



# Integrative taxonomy of *Parasabella* and *Sabellomma* (Sabellidae: Annelida) from Australia: description of new species, indication of cryptic diversity, and translocation of some species out of their natural distribution range

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Most nominal fan worm species belonging to the genus *Parasabella* Bush, 1905, and *Sabellomma* Nogueira, Fitzhugh & Silva-Rossi, 2010 (Sabellidae, Annelida) lack unique morphological diagnostic features. Species diagnoses rely on a combination of attributes, often making reference to characters that are qualitatively or quantitatively continuous. This, together with a lack of knowledge about phenotypic intraspecific variation in most species, suggests that the sole use of morphological features is insufficient to identify and characterize some of these species. Examination of collections revealed that *Parasabella* is a common and diverse group of sabellids along the Australian coastline, although it had only been recorded here twice. The genus *Sabellomma* is here reported in Australia for the first time. Comparison of morphological data and nuclear (internal transcribed spacer) and mitochondrial (cytochrome oxidase I) DNA sequence data of 30 terminals in a range of analyses allowed us to assess the monophyly of *Parasabella* and its sister-group relationship with *Sabellomma* and to examine some of the species boundaries and genetic diversity within lineages. The combined sequence data results indicate the presence of seven distinct genetic *Parasabella* lineages in Australia, four of which are assigned to previously described species (three are new records for Australia), and two are considered as a complex of species sharing a unique combination of characters, one of which is described as new. Another *Parasabella* species with distinct atypical radiolar eyes and a species of *Sabellomma* are also described as new.

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ADDITIONAL KEYWORDS: alien species – cryptic species – *Demonax* – DNA sequences – eye variability – fan worms – morphology – polychaetes – unintentional translocations.

## INTRODUCTION

*Parasabella* Bush, 1905, is a genus of fan worms (Sabellidae: Annelida) with a cosmopolitan distribution and that is mainly associated with hard substrates in shallow waters. It currently contains around 25 nominal species (Tovar-Hernández & Harris, 2010). The name *Parasabella* has recently replaced *Demonax*,

as this latter was preoccupied by a genus of cerambycid beetles and therefore considered a junior homonym (Tovar-Hernández & Harris, 2010).

*Parasabella* has been characterized by having thoracic companion chaetae that are subdistally inflated (with a hood consisting of microtubules that give a dentate appearance) and have a distally elongated mucro orientated at a right angle to the shaft (*sensu* Johansson, 1925; Knight-Jones, 1983; Perkins, 1984; Fitzhugh, 1989), features unique amongst sabellids. The genus *Parasabella* had only been recorded twice from Western Australia, as *Sabella aberrans* Augener, 1926,

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and as *Demonax leucaspis* Kinberg, 1867, reported by Monro, 1938 (the latter originally described from Peru).

Attributes traditionally used to characterize sabellid species include general overall size, relative length of radiolar crown compared with body length, number of pairs of radioles and form of distal ends, numbers of vacuolated axial cells supporting radioles, length of dorsal lips, presence and shape of radiolar eyes, pigmentation pattern, shape and length of collar, shape of first thoracic ventral shield, degree of separation of ventral shields from neuropodial thoracic tori, shape of inferior thoracic notochaetae, and length of handles of thoracic and abdominal uncini, as well as numbers of thoracic and abdominal segments (e.g. Knight-Jones, 1983; Perkins, 1984; Knight-Jones & Walker, 1985; Giangrande, 1994; Gambi *et al.*, 2001). Some of these characters have been proven to vary in *Parasabella* and other sabellids with growth (Knight-Jones, 1983; Perkins, 1984; Capa, Bybee & Bybee, 2010) and fixation process (Costa-Paiva, Paiva & Klautau, 2007) but variation and plasticity within each species is not acknowledged in traditional descriptions of species, which often refer to only a few specimens.

The genus *Sabellomma* Nogueira, Fitzhugh & Silva-Rossi, 2010, was recently erected to accommodate sabellids possessing features such as unpaired, simple eyespots along the outer margins of radioles, inter-ramal eyespots and a thorax with four to five chaetigers – all homoplastic features, as they have been reported, individually, in other sabellids (Nogueira *et al.*, 2010). Three species of *Sabellomma* have been described so far, from the Caribbean, São Paulo (Brazil), and Hawaii. Species are distinguished by pigmentation pattern, absence or presence of pinnular appendages, and the extent to which those appendages are fused to the dorsal lips, although not all of these features seem stable within the species (Nogueira *et al.*, 2010).

