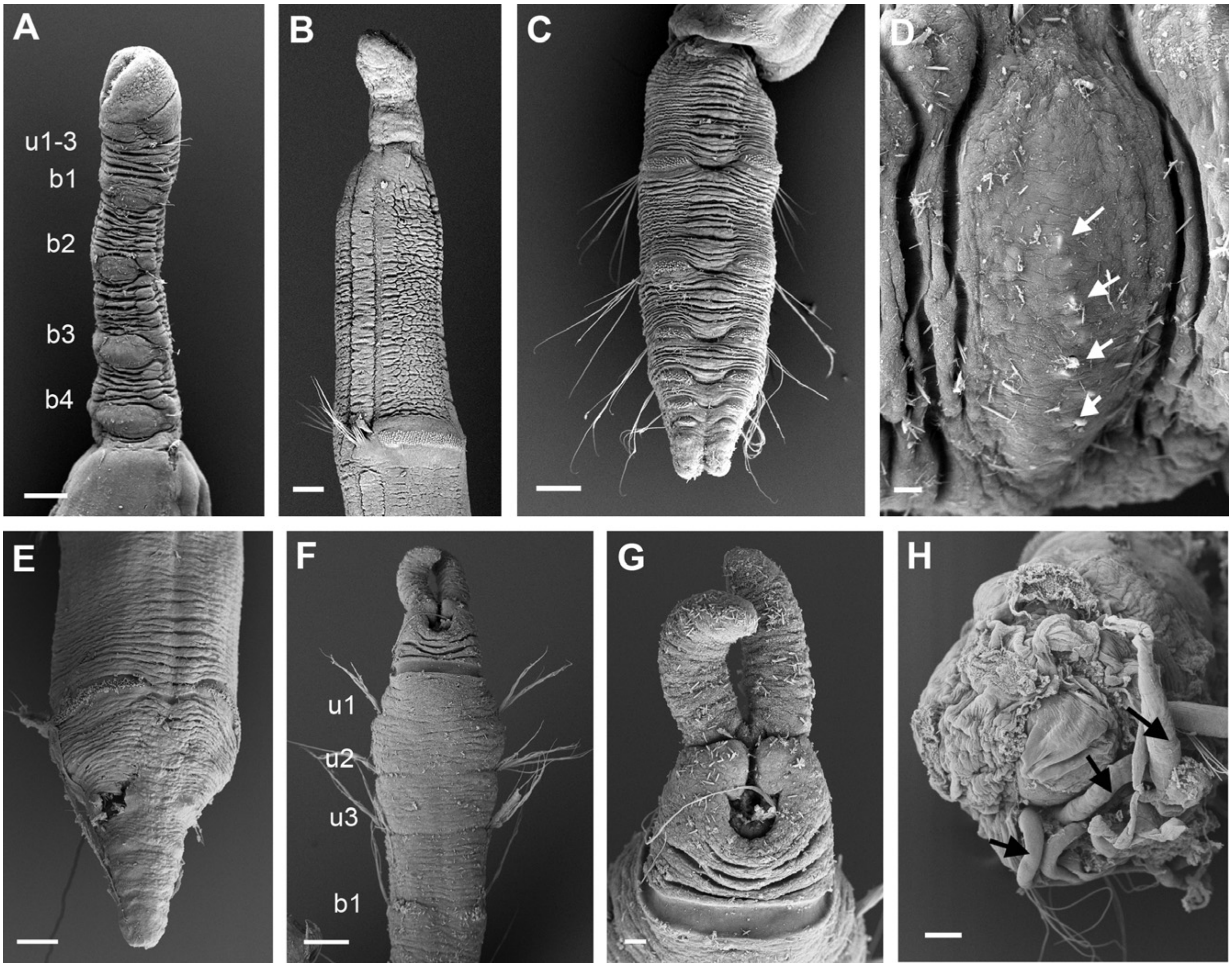

Figure 9. A–D, *Myriochele heruensis* in regeneration. A, anterior end regenerating, including uniramous and biramous segments. B, early stage of anterior end regeneration from a mid-body segment. C, regeneration of posterior end. D, detail of a torus with newly formed uncini at the point of piercing the cuticle (arrows). E, ***Myriochele australiensis* sp. nov.** Regeneration of posterior end. F–H, *Myriowenia* sp. in regeneration. F, anterior end, ventral view. G, head, ventral view. H, regeneration of anterior fragment with tubular projections (arrows). Abbreviations: b1-b4, biramous segment 1 to 4; u1-u3, uniramous segments 1 to 3. Registration numbers: A, D, AM W37182; B, AM W37179; C, AM W37181; E, AM W37201; F, G, AM W37185; H, AM W37186. Scale bars: A–C, E, G, H = 100 μm; D = 10 μm; F = 20 μm.

(Fig. 7A, B). Mouth anterior-ventral (Figs 7A, 8A), with two large lateral lips (Figs 7A, B, 8A, B). First three segments uniramous, with only notochaetae, no segmental grooves between them. First chaetiger about half length of second and twice that of the third one (RLUS = 2:4:1). Oesophageal commissures evident as a white ventral longitudinal band. First two chaetigers with long capillary notochaetae (Figs 7A, B, 8A–C), compared to subsequent ones. Acicular chaetae arranged in ventral-most part of fascicle, from segment 3 (Fig. 8E, F, H). Capillary chaetae with proximal part smooth or slightly striated (Fig. 8D) and mid and distal end with sculptures resembling scales (Fig. 8F, G); acicular chaetae smooth (Fig. 8H). Chaetigers biramous from segment 4. First biramous chaetiger at least 1.5 times as long as uniramous region; second and third biramous segments (chaetigers 5 and 6) twice the length of first biramous; fourth biramous chaetiger the longest, about three times longer than first biramous chaetiger (RLFBS = 1:2:2:3). Chaetae of first biramous segment (chaetiger 4) located just posterior to notochaetae of third chaetiger (Fig. 8E). Biramous segments with capillary and acicular chaetae on notopodia, similar to those described in anterior segments. Neuropodial tori with about ten rows of teeth on anterior segments (Fig. 8I). Uncini bidentate, with curved teeth and tips pointing upwards, obliquely

Table 4. Comparison of *Myriochele heruensis* and some morphologically similar species in the genus (‘*danielsseni*-group’)

	Myriochele danielsseni sensu Nilsen & Holthe, 1985	*Myriochele danielsseni sensu* Imajima & Morita 1987	*Myriochele striolata* Blake, 2000	*Myriochele heruensis* Gibbs, 1971
Type locality	Norway	Japan	California	Solomon Islands‡
Length (mm)	15–20	19–22	7–8	4–20
Width (mm)	0.65–0.9	0.8–1.0	0.25–0.35	0.2–0.5
Uniramous segments	3	3	3	3
Biramous segments	12	17	13–14	9–15
Eyespots	Present*	Present	Present	Present
RLUS	2:4:1	nd	2:4:1	2:4:1
First biramous chaetiger/uniramous region	1.3	1.3	> 1.5	1.3
Elongated segments (biramous chaetigers)	4–7 (1–4)	6–8 (3–5)	4–5 (1–2)	4–7 (1–4)
Most elongated segment (biramous chaetiger)	Seventh (fourth)†	nd	Fifth (second)	Seventh (fourth)
Acicular chaetae	Present	Present	Absent	Present
Unicinal teeth arrangement	Oblique	Oblique	Oblique	Oblique
Pygidium	Two short lobes	Two short lobes	Two short lobes	Two short lobes
RLFBS	1:1.5:1.5:1.5	nd	nd	1:2:2:3
Tube	Sand, spicules, and foraminiferans	Sand and foraminiferans	Sand	Sand, spicules, and foraminiferans
Pigment in prostomium	nd	Present	nd	Present
Regeneration	nd	nd	Anterior	Anterior and posterior

*Only in some populations.

†Although author’s drawings and formula of relative length do not correspond with this observation (see Nilsen & Holthe, 1985: fig. 5).

‡Although the types were collected in the Solomon Islands, the scoring of this table has been completed with additional material from Australia.

nd, no data available; RLFBS, relative length of first biramous segments; RLUS, relative length of uniramous segments.

arranged (Fig. 8J, K). Posterior chaetigers becoming shorter and narrower, ending in a narrow pygidium provided with two lateral lobes ((Figs 7C, 8L, M). Most specimens are colourless or pale yellow (Fig. 7A–C) but others have a row of pigment along the anterior margin of the head. Similarly, in some specimens, the eyespots seem to have faded with preservation. Several specimens showed anterior or posterior ends regenerating at different stages (Fig. 9A–D), with anterior regeneration being the most common. Tube encrusted with sea urchin spines and sand grains in no regular pattern (Fig. 7D).

Ecological notes: Myriochele heruensis was previously reported on sandy bottoms at 16 m depth (Gibbs, 1971). Our specimens were found in sheltered bays and estuaries of New South Wales and Victoria and in some deep water exposed environments (Fig. 14), on sand and muddy sand substrates from 15 to 85 m depth.

Distribution: The species was originally described from the Marovo Lagoon (Vangunu Island) in the New Georgia Group of the Solomon Islands (Gibbs, 1971). This is the only report of the species since the original description.

Remarks: We have assigned these specimens to *My. heruensis* as both populations share several morphological features considered as diagnostic. This species is characterized by the presence of a dorsal swollen area on the head, an anterior groove located across the dorsal surface of the prostomium and with an anterior margin of the head that varies amongst specimens. This head plasticity had already been reported by Gibbs (1971) who highlighted that the anterior groove is shallow when the prostomium is protracted and appears as a fold when it is contracted. Another two diagnostic features are the presence of a distinctive oblique cephalic groove (dorsolateral sulcus, according to Nilsen & Holthe, 1985) and an enlarged segment 7. Gibbs (1971) does not report the presence of acicular chaetae; in our opinion they probably were unnoticed by the author because other characters – body size, RLUS, shape of uncini and pygidium, and especially the head characteristics (prostomial groove and dorsal humpback) – are fully consistent with our material.

Other species of *Myriochele* sharing a similar head shape are *Myriochele danielsseni* Nilsen & Holthe, 1985, (European Atlantic and ?Japan) and *Myriochele striolata* Blake, 2000, (East Pacific) which also share with the new species the large number of transverse wrinkles along the body (numerous transverse ventral thoracic furrows, according to Blake, 2000). *Myriochele heruensis* differs from the original description of *Myrioc. danielsseni* in the relative number and the length of anterior biramous segments (see Table 4). Segment 7 (fourth biramous chaetiger) is the longest in the new species (RLFBS = 1:2:2:3) and segments 5–7 (second to fourth biramous chaetiger) are the longest in *Myrioc. danielsseni* (RLFBS = 1:1.5:1.5:1.5). The specimens identified as *Myrioc. danielsseni* from Japan (Imajima & Morita, 1987) and proposed here to be conspecific with *Myrioc. striolata* (Blake, 2000) differ from the original description of both species and from *Myrioc. heruensis* in that feature, as segments 6–8 are the most elongated (see Table 4 for comparisons amongst the species). *Myriochele heruensis* is distinguished from *Myrioc. striolata* by the overall number of body segments, with more than ten present in the new species and always with fewer than ten present in *Myrioc. striolata* (Blake, 2000), and in the position of the most elongated segment, being the fourth biramous chaetiger (segment 7) in *Myrioc. heruensis* and the second biramous chaetiger (segment 5) in *Myrioc. striolata*. Moreover, *Myrioc. heruensis* possesses acicular chaetae on notopodia from segment 3 whereas this type of chaetae is apparently absent in *Myrioc. striolata* (Blake, 2000). *Myriochele heruensis* and the Japanese population of *Myrioc. danielsseni* are the only species described as having pigment bands on the head, whereas the two other taxa have been described as lacking colour pigment (Nilsen & Holthe, 1985; Blake, 2000). These two species are also distinguished by the other features mentioned above (see also Table 4). *Myriochele danielsseni*, *Myrioc. striolata*, and *Myrioc. heruensis* form a well-characterized group of species sharing several morphological features, as stated above. Specimens described and illustrated by Gibbs (1972) as *Myriochele* sp., from the Cook Islands resemble those described herein as *Myrioc. heruensis*. However, some features cannot be compared because the three specimens of *Myriochele* sp. were incomplete and there is no mention of the acicular chaetae. It would be interesting to assess the relationships of this group of species with other species of *Myriochele* in a phylogenetic framework.