The aims of the present study were the revision of the Australian species of *Parasabella* and *Sabellomma* and their characterization by morphological and molecular diagnostic features. DNA sequences were used to assess the monophyly of *Parasabella*, and species boundaries and intraspecific genetic diversity in some cases. It is herein revealed that *Parasabella* is common and widely distributed along the Australian coasts and the results include the description of new species and new records for the genus. The delimitation of *Parasabella* species by morphological means proved to be difficult in some cases owing to the broad and continuous range of character states and/or a wide range of combination of a few attributes (some traditionally considered as diagnostic) observed in specimens. The presence of cryptic species (groups of individuals with morphologically similar yet distinguishable lineages and with reciprocal monophyly and considerable genetic dis-

tinctness) and unreported cases of translocations out of the considered natural distribution range (distant and disjunct populations showing little or no genetic variation) may explain why recognizing these species is not an easy task. Moreover, we report high genetic intraspecific variability and correlations between genetic and geographical structure in some of the Australian species. *Sabellomma*, a closely related genus, is also reported in Australia for the first time, and a new species is described.

## MATERIAL AND METHODS

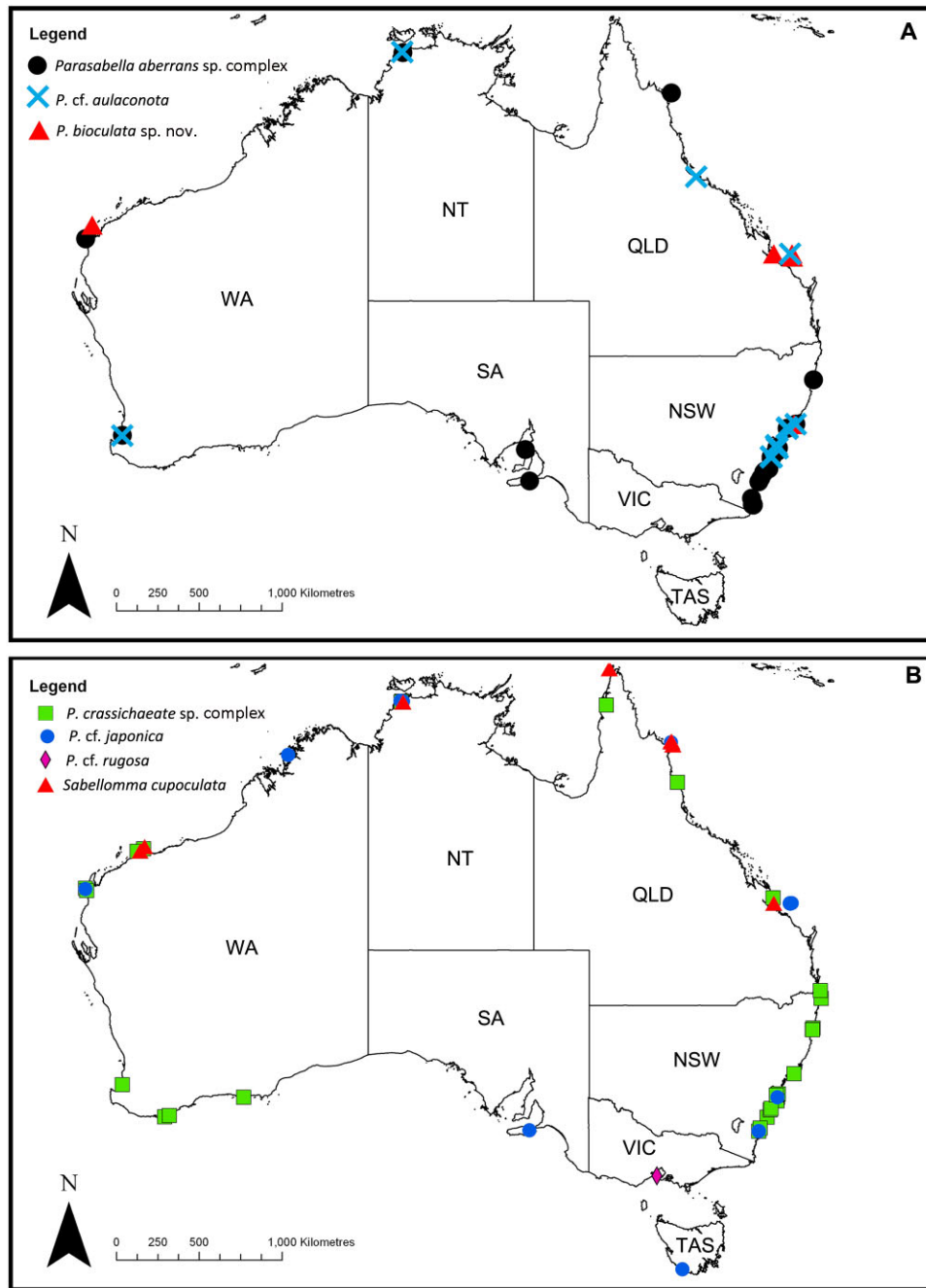
### MATERIAL EXAMINED

For the morphological studies, specimens of *Parasabella* were examined from collections housed at the Australian Museum, Sydney (AM), the Museum and Art Gallery of the Northern Territory, Darwin (MAGNT), and Museum Victoria, Melbourne (NMV). Types and additional material were loaned from the Zoological Museum Copenhagen (ZMUC), Swedish Museum of Natural History (SMNH), and Uppsala University Museum of Evolution (UPSZMC) for comparison. Newly collected material was used for life examination and colour photography. Some preserved specimens were stained with methylene blue to enhance details and increase resolution for photography with a Leica MZ16 microscope and Spot flex 15.2 camera attachment. In the Taxonomic section, the material examined is cited from Western Australian localities, clockwise, around Australia, number of specimens in parentheses. Complete details about collections are given in the Appendix and mapped in Figure 1A, B. Unless indicated otherwise, material was fixed in 5–10% formalin and is preserved in 70–80% ethanol.