The finding of an individual split into two parts inside the tube, with each part in the process of regenerating the missing half, could be an indication of reproduction by schizotomy as described for *Myrioc. danielsseni* (Aguirrezabalaga, Gil & Viéitez, 2000). However, we cannot confirm this type of reproduction in our material.

***MYRIOCHELE AUSTRALIENSIS* SP. NOV.**

(FIGURES 9E, 10, 11, 14, TABLES 1, 5

Holotype: AM W20675, New South Wales, east of Long Reef, 33°44′43″S, 151°22′43″E, sand, 60 m, 13.iv.1989.

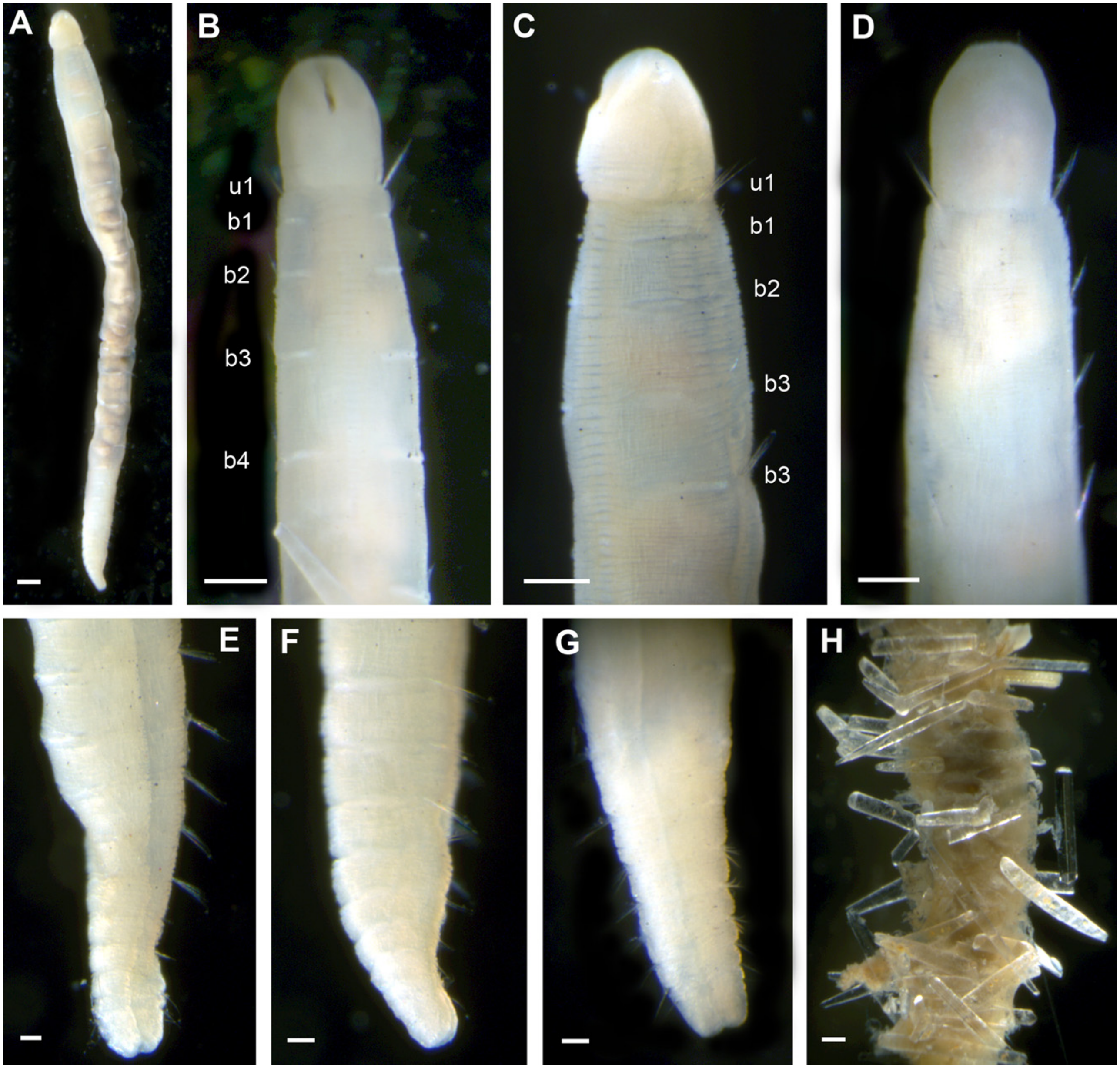

Figure 10. ***Myriochele australiensis* sp. nov.** A, complete specimen, lateral view. B, anterior end, ventral view. C, anterior end, lateral view. D, anterior end, dorsal view. E, posterior end, ventral view. F, posterior end, lateral view. G, posterior end, dorsal view. H, tube. Abbreviations: b1-b4, biramous segments 1 to 4; u1, uniramous segment 1. Registration numbers: A–H, paratypes AM W20675. Scale bars: A–D = 200 µm; E–H = 30 µm.

Paratypes: AM W37827, same sample (42 specs).

Other material examined (Appendix 1): New South Wales (175 specs): Malabar, Cobblers, Cape Banks, Wattamolla, Basspoint, Murramarang National Park; Victoria (1 spec.), Bass Strait.

Description of holotype: Specimen measuring 7.5 mm long and 0.5 mm wide, with 26 chaetigers. Body cylindrical in cross section (Fig. 10A) with tapering anterior and posterior ends (Figs 10B–G; 11A–C, L, M). Epithelium wrinkled. Longitudinal ciliated grooves present along body in ventral, lateral, and dorsal sides, the dorsal being wider and more obvious (Fig. 11C–E). Head rounded, slightly wider than the rest of body, with anterior margin slightly pointed from ventral view and distinctly set off from segmented region by constriction (Figs 10B–D; 11A–C). Eyespots not observed. First chaetiger uniramous (Fig. 11A, B); second and third biramous, increasing

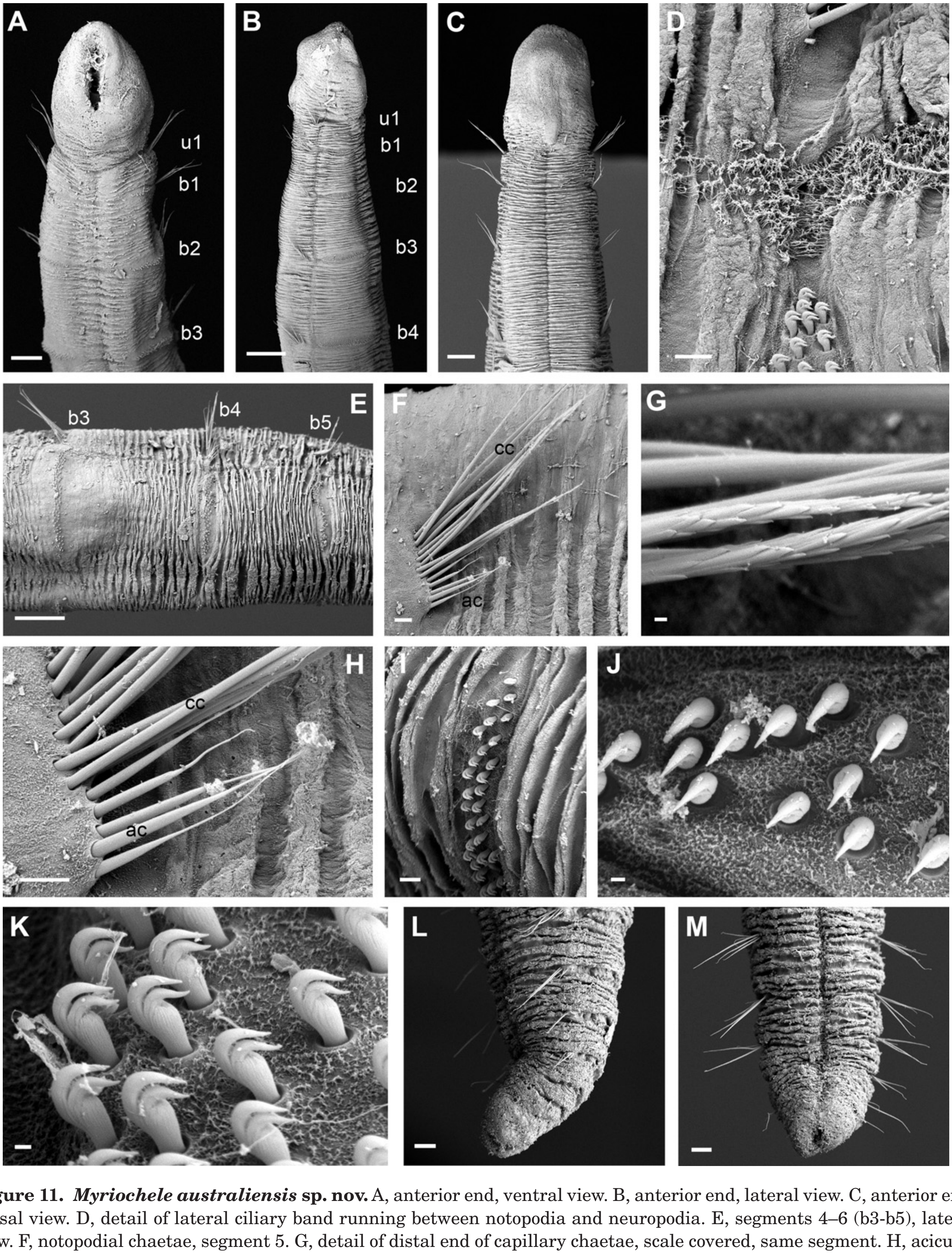

Figure 11. ***Myriochele australiensis* sp. nov.** A, anterior end, ventral view. B, anterior end, lateral view. C, anterior end, dorsal view. D, detail of lateral ciliary band running between notopodia and neuropodia. E, segments 4–6 (b3-b5), lateral view. F, notopodial chaetae, segment 5. G, detail of distal end of capillary chaetae, scale covered, same segment. H, acicular chaetae, same segment. I, uncinal field, segment 2. J, detail of uncini, top view. K, detail of uncini, side view. L, posterior end, lateral view. M, posterior end, dorsal view. Abbreviations: ac, acicular chaetae; b1-b5, biramous segments 1 to 4; cc, capillary chaetae; u1, uniramous segment 1. Registration numbers: A, AM W37200; B–D, F–I, K, L, AM W37198; E, AM W37199; J, M, AM W37197. Scale bars: A, C, E = 100 μm; B = 200 μm; D, F, H, I = 10 μm; G, J, K = 1 μm; L, M = 30 μm.

Table 5. Comparison of ***Myriochele australiensis* sp. nov.** and other morphologically similar species in the genus

	Myriochele antarctica (Hartman, 1967)	*Myriochele japonica* (Imajima & Morita, 1987)	*Myriochele malmgreni* (Parapar, 2006)	*Myriochele islandica* (Parapar, 2003a)	***Myriochele australiensis* sp. nov.**
Type locality	Antarctica	Japan	Iceland	Iceland	Australia
Shape of head	Rounded	Rounded	Rounded	Rounded*	Rounded
Body shape	Short and thick (maximum 15 × 2 mm)	Short (11 × 1 mm)	Small and slender (maximum 10 mm long)	Small and robust (5–10 mm long)	Small and robust (4–8 × 0.5 mm)
Number of segments	31	19–22	28	19	24–35
Posterior end (in section)	Rounded	Flattened	Rounded	Flattened	Rounded
First segment with acicular chaetae	nd	5	3	2	5
Number of capillaries in midbody	nd	12–13	9–10	40	8–13
Number of acicular chaetae in midbody	nd	8–9	8–9	20	5–9
RLAS	nd	1:1.5:2	1:1.5(2):5	1:2:4	1:2:3
Parapodia anterior segments (‘thoracic formula’)	U : B : B	U : B : B	U : B : B	U : B : B	U : B : B
Rows of uncini in neuropodial tori	3–4	2–4	3–5	2–5	2–4
Longest segments	nd	5–7	4–6	4–6	4–6 (5 longest)
Uncinal teeth arrangement	Horizontal	Vertical	Vertical	Vertical	Vertical
Eyespots	Absent	Absent	Absent	Absent	Present
Pygidium	Two large lobes	Two lobes and five papillae	Bilobed	Four lobes	Bilobed
Documentation of regeneration	nd	nd	nd	Anterior	Anterior

*The author described it as ‘rounded to quadrangular’.