For the molecular analyses, recently collected specimens were fixed in 100% ethanol. Tissues for DNA extractions were removed from abdominal regions. The anterior ends, left intact as vouchers, are housed in the Australian Museum (Table 1). A total of 43 specimens was selected for DNA sequencing, comprising at least five members of each Australian morphotype and attempting to include different populations along their distribution range. Specimens from Hawaii and Florida (USA) were also included for comparison. Nevertheless, amplification and/or sequencing did not succeed for all samples. The genus *Pseudopotamilla* and *Megalomma* Johansson, 1925, were considered as outgroups. Collection data together with GenBank accession numbers are given in Table 1.

### MORPHOLOGICAL DATA

Light microscopy photographs were taken with a Leica MZ16 microscope with a Spot flex 15.2 camera attached. Parapodia, usually from the fifth thoracic



**Figure 1.** Maps with collecting sites in Australia. A, *Parasabella aberrans* spp. complex, *Parasabella* sp. cf. *Parasabella aulacnota*, *Parasabella bioculata* sp. nov. B, *Parasabella crassichaetae* sp. nov. complex, *Parasabella* sp. cf. *Parasabella japonica*, *Parasabella* sp. cf. *Parasabella rugosa*, *Sabellomma cupocolata* sp. nov.

chaetiger and midabdominal region, were mounted on microscope slides to examine chaetae. The internal structure of the radioles was examined by mounting on slides thin transverse sections taken from the base level and from the mid-length. Line drawings were drawn to scale with a drawing tube attached to either a stereo- or compound microscope and digitized in Adobe ILLU-

STRATOR. Some specimens were dehydrated in ethanol, critical point-dried, covered with 20 nm of gold, and examined using a Zeiss Evo LS15 scanning electron microscope, using Robinson backscattered and Everhart-Thornley secondary electron detectors.

The nomenclature for chaetal morphology follows that proposed by Fitzhugh (1989) with some modifications.

**Table 1.** Collection information on the specimens used for the phylogenetic analyses, vouchers, and GenBank accession numbers

Species	SPEC. #	Voucher	cox1	ITS	Locality	Depth (m)	Habitat
<i>Pseudopotamilla</i> sp.	–	W.30009	KP938253	KP938223	Darwin, NT, Australia	1	Coral rubble
<i>Megalomma splendida</i>	–	HM473463	–	–	Canada, GenBank		
<i>Parasabella aberrans</i>	PS 07	W.37031	KP938268	KP938240	Ningaloo, WA, Australia	6.4	Coral rubble
	PS 08	W.37032	KP938269	KP938241	Ningaloo, WA, Australia	6.4	Coral rubble
	PS 29	W.37050	KP938265	KP938243	Kurnell, NSW, Australia	17.8	Rock epifauna
	PS 30	W.37051	KP938266	KP938244	Kurnell, NSW, Australia	17.8	Rock epifauna
	PS 31	W.37052	KP938267	KP938245	Kurnell, NSW, Australia	17.8	Rock epifauna
	PS 26	W.32586	–	KP938242	Coffs Harbour, NSW, Australia	12.7	Rock epifauna
	PS 14	W. 37038	–	KP938246	Heron Island, QLD, Australia	15	Coral rubble
	PS 15	W. 37039	–	KP938247	Heron Island, QLD, Australia	10	Coral rubble
	PS 42	W.37062	–	KP938248	Heron Island, QLD, Australia	15	Coral rubble
	PS 20	W.37042	–	KP938249	Jolong Reef, NSW, Australia	20.5	Sediment on rock
<i>Parasabella</i> sp. 1	PS 17	W.32563	–	KP938224	Hutchinson Island, Florida, USA	1.6	Intertidal epifauna
	PS 19	W.37041	–	KP938225	Sydney Harbour, NSW, Australia	4.4	Pontoon epibionts
<b><i>Parasabella crassichetae</i></b> <b>sp. nov.</b>	PS 03	W.37028	–	KP938226	Kiama, NSW, Australia	22.4	Rock epifauna
	PS 21	W.37044	–	KP938227	Kurnell, NSW, Australia	17.8	Rock epifauna
	PS 23	W.37046	–	KP938229	Jolong Reef, NSW, Australia	22.5	Pontoon epibionts
	PS 24	W.37047	–	KP938230	Jolong Reef, NSW, Australia	22.5	Pontoon epibionts
	PS 28	W.37049	–	KP938228	Jolong Reef, NSW, Australia	20.5	Sediment on rock
	PS 10	W.37034	KP938262	KP938231	Coconut Island, Oahu, Hawaii	0	Rock epifauna
	PS 11	W.37035	KP938263	KP938233	Coconut Island, Oahu, Hawaii	0	Rock epifauna
	PS 12	W.37036	KP938264	KP938232	Coconut Island, Oahu, Hawaii	0–1	In a rope
	PS 16	W. 32579	–	KP938234	Darwin, NT, Australia	0.5	Rock epifauna
	PS 09	W.37033	–	KP938235	Sydney Harbour, NSW, Australia	11.8	Pontoon epibionts
<i>Parasabella</i> sp. 2	PS 09	W.37033	KP938258	KP938236	Ningaloo, WA, Australia	3	Coral rubble
	PS 38	W.37058	KP938261	KP938238	Heron Island, QLD, Australia	20	Coral rubble
<i>Parasabella</i> sp. cf. <i>Parasabella aulacnota</i>	PS 01	W.37043	KP938259	KP938237	Jolong Reef, NSW, Australia	20.5	Sediment on rock
	PS 22	W.37045	KP938260	KP938239	Kurnell, NSW, Australia	17.8	Rock epifauna
<b><i>Sabellomma cupocolata</i></b> <b>sp. nov.</b>	PS 06	W.37030	KP938254	KP938250	Lizard Island, QLD, Australia	20	Coral rubble
	PS 37	W.37057	KP938255	KP938251	Lizard Island, QLD, Australia	30	Coral rubble
	PS 40	W.37060	KP938257	–	Heron Island, QLD, Australia	30	Coral rubble
	PS 41	W.37061	KP938256	KP938252	Lizard Island, QLD, Australia	22	Coral rubble