B, biramous; nd, no data available; RLAS, relative length of anterior segments; U, uniramous.

in length progressively, with RLAS = 1:2:3 (Fig. 11A–C). Following chaetigers similar in length to posterior end, where they are progressively shorter and thinner (Fig. 10E–G). Notopodia with capillary chaetae with proximal third smooth and distal end with scale covering (Fig. 11G), diminishing in length ventrally within each fascicle. Acicular chaetae present from segment 5 (Fig. 11F), about one third the length of capillaries with no ornamentation and abruptly tapered tips (Fig. 11H). Neuropodial tori narrow and nearly rectangular, with uncini arranged in two to three irregular rows in anterior segments (Fig. 11I, J) to three to four in middle segments (Fig. 11K). Uncini with two teeth arranged vertically, similar in size, curved and with tips slightly pointing upwards (Fig. 11K). Posterior end cylindrical, distally tapered, with compressed segments slightly directed dorsally (Fig. 11L). Pygidium consisting of two low lateral lobes (Fig. 11M). Tube with cylindrical middle section and long tapering ends, covered with sponge spicules (Fig. 10H).

Variation: Specimens found to be between 4–8 mm in length and 0.4–0.6 mm in width with 24–35 segments, with the exception of those exhibiting anterior or posterior regeneration. The shape of the head varies amongst the specimens, being in some wider than the rest of the body but in others not obviously wider. Anterior shape also diverges amongst specimens, being pointed to rounded. Brownish lateral eyespots have been observed on the head of some specimens, but are not always present (like in the holotype), so they probably fade after preservation. Several specimens showed posterior end regenerating at different stages (Fig. 9E).

Ecological notes: Myriochele australiensis sp. nov. has been found in several localities in New South Wales, in open water environments (not estuaries) (Fig. 14) at around 60–80 m depth and mostly in sandy sediments. It is sympatric with *Myrioc. heruensis* and *G. quelis* sp. nov. (see Fig. 14 and Appendix 2).

Etymology: The name of this species follows the tradition of many species of the former genus *Myrioglobula* of naming the taxon after the country in which it was discovered, in this case Australia.

Remarks: Myriochele australiensis sp. nov. is characterized by the presence of only one anterior uniramous chaetiger, which using the traditional classification would have classified it as a species of *Myrioglobula*. This new species is unique amongst other species sharing this feature because it possesses peristomial eyes (Table 5), although this feature should be used with caution as eyespots appear to fade in preserved material and could have been overlooked in the other taxa. *Myriochele australiensis* sp. nov. is distinguished from *Myriochele antarctica* (Hartman, 1967) comb. nov. in the arrangement of the uncinal teeth, positioned in a vertical row in *Myrioc. australiensis* sp. nov. and other species of the genus but side by side in *Myrioc. antarctica* (Table 5). *Myriochele australiensis* sp. nov. shares with *Myriochele malmgreni* (Parapar, 2006) comb. nov., from Iceland, the shape of the pygidium with two blunt lobes; unlike *Myriochele islandica* (Parapar, 2003a) comb. nov., which has a tetra-lobed pygidium and *Myriochele japonica* (Imajima & Morita, 1987) comb. nov., with a pygidium consisting of two large lobes and five papillae. However, *Myrioc. australiensis* sp. nov. and *Myrioc. malmgreni* comb. nov. differ in the relative length of anterior segments (1:2:3 in the former and 1:1.5:5 in the latter) and in the appearance of the anterior-most acicular chaetae on notopodia, being in the fifth segment in *Myrioc. australiensis* sp. nov. and in the third in *Myrioc. malmgreni* comb. nov.

The uncini of *Myrioc. australiensis* sp. nov. (Fig. 11K) show a characteristic 'S' shape with a prominent subrostral process and the tip of the teeth pointing upwards slightly (Fig. 15L). These features were previously observed in three of the four species hitherto described in the genus *Myrioglobula*: *Myrioglobula japonica* (Imajima & Morita, 1987; Figs 9F, 10F), *Myrioglobula islandica* (Parapar, 2003a; Fig. 8C), and *Myrioglobula malmgreni* (Parapar, 2006; Fig. 11G) but not in the *Myrioglobula* type species: *Myrioglobula antarctica*.

Myriochele australiensis sp. nov. resembles *Myriochele minor* Caullery, 1944, recorded from the Flores Island, Indonesia, in the shape of the head, elongated and with a rounded anterior end, and in the shape of the mouth. However, they differ in thoracic formula, U : B : B in *Myrioc. australiensis* sp. nov. and U : U : U in *Myrioc. minor*; in the shape of the pygidium, bilobed in the new species and with three lobes (to dorsal and one ventral) in *Myrioc. minor*; and in the relative length of the anterior segments, RLAS = 1:2:3:3:4:3 in *Myrioc. australiensis* sp. nov. and RLAS = 1:1:1:1: 4 in *Myrioc. minor*.

GENUS *MYRIOWENIA* HARTMAN, 1960

Myriowenia Hartman, 1960; Blake, 2000.

Diagnosis: Head with large anterior grooved palps and bilobed prostomium; mouth anteroventral, with ventral pharyngeal organ. Breakage groove between head and first segment. First three segments uniramous, with capillary notochaetae. Biramous segments with capillaries on notopodia and neuropodial tori with fewer than five rows of bidentate uncini, with teeth arranged in a vertical position, dissimilar in size and proximal larger.

Type species: Myriowenia californiensis Hartman, 1960, by original designation.

Remarks: Members of this genus can be distinguished from others in the family by the presence of a pair of anterior grooved palps and anterior prostomial lobes. In addition, they display uncinal teeth dissimilar in size with the distal tooth being much smaller than the proximal one, a possible reason why some authors have considered this distal tooth as absent (e.g. Blake, 2000). The ornamentation of the capillary chaetae has also been proposed to be a possible distinguishing feature of *Myriowenia* as the 'scales' are smaller than in other genera (Blake, 2000).

MYRIOWENIA SP.

FIGURES 9F–H, 12 AND 13, TABLE 6

Material examined (Appendix 1): New South Wales (128 specs), south of Sydney: Cobblers, Wattamolla, Bass Point, Cape Banks and Marley, in sandy bottoms, 40–70 m.

Description: Largest complete specimen measuring 14 mm long and 0.8 mm wide, with 55 chaetigers. Body cylindrical in cross section (Fig. 12A–C), with slightly tapering posterior end. Epithelium wrinkled in head and anterior segments. No longitudinal ciliated grooves present. Nervous system evident as white ventral longitudinal band. Head region rounded, wider than rest of the body in most specimens, distinctly set off from segmented region by constriction (Figs 9F, G, 12A–F, 13A–D). Two anterior grooved palps similar in length to uniramous region (Figs 12A–F, 13A–C), with rounded anterior lobes on each base ((Figs 12E, 13A, E). Anteroventral mouth with ventral pharyngeal organ and dorsolateral fold present and exposed in some specimens (Fig. 13A, E). Eyespots not observed. First three chaetigers uniramous (Figs 12A, B, 13B), similar in length or first one slightly longer (Figs 12A, B, 13B); biramous segments also similar in length (Fig. 12A–C) to posterior end, becoming progressively shorter and thinner (Figs 12H, I, 13M). Notopodia with capillaries (Fig. 12G) with proximal end smooth and distal end with scale covering (Fig. 13F); diminishing in length ventrally within each fascicle. Acicular chaetae absent. Neuropodial tori narrow, with uncini arranged in two to three irregular rows in anterior and middle segments (Fig. 13G) to one short row consisting of one or two uncini in posterior segments (Fig. 13L). Uncini with two curved teeth, arranged one above the other, distal tooth smaller than proximal one (Fig. 13G–I). Posterior end cylindrical, distally tapered, with compressed segments; pygidium as a rim encircling anus (Figs 12H, I, 13M). Tube very thin and flexible only covered by a few fine sand grains, not heavily cemented. Several specimens with posterior ends exhibiting regeneration processes at the broken posterior end of the body ((Figs 9H, 12J–K). Colour of specimens pale yellow after preservation.

Ecological notes: Specimens found in sandy bottoms and at 40–70 m depths, in localities south of Sydney, New South Wales (Fig. 14).

Remarks: Three species of *Myriowenia* have been described so far, *Myriow. californiensis* Hartman, 1960, from California (Fig. 15H), and two others from the Gulf of Mexico, *Myriowenia gosnoldi* Hartman, 1965, (Fig. 15G) and *Myriowenia* sp. A Milligan, 1984 (see Table 6). Differences amongst these species have not been addressed in previous studies because in most cases insufficient material was available or its condition was not optimal to check intraspecific variation. For example, what has been interpreted as a cylindrical head in *Myriow. gosnoldi* and *Myriowenia* sp. A (Hartman, 1965; Milligan, 1984) has also been observed in some of the specimens from New South Wales (e.g. Fig. 12D) and could be because of the flexibility of this region, but certainly is not a diagnostic character of these species.

The presence of 'a pair of pygidial cirri' in *Myriow. gosnoldi* (Hartman, 1965; 347: fig. 44b) resembles the regeneration processes that we have also observed in some broken fragments. Some Australian specimens of *Myriowenia* sp., like other oweniids herein described, show a certain type of filamentous processes in the fragmented posterior body part. These processes resemble extensions of the body integument (Fig. 12J, K), resulting in a different appearance of the posterior end when compared with complete (intact) specimens, with the posterior segments being compressed and slightly thinner towards the low rim pygidium (Fig. 12H, I). Moreover, in some Australian specimens other processes appear to originate from the side pores of some midbody segments (Fig. 13J, K). The true composition of these processes and their function are unknown and deserve more investigation. The main character that separates *Myriowenia* sp. and *Myriow. gosnoldi* or *Myriowenia* sp. A is the absence of a collar membrane between the cephalic and the segmented region (present in both *Myriow. gosnoldi* and *Myriowenia* sp. A). *Myriowenia* sp. is therefore more similar to *Myriow. californiensis* (*sensu* Hartman, 1960 and Blake, 2000), in sharing

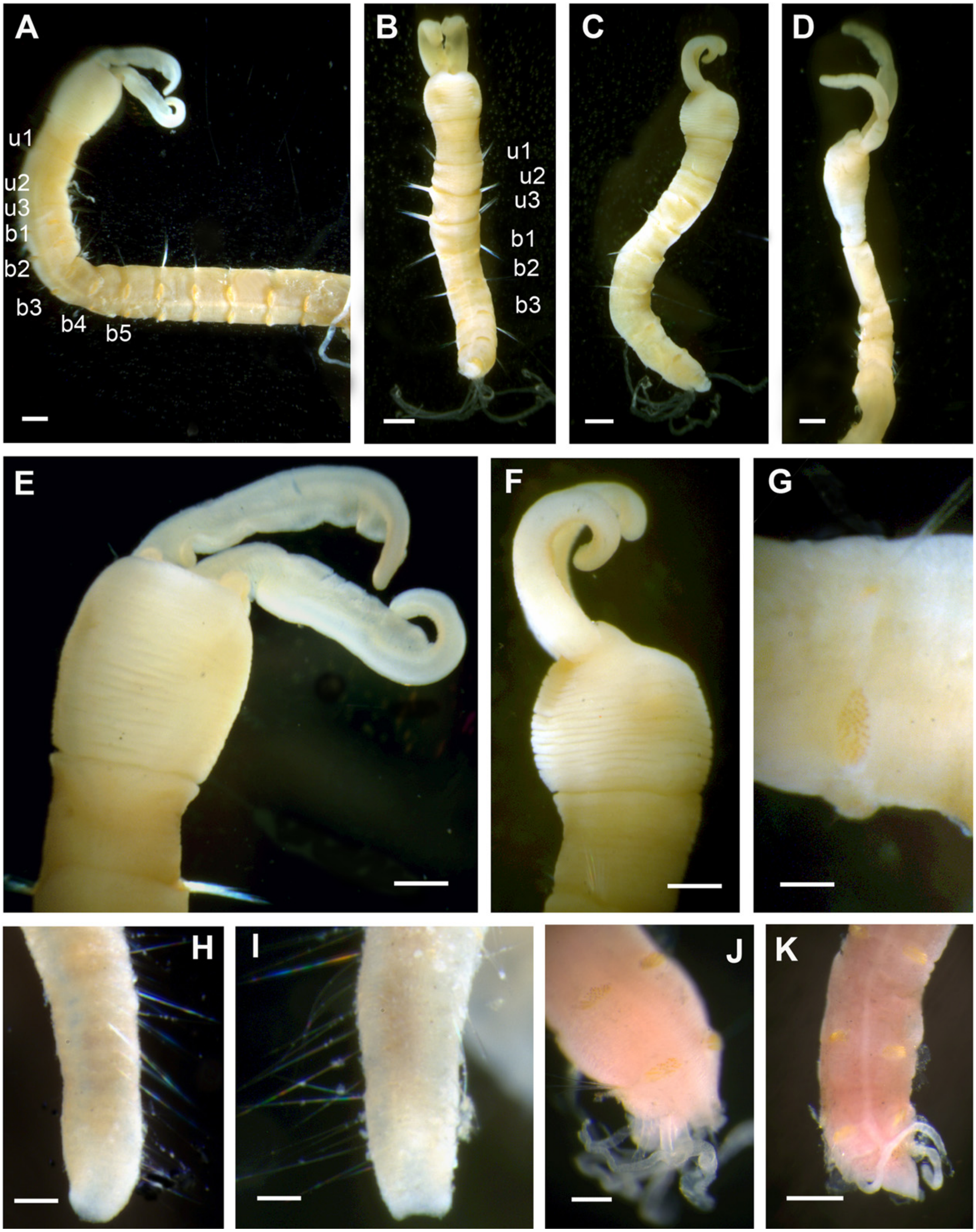

Figure 12. *Myriowenia* sp. A, specimen in lateroventral view. B, specimen regenerating posterior end, ventral view. C, specimen regenerating posterior end, lateral view. D, anterior end, lateral view. E, anterior end, ventral view. F, anterior end, lateral view. G, chaetiger 5, lateroventral view. H, posterior end, lateral view. I, posterior end, ventral view. J, regeneration of posterior end, dorsal view. K, regeneration of posterior end, ventral view. Abbreviations: b1-b5: biramous segments 1 to 5; u1-u3: uniramous segments 1 to 3. Scale bars: A–D = 400 μm; E, F = 200 μm; G = 50 μm; H–K = 100 μm.

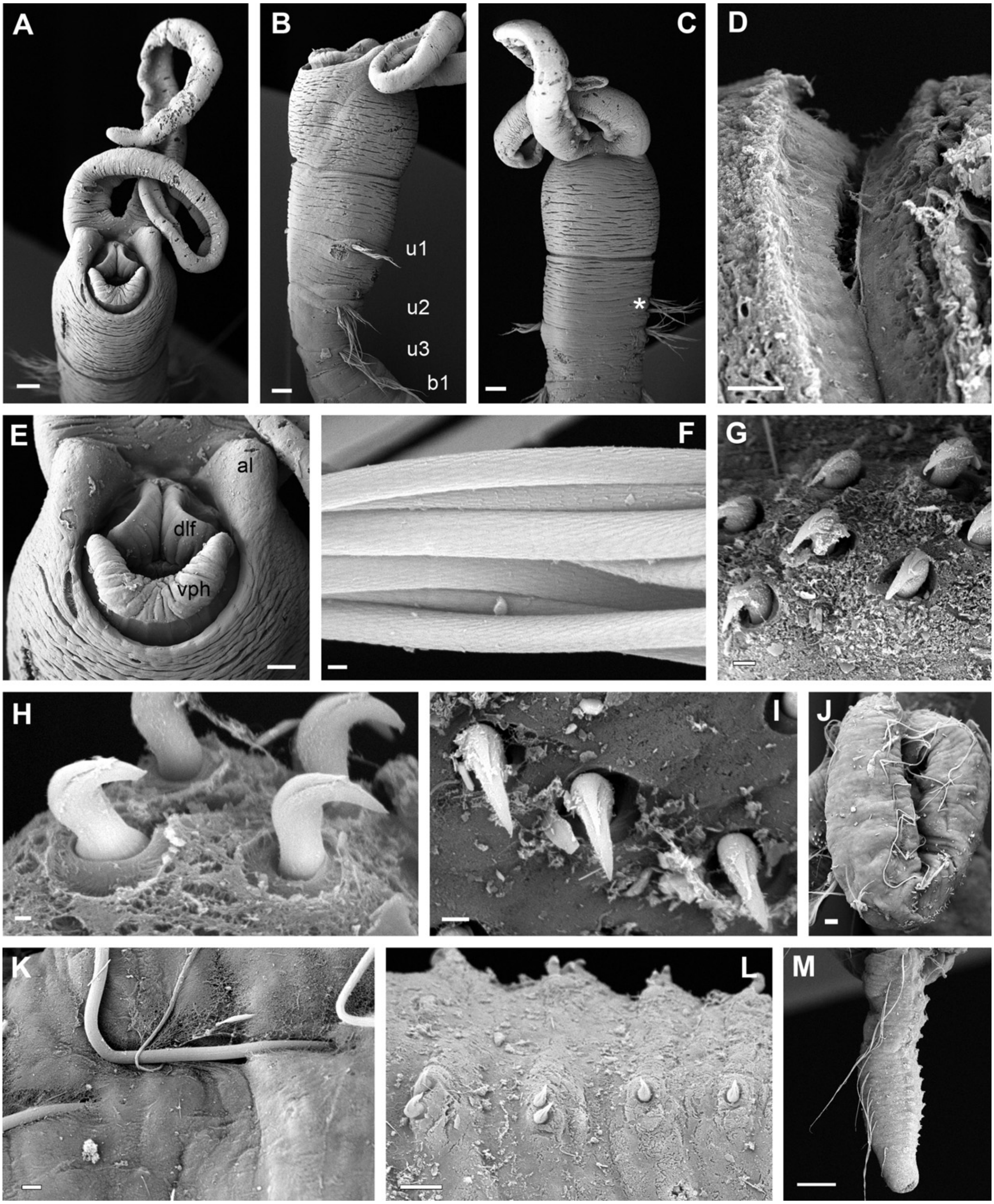

Figure 13. *Myriowenia* sp. A, anterior end, frontal view. B, anterior end, lateral view. C, anterior end, dorsal view. D, detail of cephalic groove (between head and first segment). E, detail of mouth opening and anterior head structures. F, notopodial capillary chaetae, segment 2. G, rows of uncini, segment 6. H, detail of uncini, segment 8, side view. I, detail of uncini, segment 6, top view. J, midbody, with parapodial tubular projection. K, detail of tubular projections. L, uncini in posterior segments. M, posterior end, lateral view. Abbreviations: al, anterior lobes; b1, biramous segment 1; dlf, dorsolateral folds; u1-u3, uniramous segments 1 to 3; vph, ventral pharyngeal organ; asterisk, asymmetrical first segment. Registration numbers: A–C, E, F, AM W37186; D, G, I, AM W37187; H, J, K, AM W37185; L, M, AM W37189. Scale bars: A–C = 200 μm; D, J = 20 μm; E, M = 100 μm; F, G = 2 μm; H, I = 1 μm; K = 3 μm; L = 10 μm.

Table 6. Comparison of *Myriowenia* sp. and the other previously described species in the genus

	Myriowenia californiensis Hartman, 1960	*Myriowenia gosnoldi* Hartman, 1965	*Myriowenia* sp. A Milligan, 1984	*Myriowenia* sp.
Type locality	California	Western North Atlantic	Gulf of Mexico	New South Wales, Australia
Size (mm; length vs. width)	> 22 × 1.3*	> 20 × 1†	29 × 1	14 × 18
Number of segments	> 29*	> 10†	max 32	max 55
Collar on anterior margin of segment 1	Absent	Present	Present‡	Absent
Uniramous segments relative length (length/width)	Short	Long	Short	Short
Chaetae in uniramous parapodia	12–15*	nd	Around 35	15–24
Tentacle-like pygidial cirri	Absent	Present†	Absent	Absent
Habitat	Mud or mixed sediments, up to 106 m	97–530 m	Fine sand, 12–33 m	Sand, around 60 m

*According to Blake (2000).

†The specimen described by Hartman (1965) is probably an anterior fragment undergoing regeneration.

‡Segment 2 according to author's description, but not from drawings (Milligan, 1984: fig. 46-4).

nd, no data available.

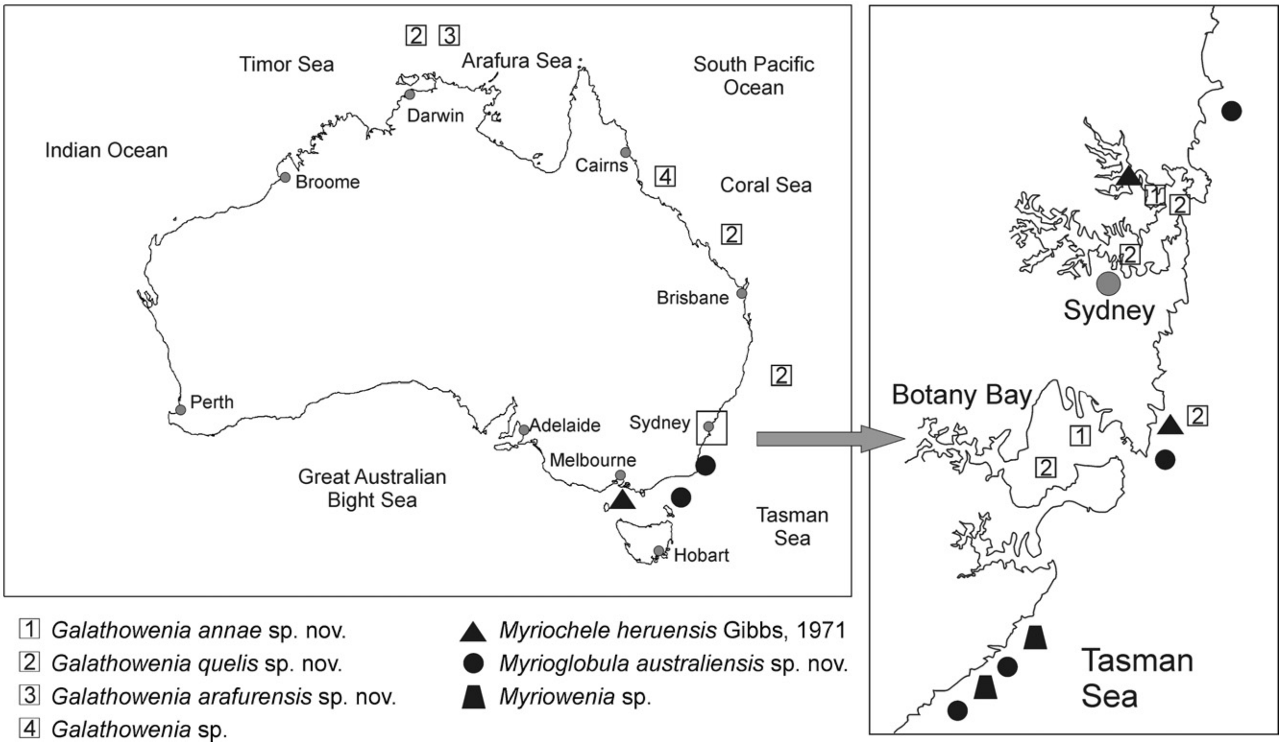

Figure 14. Distribution of Australian oweniids except for members of genus *Owenia*.

the presence of short uniramous segments. However, because the pygidium and posterior segments have not been described in *Myriow. californiensis*, we cannot compare these two, probably disjunct, *Myriowenia* species in detail.