Abbreviations used for Australian states: NSW, New South Wales; QLD, Queensland; NT, Northern Territory; WA, Western Australia. *cox1*, cytochrome oxidase I; ITS, internal transcribed spacer; SPEC. #, specimen number.



*Parasabella* species show broadly hooded inferior thoracic chaetae as figured by Perkins (1984) and Fitzhugh (1989). However, a range of forms from those with broader hoods and distal ends narrowing abruptly (herein referred to as type A, Fig. 2A), and those with more slender hoods and a progressively tapering distal tip (referred to as type B, Fig. 2B–F), have also been observed (similar to classification of chaetae of species of *Megalomma*, Capa & Murray, 2009). Moreover, some chaetal ratios were also measured to allow comparisons amongst species (e.g. Table 2). These are the maximum width of the hood with respect to shaft width, and total length of the hood with respect to maximum width (Fig. 5A). Several measurements were also taken for the uncini. These are: the ratio of the length of the handle divided by the length from the tip of the main fang to the breast (Fitzhugh, 1989; Rouse & Fitzhugh, 1994) and the length of the neck with respect to the length of the breast (Fig. 5K).

Companion chaetae have also been redefined herein in order to incorporate the variation observed amongst the species of *Parasabella* and *Sabellomma*. Most sabellids with companion chaetae have a proximal shaft with a tapering distal hood almost perpendicular to the shaft and parallel to the body wall. The distal hood is symmetrical or asymmetrical, with minute striations at the proximal side of the hood (e.g. *Sabellomma* Nogueira *et al.*, 2010 or *Megalomma* Fig. 2H, I). This shape is herein referred to as transversely flattened (Fig. 2H, I), alluding to the flattening of the hood in the plane perpendicular to the longitudinal axis of the shaft. In members of *Parasabella*, the companion chaetae are atypical because they are subdistally enlarged with conspicuous serrations along the edge, and the distal hood, also tapering, is orientated at a right angle (e.g. Knight-Jones, 1983; Perkins, 1984). They have also been described as companion chaetae with bulbous avicular heads, with a thin mucro arising between the toothed crest and beak (e.g. Knight-Jones & Perkins, 1998). These are herein referred to as companion chaetae with hoods compressed laterally (Fig. 2J, K) because they are compressed side-to-side in the same plane as the longitudinal axis of the shaft (Fig. 2J, K). The new *Sabellomma* species described herein possesses transversely flattened companion chaetae in which the hood is very thin and almost needle-like (Fig. 2L, M), a form that appears to be midway between the related genera *Megalomma* and *Parasabella* (Fig. 2H–M).