OWENIA DELLE CHIAJE, 1844, EMENDED

Owenia Delle Chiaje, 1844; Nilsen & Holthe, 1985; Blake, 2000.

Ammochares Grube, 1846.

Ops Carrington 1865.

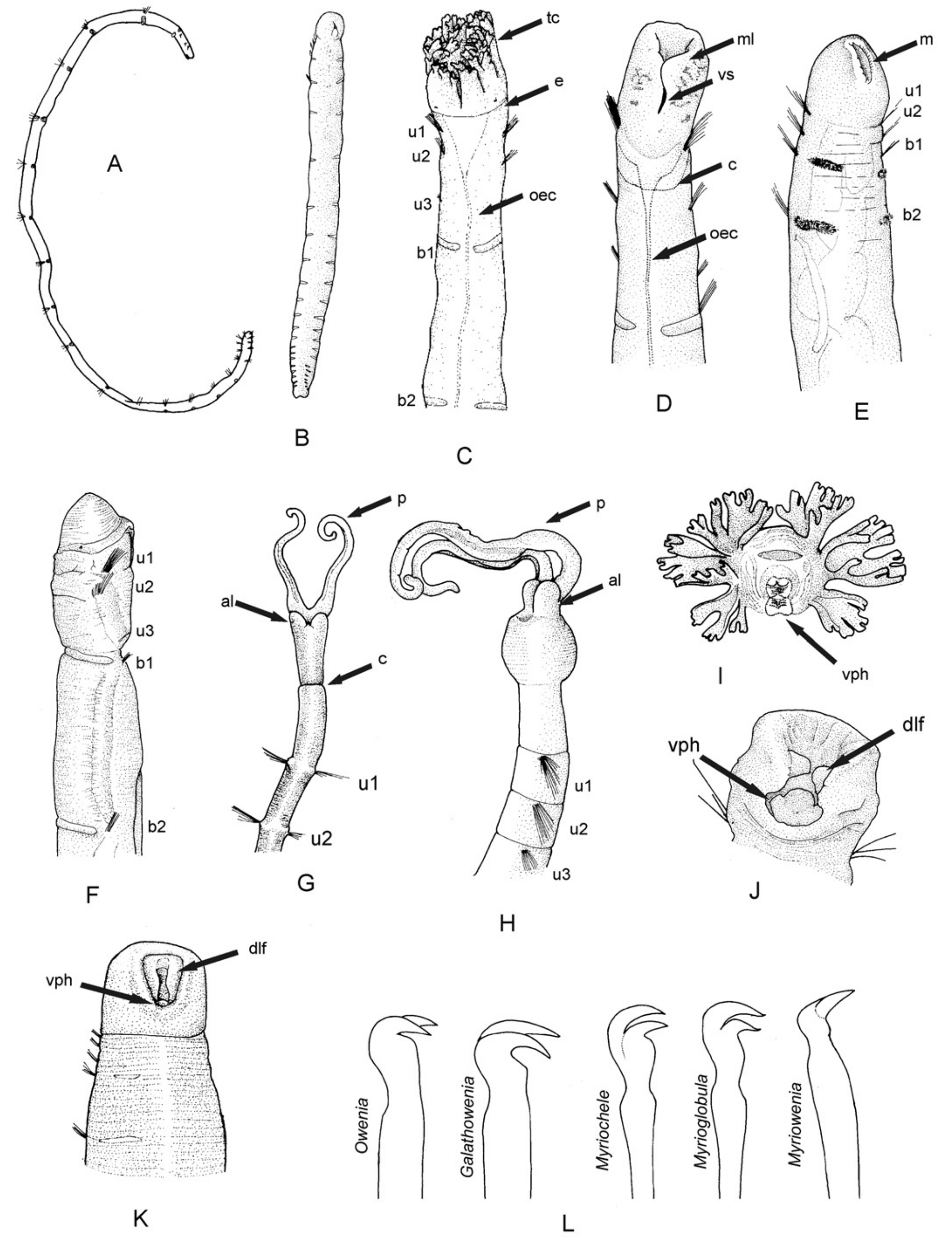

Figure 15. Stylized drawings of main morphological features in some representative species of Oweniidae genera (all redrawn from originals with permission). A, *Galathowenia oculata*. B, *Myriochele heeri*. C, *Owenia fusiformis*. D, *Galathowenia oculata*. E, *Myriochele olgae*. F, *Myriochele danielsseni*. G, *Myriowenia gosnoldi*. H, *Myriowenia californiensis*. I, *Owenia fusiformis*. J, *Galathowenia oculata*. K, *Myriochele heeri*. L, generalized drawings of disposition of the uncinal teeth in all genera. A, after Milligan (1984: 46–49, fig. 46.6a). B, after Nilsen & Holthe (1985: 20, fig. 3B). C, after Hartmann-Schröder (1996: 477). D, after Imajima & Morita (1987: 95, fig. 6). E, after Blake (2000: 112, fig. 5.5). F, after Imajima & Morita (1987: 93, fig. 5). G, after Hartman (1965: 347, fig. 44a). H, after Hartman (1960: 209, fig. 16.5). I, after Drasche (1885: plate 1, fig. 2). J, after a SEM picture in Purschke & Tzetlin (1996: 4, fig. 10B). K, after Parapar (2006: 530, fig. 7A). L, from diverse sources cited above. Abbreviations: al, anterior lobes; b1-b2, biramous segments 1 to 2; c, collar; dlf, dorsolateral folds; e, eyespots; m, mouth; ml, mouth lips; oec, oesophageal commissure; p, palps; tc, tentacular crown; u1-u3, uniramous chaetiger and position on body; vph, ventral pharyngeal organ; vs, ventral slit.

Emended diagnosis: Body thick and rigid. Head with prostomial tentacular crown. Anterior elongate mouth surrounded by membranous lips. Anterior three segments with capillaries only; third notopodia dorsal with respect to other anterior notopodia. Biramous segments with capillaries on notopodia and more than 20 irregular rows of bidentate uncini with teeth always arranged side by side on neuropodial tori. Pygidium as a terminal rim or with a pair of weakly developed lobes. Tube generally tapering towards both ends and covered with foreign objects imbricated like roof tiles.

Type species: Owenia fusiformis Delle Chiaje, 1844, by original designation.

Remarks: Some of the features on the tree (Fig. 1B) that appear as synapomorphies of this genus, such as the presence of a peristomial collar or the presence of eyespots, are actually absent in some species not considered in the present study (see for example Ford & Hutchings, 2005) and therefore they have not been included in this emended diagnosis. The type species was widely reported from around the world from intertidal to deep waters (e.g. Hartman, 1959; Dauvin & Thiébaut, 1994). However, more recently this cosmopolitan pattern has been questioned and a series of cryptic species have been described (e.g. Koh & Bhaud, 2001; Koh *et al*., 2003; Ford & Hutchings, 2005) or genetic lineages suggested (Jolly *et al*., 2006). Suites of new characters have been shown to be useful to separate species (e.g. Blake, 2000; Koh & Bhaud, 2003; Ford & Hutchings, 2005).

AUSTRALIAN SPECIES OF *OWENIA*

Within Australian waters, three species of *Owenia* have been described recently (Ford & Hutchings, 2005) and are not dealt in detail herein. They are distinguished from each other in minor morphological features such as the absence (*Owenia bassiensis* Ford & Hutchings, 2005) or presence (*Owenia australis* Ford & Hutchings, 2005 and *Owenia mirrawa* Ford & Hutchings, 2005) of the peristomial collar and the level and relative length of the ramifications in the tentacles forming the tentacular crown.

DISCUSSION

POSITION OF OWENIIDAE

The relationships of Oweniidae with other polychaetes have been debated for some decades with conflicting points of view (Liwanow & Porfirjewa, 1967; Bubko, 1973; Rieger, 1976, 1988; Smith *et al*., 1987; Minichev & Bubko, 1992; Westheide, 1997; Eeckhaut *et al*., 2000; Rousset *et al*., 2004; Struck *et al*., 2007, 2008; Zrzavý *et al*., 2009). Morphological data suggest that the presence of monociliated cells (Gardiner, 1978) and the nephridial type in the mitraria larvae (Smith *et al*., 1987) are plesiomorphic conditions (Rieger, 1976; Smith *et al*., 1987) and are indicative of the basal position of the oweniids within the annelid tree (Rieger, 1986; Smith *et al*., 1987; Westheide, 1997). These conclusions are also supported by some molecular studies (Struck *et al*., 2008; Zrzavý *et al*., 2009). Nevertheless, other authors advocate a close relationship of Oweniidae and Siboglinidae, a more derived group of Annelida, based on the presence of the intra-epidermal nerve cord (Rousset *et al*., 2004; Struck *et al*., 2007; Capa *et al*., 2011) and the type of hooks (Meyer & Bartolomaeus, 1996). In the present analyses, based only on morphological data, a close relationship of Oweniidae and Magelonidae is suggested (with low support) based on the absence of nuchal organs, fusion of prostomium and peristomium, presence of ventral buccal organ, and monociliated epidermal cells. These results should however be taken with caution. The absence of nuchal organs could well be interpreted as a secondary loss that has also occurred in some other polychaetes (Purschke, 1997, 2005). The fusion of prostomium and peristomium in *Magelona*, being limited to the lips (Rouse & Fauchald, 1997), needs further investigation (Rouse & Pleijel, 2001) as there are some opposing argu-

KEY TO OWENIIDAE GENERA

1\. Head with a tentacular crown, uncini with teeth similar in size and arranged side by side .... *Owenia*
– Head and uncini different 2
2\. Head with a pair of long and grooved palps and with anterior lobes, uncini with dissimilar sized teeth arranged vertically (one above the other) .... *Myriowenia*
– Head and uncini different 3
3\. Anterior end truncated, mouth terminal, continuing ventrally as a slit, breakage groove between first and second segment, notopodia with only capillary chaetae, uncini with teeth of similar size and generally arranged obliquely .... *Galathowenia*
– Anterior end rounded, mouth terminal or slightly ventral but without a ventral slit, notopodia with capillary and acicular chaetae; uncini with teeth of similar size and generally arranged vertically .... *Myriochele*

KEY TO AUSTRALIAN OWENIIDAE

1. Head with a tentacular crown (*Owenia*) 2
– Head without a tentacular crown 4
2. Three pairs of branchiae, peristomial collar absent .... *Owenia bassiensis*
– Four pairs of branchiae, peristomial collar present 3
3. Branchiae lacking any major ramification .... *Owenia australiensis*
– Branchiae with several ramifications at base of branchial crown .... *Owenia mirrawa*
4. Head with a pair of palps, long and grooved .... *Myriowenia* sp.
– Head without palps 5
5. Head rounded, mouth terminal or slightly elongated ventrally but not forming a ventral slit, capillary and acicular chaetae present (*Myriochele*) 6
– Head elongated and truncated anteriorly, mouth terminal continuing ventrally as a slit; only capillary chaetae present (*Galathowenia*) ....
6. Three uniramous anterior segments, head provided with a dorsal bulge and an oblique cephalic groove .... *Myriochele heruensis*
– One uniramous anterior segment, head rounded with no bulge or oblique cephalic groove .... ***Myriochele australiensis* sp. nov.**
7. Body slender, thread-like, about 15 mm long and 0.2 mm wide, pygidium with two blunt lobes or three short dissimilar lobes 8
– Body robust, about 30 mm long and 0.6 mm wide, head region with large brown-red pigment spots; pygidium with seven to eight lobes of similar size .... ***Galathowenia arafurensis* sp. nov.**
8. Head region with brown-red pigment spots; pygidium with three digitiform lobes of different sizes .... ***Galathowenia annae* sp. nov.**
– Head region without brown-red pigment spots; pygidium rim-liked or with two low lobes 9
9. At least segments 5 and 6 with tegumental flaps behind notopodia* .... *Galathowenia* sp.
– No flaps behind notopodia .... ***Galathowenia quelis* sp. nov.**

*Character only discernible using SEM. This species is still not fully characterized.

ments suggesting that it is recognizable behind the prostomium (e.g. Jones, 1968; Hutchings, 2000; Aguirrezabalaga, Cebeiro & Fiege, 2001). The presence of a buccal organ is also common in several polychaete groups (Orrhage, 1973; Purschke & Tzetlin, 1996; Tzetlin & Purschke, 2005) that are not necessarily related (e.g. Zrzavý *et al.*, 2009). The position of the Magelonidae has still not been assessed and contradicting hypotheses have been proposed. It has generally been related with spioniform taxa (e.g. Fauchald, 1977) or within Spionida (*sensu* Rouse & Fauchald, 1997) but analyses of molecular data suggest the paraphyly of Spionida (e.g. Rousset *et al.*, 2004, 2007; Zrzavý *et al.*, 2009) and sister-group relationship of magelonids has not been assessed. Magelonidae have been related to some cirratuliforms not included in Spionida *s.s.* (Rousset *et al.*, 2004), to protrodrilids (Rousset *et al.*, 2007), or have a variable position depending on the type of analyses and data sets (Zrzavý *et al.*, 2009). If the magelonid terminal is omitted from the analyses, Siboglinidae is recovered as a sister group of Oweniidae in nonweighted and implied weighted data sets (as suggested by Liwanow & Porfirjewa, 1967; Rouse & Fauchald, 1997; Eeckhaut *et al.*, 2000; Rousset *et al.*, 2004; Struck *et al.*, 2007; Capa *et al.*, 2011).

OWENIIDAE RELATIONSHIPS AND CHARACTER TRANSFORMATION

Our results endorse the monophyly of the Oweniidae (as did Sene-Silva, 2002) and four of the traditional oweniid genera if some synonymizations and nomenclatural changes are carried out. The monophyly of *Owenia* and *Myriowenia* has never been questioned owing to the presence of their characteristic head appendages (tentacular crown and grooved palps, respectively). However, the position of these groups differs in the literature. The hypothesis proposed by Sene-Silva (2002) recovered *Myriowenia* as the basal oweniid and *Owenia* as the most derived. Other authors (e.g. Nilsen & Holthe, 1985) also suggested this hypothesis based on the arrangement of uncinal teeth, with vertically arranged teeth in *Myriowenia* as the plesiomorphic condition, also found in other polychaetes, and side by side in *Owenia* as the apomorphic condition. In our hypothesis the position of *Owenia* depends on methodological procedures and although its position in the nonweighted analyses is uncertain, low concavity values topologies support the hypothesis of the apomorphic condition of the uncini with side by side teeth (Fig. 1C). However, the results with higher values of *k* imply that the oblique arrangement of uncinal teeth is the derived condition (Fig. 1D).

The genus *Galathowenia* was defined by the shape of the prostomium with a ventral cleft (Kirkegaard, 1959) as opposed to the rounded anterior end in *Myriochele* (Kirkegaard, 1959, 1983; Fauchald, 1977; Blake, 1984, 2000; Parapar, 2001, 2003b, 2006), although this genus has been considered a junior synonym of *Myriochele* by some authors (e.g. Blake & Dean, 1973; Nilsen & Holthe, 1985; Hartmann-Schröder, 1996; Cantone & Di Pietro, 1998; Sene-Silva, 2002). After our analyses (Fig. 1C, D), we consider this genus as a valid taxon based on the shape of the head. We consider that the results obtained by Sene-Silva (2002) could be explained because no direct observation of specimens was carried out and the character scoring was performed from the literature (see Parapar, 2006, for further comments). Moreover, Sene-Silva's results were incorrectly interpreted because some of the terminal taxa in his study, such as *G. pygidialis* and *G. fragilis*, were considered as members of *Myriochele* instead of *Galathowenia* (Blake, 2000; Parapar, 2003a).

As a consequence of our results, with *Myrioglobula* paraphyletic and its species recovered scattered within *Myriochele* (Fig. 1A–D), we propose the former as a junior synonym of the latter. Some years ago, Parapar (2003c, 2006) proposed the use of the *Myriochele–Myrioglobula* group after finding that the number of anterior uniramous segments showed high interspecific variability and that some species were characterized by having an alternating uniramous/biramous pattern. Members of this clade share the presence of acicular chaetae with an elongated tapering distal end and a smooth surface, unique amongst polychaetes, and the shape of the head, similar in width to the segments and with a rounded anterior margin. Some authors have suggested *Myrioglobula* as a basal oweniid because of the presence of one uniramous anterior segment, a feature shared with sabellids and terebellids (Meyer & Bartolomaeus, 1996), but this hypothesis is rejected herein and the presence of one uniramous segment is considered as a convergence in some species.

The shape of the uncini and arrangement of their teeth is a character frequently used in oweniid generic and species diagnoses. According to our phylogenetic hypothesis, this feature is informative and unambiguously characterizes *Myriowenia*, with teeth arranged vertically and *Owenia*, with side by side teeth. The teeth arranged obliquely was also one of the synapomorphies of the *Galathowenia–Myriochele s.s.* clade in some of the analyses (Fig. 1D), but this was not the case either in the nonweighted data set analyses or when the concavity values were low (Fig. 1A–C). Most *Galathowenia* show teeth similar in size, displayed in an oblique arrangement, but there is one exception, *G. pygidialis*, not included in our analyses, with teeth in a side by side position (Hartman, 1960; Blake, 2000). Members of *Myriochele s.s.* bear similar-sized teeth in a vertical arrangement, with the exceptions of *G. australis* (transferred to this clade in the present paper) and *Myrioc. heruensis*, which have them in an oblique position. Similarly, all the described species within the genus *Myrioglobula* show all the teeth in this vertical arrangement, with only the exception of *Myriog. antarctica*, the type species of the genus.

CONCLUSIONS

The reconsideration of morphological features and the phylogenetic analyses of the type species and other members of the Oweniidae have improved our understanding of the relationships of these polychaetes and the systematics of the group. However, there are still some matters that need further investigation. These include resolving the position of Oweniidae within the annelid tree and some of the generic relationships. Owing to the difficulty of finding additional external morphological characters in such morphologically simple forms, we suggest that the use of DNA sequence data to assess these issues could be illuminating.

The revision of the oweniid fauna in Australia has revealed a higher diversity than previously known. Four species belonging to the genus *Galathowenia*, two belonging to *Myriochele*, and one to *Myriowenia* were registered after the study of museum collections, with four of them described here as new. Descriptions of two other species can be undertaken when new material becomes available or a revision of the genus *Myriowenia* is undertaken. Nevertheless, we suspect that this is only part of the picture because there are wide collection gaps in most of Western Australia, South Australia, and in deep waters (deeper than 100 m). Future collecting in these geographical areas and environments will almost certainly increase the oweniid diversity in Australia. Our results, together with the three *Owenia* species recently described (Ford & Hutchings, 2005), suggest a high endemicity of members of the group in Australia. However, collections from nearby archipelagos should also be studied and compared with the Australian fauna in order to confirm this endemicity.

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APPENDIX 1

MATERIAL EXAMINED

***Galathowenia annae* sp. nov.** A total of 74 specimens examined.

New South Wales, Australia (this study).

Botany Bay: 73 specimens in total. AM W37222-37228 and unregistered material (5 samples), approximately 33°58′S, 151°12′E, 13–18 m, fine sand and mud, (65 specs), AM W37208, W37064, [4 specs on scanning electron microscopy (SEM) pins]; unregistered material, F.A.C. study 1992 by AM Stn G1-1-2 (2 specs); AM W23543-23645, Weeney Bay, 34°01′3″S, 151°09′7″E, 1 m, mud, NSW Environmental Protection Agency (EPA-AM) Contaminated Sediments Joint Project (6 specs).

Pittwater: 1 specimen in total. AM W37190, 33° 35′44″S, 151°18′44″E, muddy sand, 17 m, on SEM pin.

***Galathowenia quelis* sp. nov.** A total of 270 specimens examined.

New South Wales, Australia (this study).

Botany Bay: 166 specimens in total. AM W21559-21560 + unregistered material (43 samples), off Port Botany, 33°58′45″S, 151°11′01″E, around 7 m, iv.1992 (103 specs); AM W23546–23547, Weeney Bay, 34°01′3″S, 151°09′7″E, 1 m, mud, EPAAM Contaminated Sediments Joint Project iii.1995 (2 specs); AM W37824-37826 + unregistered material (8 samples), around 33°58′S, 151°12′E, 15–18 m, fine sand and muddy sand, vii.1992 (51 specs); AM W37823, off Port Botany, 33°58′33″S, 151°11′43″E, 16.5 m, sandy mud, ix.2004 (9 specs); AM W37824, 800–1000 m off Port Botany, 33°58′45″S, 151°11′1″E, 7 m, 28.vii.1992 (1 spec.).

Malabar: 6 specimens in total. AM W33845, 33°58′33″S, 151°16′51″E, 60 m, sand, Fisheries Research Institute, DOOM Stn 4B1, Jan. 1990 (3 specs); unregistered material (2 samples), EPA Malabar Deep Ocean Outfall Study, between 33°58′S, 151°17′E and 33°58′S, 151°17′E, around 80 m, iv.–v.1996 (3 specs).

Port Jackson: 1 specimen. AM W27743, Sydney Cove, 33°51′33″S, 151°12′31″E, 10 m, fine sediment bottom, v.2001.

Pittwater: 83 specimens in total. AM W37822, west of Sand Point, 33°35′44″S, 151°18′20″E, sandy mud, 15.6 m, 2.xii.2004 (6 specs); AM W23721-23724, approximately 33°35′S, 151°18′E, 13–17 m, muddy sand, vi. and x.1994, and v.1995, (15 specs); AM W32541 + unregistered material (13 samples), approximately 33°35′44″S, 151°18′44″E, 15–18 m, fine sand and muddy sand, ix.–xii.2004 (62 specs).

Queensland, Australia (this study).

Shoalwater Bay: 12 specimens in total. AM W202715, Triangular Islets, 22°23′S, 15°31′E, 1981 (12 specs).

Northern Territory, Australia (this study).

Arafura Sea: 2 specimens in total. AM W34018 and AM W34024, Area C East, 9°21′23″S, 134°04′58″E, and 9°23′37″S, 134°10′18″E, respectively, RV Southern Surveyor Arafura Sea Cruise, v.2005 (2 specs).

***Galathowenia arafurensis* sp. nov.** A total of 5 specimens examined.

Northern Territory, Australia (this study).

Arafura Sea: 5 specimens in total. NTM W21072, 9°23′6″S, 134°10′37″E, 88 m (1 spec.); NTM W21073, 9°50′118″S, 134°17′762″E, 83 m (1 spec.); AM W34019, RV Southern Surveyor (SS05/2005), 9°22′2″S, 133°39′53″E, in bioturbated soft bottom with detritus, 112–233 m, v.2005 (1 spec.); AM W34020, RV Southern Surveyor (SS05/2005), 9°47′59″S, 135°22′00″E, in bioturbated soft bottom with detritus, 112–233 m, v.2005 (1 spec.); AM W34017, same sample (1 spec. on SEM pin).

Galathowenia sp. A total of 44 specimens examined.

Queensland, Australia (this study).

Halifax Bay: 44 specimens in total. AM W38452-38458, north of Townsville, 19°9–10′S, 146°37′E, 1985.

Galathowenia africana Kirkegaard, 1959. A total of 3 specimens examined.

West Africa (Guinea, Congo) (Kirkegaard, 1959)

ZMUC POL-1522 (holotype). ZMUC POL-1523 (2 paratypes).

***Myriochele australiensis* sp. nov.** A total of 219 specimens examined.

New South Wales, Australia (this study). A total of 218 specimens examined.

East of Long Reef: A total of 43 specimens. AM W20675 and AM W37827, 33°44′43″S, 151°22′43″E, 1989, 60 m, sand.

East of Malabar: A total of 45 specimens. AM W38594-38595 + unregistered material (9 samples), EPA Malabar Deep Ocean Outfall Study, approximately 33°58–59′S, 151°17′E, 60 –80 m, 1995–1998.