A table with all currently accepted species of *Parasabella* (after Tovar-Hernández & Harris, 2010) is presented to allow comparison of suggested valid diagnostic features (Table 2). Three species were excluded because little or no information on most features is available for them: *Parasabella columbi* (Kinberg, 1867), from Argentina, *Parasabella fernandezensis*

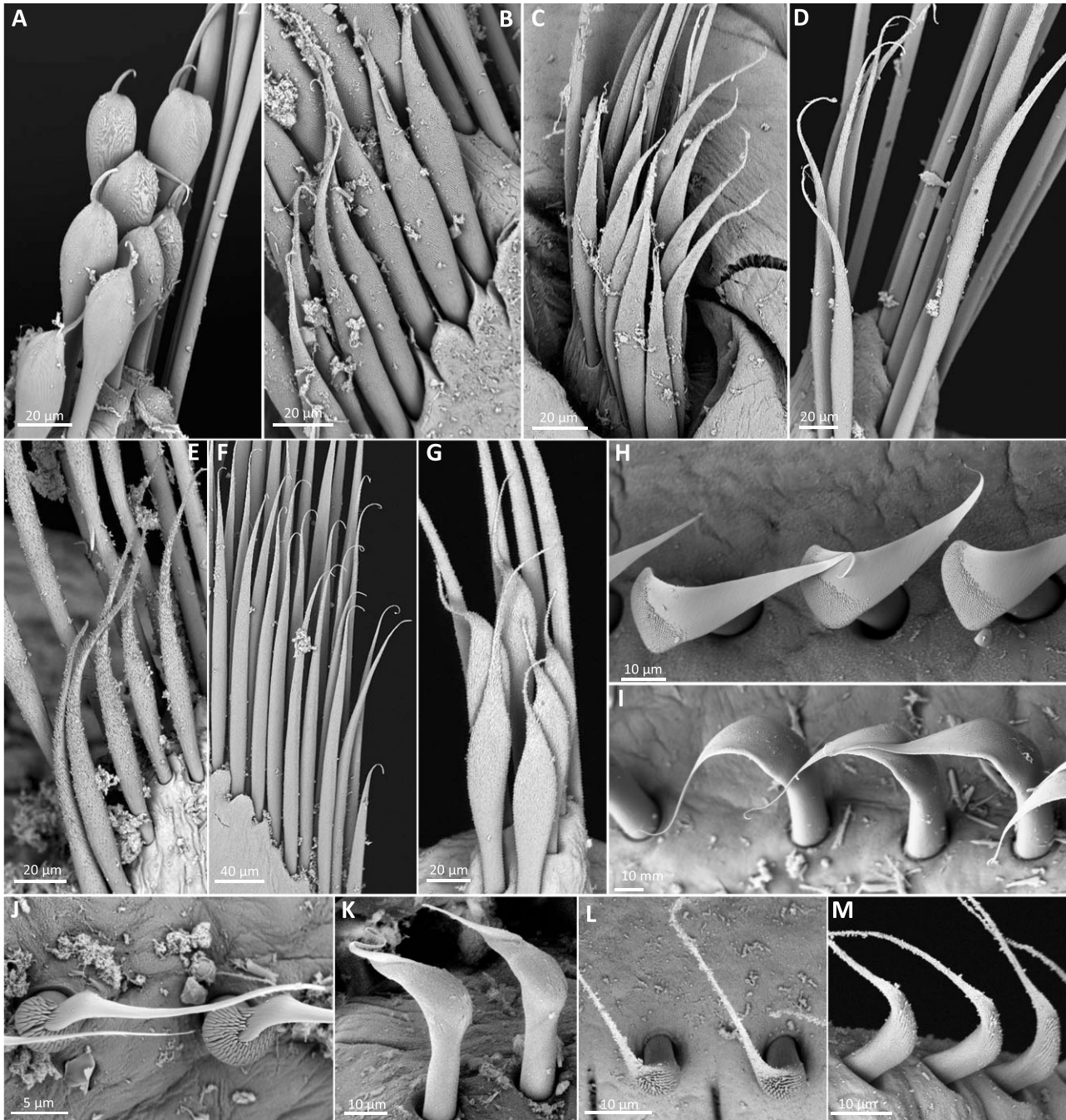
(Augener, 1922), from Juan Fernandez, Chile, and *Parasabella rufovittata* (Grube, 1881) from Singapore. By contrast, *Parasabella fullo* (Grube, 1878), omitted from Tovar-Hernández & Harris (2010), is included as we consider it to be a valid taxon, together with the new species described herein.

#### DNA EXTRACTION, AMPLIFICATION, AND SEQUENCING

Genomic DNA was extracted from muscle tissue using standard protocols for the DNeasy Blood and Tissues Kit (QIAGEN Pty Ltd). Sequences of 623–658 bp of the mitochondrial gene cytochrome oxidase I (*cox1*) from 18 individuals, and 538–787 bp of the region including the nuclear gene ribosomal internal transcribed spacers 1 and 2 (ITS1 and ITS2) with flanking regions of 18S rDNA and 28S rDNA, from 31 specimens, were obtained. The primers used were LCO11490 and HCOI2198 for *cox1* (Folmer *et al.*, 1994), and ITSF and ITSR for ITS1 and ITS2 (Chen *et al.*, 2002). PCR mixtures contained 1× QIAGEN PCR buffer, 0.5× Q Solution, 3.5 mM MgCl<sub>2</sub>, 0.05 mM of each deoxynucleotide (dNTP), 10 pmol of each primer, 1 unit of QIAGEN Taq DNA polymerase, and 50–100 ng of whole genomic DNA, and were made up to 25 µL total volume with double-distilled H<sub>2</sub>O. Amplifications were performed on a MastercyclerS Gradient (Eppendorf Inc). The PCR thermal cycling profile was 94 °C for 2 min, followed by 35 cycles of 94 °C for 20 s, 50 °C for 40 s, 72 °C for 1 min, and 5 min of final extension at 72 °C. Successful amplifications were then purified using the ExoSAP-IT PCR purification system (USB Corporation), and then bidirectionally sequenced, using the original PCR primers, at an external sequencing facility using BigDye v. 1.1 (Applied Biosystems). Chromatograms were annotated with the program SEQUENCHER v. 5.1 (Gene Codes Corporation). ITS1 and ITS2 sequence chromatograms showed no evidence of double peaks (which would suggest the presence of multiple copies), so cloning was not pursued.