South-east of Bate Bay: A total of 38 specimens. AM W38592-38593 + unregistered material (2 samples), The Ecology Lab, Ready-Mixed Industries (RMI)/ Pioneer Study, 34°4′36″S, 151°13″E, vi.–vii.1990.

East of Cape Banks: A total of 35 specimens. AM W38591 + unregistered material (5 samples), The Ecology Lab, RMI/Pioneer Study, 34°00′S, 151°16′E, 65–70 m, 1990–1991.

East of Wattamolla: A total of 10 specimens, unregistered material (3 samples), The Ecology Lab, RMI/ Pioneer Study, 34°08′00″S, 151°08′50″E, 29.x.–14.xi.1990.

East of Bass Point: 1 specimen. AM W38590, 34°36′S, 150°54′E, 65–70 m, The Ecology Lab, RMI/ Pioneer Study, vi.1990.

Murramarang National Park: A total of 46 specimens.AM W33846, North Head Lagoon, 35°45′55″S, 150°15′53″E, 1 m, sand, K. Mikac, vi.2000.

Victoria, Australia (this study). 1 specimen examined. Bass Strait, MV F136277, 39°45′9″S, 145°33′5″E, 74 m (1 spec.)

Myriochele heruensis Gibbs, 1972. A total of 1092 specimens examined.

Victoria, Australia (this study).

Port Phillip Bay. Around 828 specimens in total. AM W16313, 38°16′18″S, 144°41′30″E, sand, silt-clay, 24 m, (383 specs); AM W16202, 38°16′18″S, 144°41′30″E, 19 m, sand, silt, clay, (55 specs); AM W16312, 38°16′18″S, 144°41′30″E, sand, silt, clay, (105 specs); MV F136518, Environmental study benthic survey, 38°09′3″S, 145°03′5″E, sand, 1969–1973 (74 specs); MV F136511, environmental study benthic survey, 38°16′3″S, 144°51′5″E, 1969–1973 (183 specs); MV F136496, environmental study benthic survey, 38°09′3″S, 144°44′8″E, 1969–1973 (28 specs).

New South Wales, Australia (this study).

East of Malabar. A total of 178 specimens. AM W38494, 33°59′S, 151°17′27″E, 78.5 m, EPA Malabar Deep Ocean Outfall Study, vi.1996; AM W33841, 33°58′43″S, 151°17′48″E, 82 m, EPA Malabar Deep Ocean Outfall Study, 1995 (3 specs); other unregistered material, EPA Malabar Deep Ocean Outfall Study, 1995–1998, 19 samples, (141 specs); AM W24307, 33°58′34″S, 151°16′52″E, Fisheries Research Institute (NSW), sand, 60 m (34 specs).

Pittwater. Approximate number of 12 specimens. AM W23719, 33°35′58″S, 151°18′21″E, 13.9 m, muddy sand (2 specs); AM W23720, 33°35′52″S, 151°18′38″E, 16.4 m, muddy sand (5 specs); AM W23725, 33°35′50″S, 151° 18′41″E, 16.5 m, sandy mud (1 spec.); AM W23726, 33° 35′46″S, 151°18′20″E, 14.9 m, muddy sand (3 specs); AM W23727, 33°35′53″S, 151°1838′E, 16.9 m, muddy sand (1 spec.); AM W38588, 33°35′51″S, 151°18′21″E, 13.5 m, muddy sand, Federal Airports Commission (FAC) Study by Australian Museum, 1994 (several specs).

Murramarang National Park: A total of 74 specimens; AM W33847, North Head Lagoon, 35°45′55″S, 150°15′53″E, 1 m, sand, K. Mikac, vi.2000.

Myriochele heeri Malmgren, 1867. A total of 6 specimens examined.
Iceland (Parapar, 2006).
MNCN 16.01/10535 (sample 2400, 6 specs).

Myriochele islandica (Parapar, 2003). A total of 5 specimens examined.
Iceland (Parapar, 2003a).
MNCN 16.01/9023 (sample 2692, 5 paratypes).

Myriochele malmgreni (Parapar, 2006). A total of 3 specimens examined.
Iceland (Parapar, 2006).
MNCN 16.01/10547 (sample 2474, 3 paratypes).

Myriochele olgae Blake, 2000. A total of 7 specimens examined.
Iceland (Parapar, 2006).
MNCN 16.01/10542 (7 specs)

Myriochele riojai Parapar, 2003. A total of 2 specimens examined.
Bransfield Strait, Antarctica (Parapar, 2003b).
MNCN 16.01/8870 (station DR-6, holotype); MNCN 16.01/8871 (station DR-1, 1 paratype).

Myriochele robusta Parapar, 2003. A total of 2 specimens examined.
Bransfield Strait, Antarctica (Parapar, 2003b).
MNCN 16.01/8872 (station DR-7, holotype); MNCN 16.01/8873 (station DR-2, 1 paratype);

Myriowenia sp. A total of 138 specimens examined.
New South Wales, Australia (this study).

East of Bate Bay: A total of 9 specimens. AM W38459 (1 spec), AM W38466-38467 (3 specs), AM W38471 (2 specs), W38477 (1 spec.), AM W38484 (2 specs), The Ecology Lab, RMI/Pioneer Study, 34°04′36″S, 151°11′00″E to 34°06′48″S, 151°13′00″E, 65–70 m, vi.1990–i.1991.

East of Cape Banks: 1 specimen. AM W38478, 34°00′S, 151°16′00″E, The Ecology Lab, RMI/Pioneer Study, 65–70 m, 1990.

East of Wattamolla: A total of 48 specimens. AM W38460–38461 (14 specs), AM W38465 (2 specs), AM W38468–38470 (8 specs), AM W38472–38473 (4 specs), AM W38481–38483 (7 specs), AM W38485 (1 spec.), AM W38487 (5 specs), AM W38490–38493 (7 specs), The Ecology Lab, RMI/Pioneer Study, 34°08′S, 151°08′30″E, 65–70 m, 1989–1991.

East of Bass Point: A total of 80 specimens. AM W38462–38464 (8 specs), AM W38474–38476 (58 specs), AM W38479–38480 (6 specs), AM W38487–38489 (8 specs), The Ecology Lab, RMI/Pioneer Study, 34°36′S, 150°54′E, 45–70 m, 1989–1991.

APPENDIX 2

CHARACTERS AND STATES INCORPORATED IN THE ANALYSES

In this appendix, names of terminals and generic classifications correspond to the taxonomic accounts previous to the changes here proposed as a result of the present study.

1. Body shape: (0) compact (thick and rigid); (1) slender (thin and soft).

The body shape of the oweniids has been described as elongated, cylindrical, and fairly rigid (Blake, 2000; Rouse & Pleijel, 2001) but there are some differences within the group in the overall shape. Members of *Myriochele*, *Myrioglobula*, and *Owenia* have a thick, rigid body. *Myriochele* and *Myrioglobula* typically have a cigar-like body with both ends tapering, whereas *Owenia* has a truncated anterior end. *Galathowenia* and *Myriowenia* species have long and slender bodies, generally contorted after fixation and preservation.

2. Number of chaetigers: (0) < 30; (1) 30–50; (2) > 50.

This character reflects the maximum number of segments observed within a species. The number of segments can be comparatively constant within members of certain species (e.g. *Myriochele*, *Owenia*, and *Galathowenia* spp.), whereas others seem to keep growing and adding segments continually (e.g. *Myriowenia* spp.).

3. Prostomium and peristomium: (0) fused (not distinguishable); (1) separate (distinguishable).

Prostomium and peristomium of oweniids are not recognizable externally and are fused forming the head region (Nilsen & Holthe, 1985).

4. Head (prostomium + peristomium) shape: (0) globular; (1) cylindrical.

A globular head is that with rounded margins and more or less rounded or pointed anteriorly; cylindrical head is that with parallel margins and truncated anterior end. Members of *Myriochele*, *Myrioglobula*, and *Myriowenia* have a rounded, sometimes pointed anterior end (Figs 11C, 12B, 15E, H), whereas in *Galathowenia* it is typically truncated ((Figs 3D, 5D, 15D). *Owenia* possess a tentacular crown (Fig. 15C) in this position, making head shape observation difficult, but if tentacles are removed, the anterior end appears truncated.

5. Peristomial opening: (0) terminal; (1) oblique; (2) ventral slit

The ventral slit is here defined as a cleft, a continuation of an anterior mouth opening, resulting in two large anteroventral lips with high plasticity (Figs 4A, B, 15D). Taxa lacking this slit have a button-hole-shaped mouth with low lips around, in an oblique (e.g. (Figs 10B, 11A, 15E) or terminal position (e.g. Fig. 13A, B).

6. Tentacular crown: (0) absent; (1) present.

Although different names have been given to the anterior ramified and ciliated appendices arranged around the anterior margin of *Owenia* species (Fig. 15C), the origin, function, and homology to other oweniids or even polychaete structures is still unknown. According to some authors the tentacular crown is modified lips, therefore with a peristomial origin (Berkeley, 1949; Sene-Silva, 2002), but others have interpreted them as prostomial (Rouse & Fauchald, 1997; Rouse & Pleijel, 2001).

7. Palps: (0) absent; (1) present.

At this stage, it is still uncertain if the anterior appendices present in members of *Myriowenia* (Figs 12A, 13A, 15G, H) and the tentacular crown in *Owenia* are homologous, and also homologous to other polychaete palps. Sene-Silva (2002) followed Orrhage (1964, 1978, 1980) in considering them to be homologous with those present in Spionida, Terebellida, and Sabellida.

8. Well-developed anterior lobes: (0) absent; (1) present.

The origin and nature of these lobes located below the 'palps' of *Myriowenia* species (Figs 13E, 15G, H) are unknown and some authors have interpreted them as labial lobes (Sene-Silva, 2002), whereas others have considered them prostomial (Hartman & Barnard, 1960; Hartman, 1969; Blake, 2000). These lobes are absent in other taxa of Oweniidae and are a synapomorphy of *Myriowenia*.

9. Foregut: (0) occluded; (1) ventral buccal organ; (2) axial simple proboscis.

The structure of the foregut varies widely amongst polychaetes but has been classified as three different types (e.g. Dales, 1962; Purschke & Tzetlin, 1996; Tzetlin & Purschke, 2005), two of which are applicable on our terminals. Siboglinidae, in adult stage, have an occluded gut.

10. Ventral pharyngeal organ: (0) absent; (1) present.

Inside the mouth, at least some oweniids present three structures, one located on the dorsal edge and two lateroventral ones sometimes referred to as lips (Dales, 1957) (Figs 6E, 13E, 15I–K). According to some authors they are expansions of the prostomium that participate in the manipulation and selection of sediment particles for feeding purposes (Dales, 1957). The buccal organ in Oweniidae has been described as having a bulb organ that protrudes slightly from the mouth (Purschke & Tzetlin, 1996; Tzetlin & Purschke, 2005), which might have confused some authors who have described this structure as a proboscis (e.g. Blake, 2000). Homology of ventral pharyngeal organs across polychaetes has not been established (Purschke & Tzetlin, 1996 vs. Dales, 1957, who suggested that they are homologous in sedentary polychaetes). The ventral pharyngeal organ has been described as a double-lipped structure lying mid-ventrally between and beneath the ventrolateral lips and involved in tube building in *Owenia* (Watson, 1901; Wilson, 1932; Dales, 1957). Some species of *Myriochele* (Blake, 1984; Nilsen & Holthe, 1985, Hartmann-Schröder, 1996; Parapar, 2006) and *Myriowenia* (Blake, 2000) have also been described or illustrated as having a ventral pharynx.

11. Dorsolateral ciliary folds: (0) absent; (1) present.

Protrusible ciliated folds on the dorsolateral walls of the foregut are present in some polychaetes (Purschke & Tzetlin, 1996; Tzetlin & Purschke, 2005) and have been considered herein to be present at least in some oweniids (Figs 13E, 15I–K).