#### SEQUENCE ALIGNMENT, PHYLOGENETIC ANALYSES, MOLECULAR DIVERGENCE, AND DIAGNOSTIC CHARACTERS

Nucleotide sequences of *cox1* were aligned with MAFFT v. 7.0 (Katoh, 2013) using the G–INS–i strategy, recommended for sequences with global homology, and ITS1 sequences using the Q–INS–i strategy, which takes into account secondary structures. The best nucleotide substitution model fitting each marker or partition was estimated in MrAIC (Nylander, 2004) based on the Bayesian information criterion (BIC). The best partitioning scheme was selected based on BIC using the maximum likelihood (ML) values estimated in RaxML v. 7.2.8 (Stamatakis, 2006). The best ML tree was



**Figure 2.** Comparison of chaetae from different *Parasabella*, *Sabellomma*, and *Megalomma* species. A–G, thoracic inferior chaetae. A, *Parasabella crassichaetae* sp. nov. complex, with type A chaetae (broad hoods and distal ends narrowing abruptly). B–F, type B chaetae (slender hoods and with a progressively tapering distal tip). B, *Parasabella* sp. cf. *Parasabella aulaconota*. C, *Parasabella aberrans* spp. complex. D, *Parasabella bioculata* sp. nov. E, *Parasabella* sp. cf. *Parasabella japonica*. F, *Parasabella* sp. cf. *Parasabella rugosa*, G, *Sabellomma cupocolata* sp. nov., with type A chaetae. H–M, companion chaetae. H, I, with hoods transversely flattened. H, *Megalomma interrupta* Capa & Murray, 2009. I, *Megalomma phyllisae* Capa & Murray, 2009. J, K, with hoods laterally compressed; J, *Parasabella crassichaetae* sp. nov. complex. K, *Parasabella* sp. cf. *Parasabella rugosa*. L, M, with hoods transversely flattened but with very thin, almost needle-like distal mucro. L, *Sabellomma cupocolata* sp. nov., companion chaetae, top view. M, *S. cupocolata* sp. nov., companion chaetae, side view.

**Table 2.** Comparison of *Parasabella* species. Features included have been considered as diagnostic in the past and some chaetal ratios have also been included (measurements obtained from published drawings or material examined) and refer to Figure 5A and K: A/B, width hood/shaft; C/B, hood length/width; H/G, length of handle/distance from breast to main fang; E/F, length neck/breast; # cells, number of vacuolated cells supporting radioles, at base, in cross-section. *Parasabella columbi* (Kinberg, 1867), *Parasabella fernandezensis* (Augener, 1922), and *Parasabella rufovittata* (Grube, 1881) were excluded because the relevant information was not available

Gap between ventral shields and neuropodial tori	Radiolar eyes	Radiolar support # cells	Inferior thoracic chaetae			Thoracic uncini		Other features	Species	Reported distribution	References other than original description
			Type	A/B	C/B	H/G	E/F				
Absent. Thoracic ventral shields and neuropodial tori in contact	Absent	4	Type A	2-3	2-4	Short, < 1	0.2-0.3	Long dorsal lips and pinnular appendages. *Dorsal lips of medium length with one pinnular appendage. Radioles with short tips. Long dorsal lips, with 1-3 pinnular appendages.	<i>Parasabella langerhansii</i> (Knight-Jones, 1983) <i>Parasabella tommasi</i> (Giangrande, 1994)	Eastern Mediterranean, Atlantic (Madeira, UK) Mediterranean	Knight-Jones, 1983; Giangrande, 1994
		6-8	Type A	3	2.5-3	Medium, 1-1.5	0.5	Radioles with short tips. Long dorsal lips, with 1-3 pinnular appendages.	<b><i>Parasabella crassichaetae</i> sp. nov. complex</b>	Australia, Hawaii	-
		8	Type B	1.5-2	4-6	Medium, 1.5	0.3	Radioles with short tips. Medium dorsal lips with one pinnular appendage.	<i>Parasabella flecata</i> (Hoegland, 1919)	Puerto Rico	Knight-Jones, 1983
		8	Type B	1.25	5	Medium, 1.5-2	0.5-1	1-3 pinnular appendages.	<i>Parasabella jamaicensis</i> (Augener, 1924)	Jamaica	Perkins, 1984; Tovar-Hernández & Salazar-Vallejo, 2006
		?8-10	Type B	1.5	6	Medium, 1.5	1	1-3 pinnular appendages.	<i>Parasabella aulacnota</i> (von Marenzeller, 1884)	Japan	Examination of types
		8-10	Type B	2	5-6	Medium, 1-1.5	0.75		<i>Parasabella</i> sp. cf. <i>Parasabella aulacnota</i>	Australia	-
		8-10	Type A	3	3	Short, < 1	0.3	Long dorsal lips with one pinnular appendage.	<i>Parasabella brevithoracica</i> (Pillai, 1961)	Sri Lanka	Knight-Jones, 1983
		8-10	Type A	2	2-3	Medium, 1-1.5	0.2-0.5	Short dorsal lips with one pinnular appendage.	<i>Parasabella pallida</i> (Moore, 1923)	USA (California) and Mexico (Mazatlán)	Perkins, 1984; Tovar-Hernández <i>et al.</i> , 2009
		10	Type A	2-3	2-4	Medium, 1-1.5	0.2	Radioles with long tapering distal ends. One pinnular appendage.	<i>Parasabella saxicola</i> (Grube, 1861)	Mediterranean, Ireland	Knight-Jones, 1983; Giangrande, 1994
		> 10	Type A	2-3	2-3	Medium, 1.5	0.3	Short crown with long tapering tips. Long dorsal lips with one pinnular appendage.	<i>Parasabella brachycona</i> (Clararède, 1870)	Mediterranean, Ireland	Knight-Jones, 1983; Knight-Jones <i>et al.</i> , 1991; Giangrande, 1994
		13-16	Type B	1.5	5-6	Short, 1	0.3	Long dorsal lips with two pinnular appendages.	<i>Parasabella cambrensis</i> (Knight-Jones & Walker, 1985)	UK (Wales)	-
		16-20	Type B	1.5	4-5	Medium, 1-1.5	1	Dorsal swelling in thorax.	<i>Parasabella aberrans</i> (Augener, 1926)	New Zealand, Australia	Examination of types
		> 20	Type A	2-3	3-5	Medium, 1-2	0.5	Short dorsal lips with one pinnular appendage.	<i>Parasabella leucaspis</i> (Kinberg, 1867)	Widespread: western South and central America, Hawaii	Knight-Jones, 1983; Perkins, 1984.
		< 20	Type A	2-3	2-4	Medium, 1.5	0.5-1	Radioles with long tapering tips. Long dorsal lips.	<i>Parasabella media</i> Bush, 1905	Eastern Pacific Ocean (Alaska to Monterey Bay)	Examination of types Banse, 1979; Knight-Jones, 1983; Perkins, 1984



> 20	Type B	1.5	10–12	Medium, 1.5–2	0.5	‡Radioles in double rows. Medium length dorsal lips with three pinnular appendages. Radioles with short tips.	<i>Parasabella rugosa</i> (Moore, 1904)	Baja California to San Diego	Perkins, 1984
> 30	Type B	1.5	3–4	Long, 2.5–3.5	0.5–1	Radioles with long tips.	<i>Parasabella fullo</i> (Grube, 1878)	Japan	Buzhinskaja, 1985. Examination of types
?	Type B	?	?	?	1	Short collar	<i>Parasabella albicans</i> (Johansson, 1922)	Japan	Uchida, 1968, Examination of type
?	Type B	2–3	6–7	Medium, 1.5	1	Pale orange eyes present in ventral collar (needs confirmation).	<i>Parasabella octilea</i> (Pillai, 1965)	Philippines	Knight-Jones, 1983
?	Type A	2	3	Medium, 1.5	1	Radioles with blunt tips. Dorsal lips medium in length.	<i>Parasabella tenuicollaris</i> (Grube, 1870)	Mediterranean	Knight-Jones <i>et al.</i> , 1991; Giangrande, 1994
Present	Type B	2	5–6	Medium, 1.5–2	0.3–0.5	†Several small eyes randomly arranged	<i>Parasabella micropthalma</i> (Verrill, 1873)	Eastern North and South Americas	Perkins, 1984
Absent	Type A	2–3	3–4	Short, 1	0.5	Radioles with very long and strap-like tips. Long dorsal lips with one pair of pinnular appendages.	<i>Parasabella torilis</i> (Knight-Jones & Walker, 1985)	UK (Wales)	–
?	Type B	?	?	Medium, 1.5	1–1.5	Radioles with short tips. Abdominal uncini longer than wide.	<i>Parasabella japonica</i> (Moore & Bush, 1904)	Japan	–
6	Type B	1.5	9–10	Medium, 1.5	1.5–2	Abdominal uncini longer than wide.	<i>Parasabella</i> sp. cf. <i>Parasabella japonica</i>	Australia	–
6–8	Type B	2	7–8	Long, > 3	0.5	Radioles with short tip. Long dorsal lips with small pinnular appendage.	<i>Parasabella polarsterni</i> (Gambi <i>et al.</i> , 2001)	Antarctica	–
8–11	Type B	2	4–6	Medium, 1.5–2	0.3–0.5	Dorsal lips medium in length with one pair of pinnular appendages. Abdominal uncini longer than wide.	<i>Parasabella lacunosa</i> (Perkins, 1984)	Florida	–
Present	Type B	2–3	8–9	Medium, 2	1.5	One distal pair of eyes in midradioles.	<b><i>Parasabella bioculata</i> sp. nov.</b>	Australia	–