12. Cerebral eyespots: (0) absent; (1) present.

It is unclear if the eyes present in the larvae and adult stage of some oweniids (Figs 2B, 5C, 7A, 15C, D, F) have a prostomial or a peristomial origin (e.g. Capa *et al*., 2011 and references therein) but eyes associated with, embedded in, or near, the brain are commonly termed cerebral eyes (Purschke *et al*., 2006) and they are accordingly treated as homologous in the different terminals considered herein.

13. Nuchal organs: (0) absent; (1) present.

Some polychaetes lack nuchal organs and this has been considered as a loss (Purschke, 2005). Oweniidae and Siboglinidae are amongst these although some authors have suggested that in the case of Oweniidae further investigation is needed (Purschke, 1997).

14. Collar between head and first segment: (0) absent; (1) present.

Oweniid species have often been described as possessing a collar between the head and the first segment (e.g. Imajima & Morita, 1987; Hartmann-Schröder & Rosenfeldt, 1989; Dauvin & Thiébaut, 1994; Blake, 2000; Parapar, 2006) (Fig. 15G). However, we suspect that in some cases it has been confused with a fold of the epithelium as a result of contraction of the head within the anterior body segments or with a breakage groove in this position (e.g. Hartman, 1965 for *Myriowenia gosnoldi*).

15. Breakage groove between head and first chaetiger: (0) absent; (1) present.

According to our observations (we have seen several specimens regenerating the anterior ends within a sample) and the data from the literature (e.g. Aguirrezabalaga *et al*., 2000; Parapar, 2001), some species of oweniids are able to break and regenerate anterior parts of the body (Figs 6J–K, 12E, 15D). The reason why this happens is still unknown but may be related to asexual reproduction as suggested by some authors (Aguirrezabalaga *et al*., 2000; Parapar, 2001). In some individuals of certain species (e.g. *Myriowenia* spp.) a constriction between the head and the first chaetiger indicates the breakage zone.

16. Breakage groove between first and second chaetiger: (0) absent; (1) present.

In some other cases, such as some *Galathowenia* species, this constriction lies between the first and the second chaetiger (Imajima & Morita, 1987; Nilsen & Holthe, 1985; Parapar, 2001; and present study) (Figs 6B, J–K, 15D).

17. Neuropodial uncini begin: (0) segment 1; (1) segment 2; (2) segment 3; (3) segment 4.

The segmented body region is considered to be the one between the peristomium and the pygidium and therefore the first true segment is the one following the peristomium (Schroeder & Hermans, 1975; Nielsen, 2005). Other interpretations in the past have defined the peristomium as the first segment, being followed by the second segment, which would be the first chaetigerous segment (Nilsen & Holthe, 1985). Traditionally, the segmented body of oweniids has been separated in two regions, thorax and abdomen, based on the presence of uniramous or biramous parapodia (e.g. Blake, 2000). We avoided the traditional use of thorax and abdomen, common in the literature, as it lacks homology grounds (e.g. Nilsen & Holthe, 1985 vs. Parapar, 2003a, b). The first segment of all oweniids bears only notochaetae (Fig. 15C–F), but this is not the case in other polychaetes, such as *Magelona* or Siboglinidae (Rousset *et al*., 2004; Southward, Schulze & Gardiner, 2005), which lack chaetae on this segment, or members of Spionidae, which have chaetae in both rami or only in the neurochaetae (Rouse & Pleijel, 2001). *Myrioglobula* species typically present chaetae in both notopodia and neuropodia from the second segment (Fig. 11A), but this is not exclusive of this taxon, as *Myriochele robusta* was also found to present this feature (Parapar, 2003b). Some species of *Myriochele* such as *Myrioc. olgae* or *Myrioc. antarctica* have two consecutive uniramous segments and the neurochaetae appear on the third one (Blake, 2000; Cantone & Di Pietro, 2001) (Fig. 15E). In this regard, *Myrioc. robusta* is an exception in the genus. It was described as possessing uniramous segments 1 and 3 and biramous 2, 4, and onwards (Parapar, 2003b).

18. Chaetigers 4–6: (0) isometric; (1) not isometric.

In some oweniids (such as most *Owenia* and *Myrioglobula* species), the relative length of the first 'abdominal' chaetigers is fairly similar (isometric), whereas in others (such as most *Galathowenia*, *Myriochele*, and *Myriowenia*) this comparative measure varies (not isometric).

19. Chaetae emerging from body wall: (0) absent (well-developed parapodia); (1) present.

Of the terminals included herein only Oweniidae and Siboglinidae have reduced parapodia and chaetae emerging from the body wall.

20. Acicular chaetae in notopodia: (0) absent; (1) present.

Myriochele and *Myrioglobula* bear two types of notopodial capillary chaetae in at least some segments (Figs 8H, 11H). One of the types, typical of Oweniidae, is cylindrical and progressively tapering towards the end and with a smooth proximal emerged part and a distal end showing a characteristic structure of the cortex, resembling small, imbricate scales all around the chaetae. The second is the short and smooth capillaries (with no distal microstructure) with an abruptly narrowing tip, arranged ventrally to the first type of capillaries. The terminology used in the literature for the latter type of chaetae varies, being sometimes designated as short capillaries (e.g. Parapar, 2003b) and other times as acicular chaetae (Nilsen & Holthe, 1985; Imajima & Morita, 1987; Parapar, 2001, 2003a, 2006; present paper). *Galathowenia australis* is an exception amongst members of this genus as it also has acicular chaetae on some notopodia (Parapar, 2003b).

21. Anterior-most acicular notochaetae first present from: (0) first chaetiger; (1) second chaetiger; (2) third chaetiger; (3) fourth chaetiger; (4) fifth chaetiger.

The segment on which the acicular chaetae first appear varies amongst species and has been used as a specific diagnostic feature, although sometimes it shows certain intraspecific variation. For the present study we considered the anterior-most segment on which these chaetae have been observed.

22. Rows of uncini per torus: (0) 1; (1) < 8; (2) 8–20; (3) > 20.

In Oweniidae, there is a single formation site of chaetae per parapodial rami. For the neuropodia, these are located on the posterior–dorsal side of each uncinal field (Meyer & Bartolomaeus, 1996). Although the formation of these uncinal patches, formed by more or less irregular rows of uncini, starts as a single row in early stages of development (Smart & Dassow, 2009), it continues in juveniles (Meyer & Bartolomaeus, 1996), and additional rows are added in adults (Thiébaut & Dauvin, 1992; Meyer & Bartolomaeus, 1996) (Figs 3F, 4H, 6G, 8I, 11H). For these reasons, the irregular rows in Oweniidae have been interpreted as modified transverse rows (Hausen, 2005b).

23. Bidentate uncini: (0) with teeth arranged in a vertical row; (1) with teeth arranged in an oblique row; (2) with teeth arranged side by side at the same level; (3) with teeth arranged in multiple rows.

Uncini of members of the outgroup have a capitium consisting of rows of several teeth, except in *Magelona* and Chaetopteridae. Amongst the oweniids, the genus *Galathowenia* (Fig. 3H) typically has two teeth in an oblique arrangement (Fig. 15L), in the genera *Myriochele*, *Myrioglobula* (Fig. 11J, K), and *Myriowenia* (Fig. 13H, I) they are arranged in a vertical row, and in

Owenia they are arranged side by side. In the present study some exceptions were found to this pattern (i.e. *Myrioc. heruensis*).

24. Rostrum of uncini: (0) absent; (1) present.

The spines or denticles found in the uncini of Oweniidae are homologous to the capitium of the uncini of other annelids. The rostrum seems to have been reduced for members of this group (Meyer & Bartolomaeus, 1996; Bartolomaeus, 1998, contrary to Nilsen & Holthe's, 1985 interpretation). Other polychaetes have been described as lacking a rostrum, such as siboglinids and some fabriciids and chaetopterids (Bartolomaeus, 1998; Hausen, 2005a).

25. Relative size of each paired tooth of uncini: (0) equal; (1) proximal tooth larger.

Oweniids' uncinal teeth are similar in size (Figs 8K, 11K, 15L), except for *Myriowenia*, in which the proximal tooth is larger (Fig. 13H, I). Sene-Silva (2002) considered a similar character in his phylogenetic analysis of the family but misinterpreted the two teeth of oweniids as a rostrum and capitium.

26. Manubrium of uncini: (0) absent; (1) present.

Oweniidae and most of the outgroup present uncini with a well-developed manubrium (also known as a handle or shaft), whereas the Chaetopteridae lack this structure.

27. Manubrium shape: (0) slightly curved, almost straight; (1) sharply curved backwards, forming an almost 90° angle.

This feature has been omitted from most taxonomic descriptions but could reveal phylogenetic information in terms of genera. *Myriowenia* has a straight manubrium (see Hartman, 1965) whereas the rest of the oweniids exhibit a bent shape (e.g. Imajima & Morita, 1987).

28. Segmental branchiae: (0) absent; (1) present.

Although the anterior tentacles of *Owenia* have respiratory, feeding, and tube-building functions (Watson, 1901; Dales, 1957), oweniids lack the segmental branchiae that are present in other polychaete families (e.g. Spionidae).

29. Longitudinal groove on dorsum of body: (0) absent; (1) present.

Longitudinal grooves (Fig. 11C) have not been considered in taxonomic descriptions or in the previous phylogenetic study (Sene-Silva, 2002). Although variation has been observed between the terminals examined for this study, the character could be phylogenetically informative. The ventral ciliary groove in sabellids (inverted in the thoracic region) has been considered as homologous to the groove present in the anterior end of chaetopterids although the function differs amongst taxa.

30. Longitudinal grooves on body sides: (0) absent; (1) present (Parapar, 2003c: fig. 2C). Lateral grooves have been found to be ciliated (Fig. 11B, D), whereas the dorsal groove lacks cilia.
31. Longitudinal grooves on body ventrum: (0) absent; (1) present.

The ventral groove (Fig. 11A; Parapar, 2003c: fig. 2C) is often glandular and different in nature from the lateral and dorsal grooves (Parapar, 2003c: fig. 2D)

32. Pygidium: (0) rim with or without inconspicuous lobes; (1) clearly bilobed; (2) trilobed; (3) multilobed (more than three and often variable with size of specimens).

The shape of the pygidium of oweniids is a feature that shows intraspecific variation even amongst members of the same group (e.g. Parapar, 2003c). The pygidium with two long terminal cirri described for *Myriowenia gosnoldi* (Hartman, 1965: fig. 44a, b) needs further investigation. Although we were unable to examine this specimen, we believe that the posterior structures are the same as those often found in oweniids as part of the regeneration process after breakage (see Fig. 12J, K). The posterior end of the type of *Myriow. gosnoldi* does not correspond to the typical end seen in *Myriowenia* and most oweniids, in which the chaetigers become compressed and narrow towards the pygidium (e.g. Blake, 2000).

33. Intra-epidermal cord: (0) absent; (1) present.

This feature, also referred to as the basiepidermal cord (Coulon & Bessone, 1979; Orrhage & Müller, 2005), has been suggested to be an autapomorphy of a clade formed by Oweniidae and Siboglinidae (e.g. Liwanow & Porfirjewa, 1967; Rousset *et al*., 2004; Capa *et al*., 2011).

34. Oesophageal commissures shape: (0) straight; (1) Y-shaped.

In some taxa, such as *Owenia* (Fig. 15C) or some *Galathowenia* species (Fig. 15D), the oesophageal commissures descend as two lines from the eyespots, extending posteriorly to meet at an acute angle on the ventral midline, uniting with the large ganglion (Watson, 1901). These are visible as a Y-shaped white band continuing to the ventral nerve cord. A special function has been assigned to this triangular ventral area, involved in the deposition of particles outside of the tube (Watson, 1901).

35. Monociliated epidermal cells: (0) absent; (1) present.

Monociliated epidermal cells were only known from the tentacles of *Owenia fusiformis* (Gardiner, 1978) until they were described on the larval feeding tentacles of *Magelona mirabilis* (Bartolomaeus, 1995) and *Myriowenia* (Westheide, 1997). However, they have not been found in some *Myriochele* species (Westheide, 1997). This condition, present in both oweniids and magelonids, does not necessarily reflect a common origin and could be produced after truncated ciliogenesis (Bartolomaeus, 1995; Hausen, 2005a).