\*Radiolar spots described as eyes by mistake (A. Giangrande, pers. comm.).

†Examination of members belonging to this species showed that the radiolar spots are just pigment and not eyespots (Nogueira *et al.*, 2010).

‡According to Hartman (1965), radiolar eyespots are present but this is assumed here to be a mistake (after Perkins, 1984).



**Table 3.** Corrected (TrN, Tamura-Nei substitution model, below diagonal and in italics) and uncorrected (p-distance, above diagonal) pairwise genetic distances amongst *Parasabella* species cytochrome oxidase 1 sequences (including all codon positions); interspecific TrN genetic distances shown along the diagonal, in bold

	A	B	C	D	E
A. <i>Sabellomma cupocolata</i> sp. nov.	<b>0.027</b>	0.252	0.234	0.237	0.243
B. <i>Parasabella</i> sp. 2	<i>0.312</i>	–	0.227	0.234	0.250
C. <i>Parasabella</i> sp. cf. <i>P. aulacnota</i>	<i>0.283</i>	<i>0.277</i>	<b>0.016</b>	0.225	0.252
D. <i>Parasabella crassichaetae</i> sp. nov.	<i>0.289</i>	<i>0.286</i>	<i>0.275</i>	<b>0.000</b>	0.242
E. <i>Parasabella aberrans</i> spp. complex	<i>0.300</i>	<i>0.313</i>	<i>0.315</i>	<i>0.296</i>	<b>0.213</b>

**Table 4.** Corrected (TrN, below diagonal and in italics) and uncorrected (p-distance, above diagonal) pairwise genetic distances amongst *Parasabella* species internal transcribed spacer sequences; interspecific TrN genetic distances shown along the diagonal, in bold

	A	B	C	D	E	F	G
A. <i>Sabellomma cupocolata</i> sp. nov.	<b>0.003</b>	0.344	0.332	0.320	0.318	0.346	0.337
B. <i>Parasabella</i> sp. 2	<i>0.471</i>	–	0.115	0.202	0.193	0.161	0.200
C. <i>Parasabella</i> sp. cf. <i>P. aulacnota</i>	<i>0.449</i>	<i>0.126</i>	<b>0.005</b>	0.180	0.171	0.143	0.189
D. <i>Parasabella</i> sp. 1	<i>0.430</i>	<i>0.238</i>	<i>0.209</i>	<b>0.00</b>	0.223	0.224	0.234
E. <i>Parasabella</i> sp. cf. <i>P. japonica</i>	<i>0.425</i>	<i>0.226</i>	<i>0.199</i>	<i>0.269</i>	<b>0.071</b>	0.197	0.179
F. <i>Parasabella crassichaetae</i> sp. nov.	<i>0.479</i>	<i>0.189</i>	<i>0.165</i>	<i>0.274</i>	<i>0.237</i>	<b>0.106</b>	0.208
G. <i>Parasabella aberrans</i> spp. complex	<i>0.461</i>	<i>0.236</i>	<i>0.223</i>	<i>0.284</i>	<i>0.209</i>	<i>0.250</i>	<b>0.101</b>

obtained in RAxML v. 7.2.8 (Stamatakis, 2006) by optimizing the best topology out of 1000 random searches. Branch support (BS) was estimated with 1000 bootstrap pseudo-replicates (Stamatakis, 2006). Nucleotide divergence between sequence pairs within and between lineages was estimated in MEGA v. 6 (Tamura *et al.*, 2013). Only perfectly homologous regions (same length, same part of locus), eliminating uncertainties, positions containing gaps and missing data were considered (following Fregin *et al.*, 2012). Distances based in optimal substitution model (Tamura-Nei model, TrN, in this case) were used and compared with the uncorrected p-distances (Tables 3, 4). Comments about genetic distances in the Results section only refer to the corrected data. Distance between *cox1* sequences were calculated with (Table 3) and without third codon positions (not shown) and in all cases, this value was at least 50% larger for the latter.

To facilitate diagnoses, species-specific molecular diagnostic features are provided if using CAOS-Analyzer (Sarkar, Planet & DeSalle, 2008). This software can extract diagnostic character states from molecular sequences that have been hierarchically organized in a phylogenetic tree. Only nucleotides that are exclusive and unambiguous synapomorphies with a confidence factor of 1.0 were selected as diagnostic and if forming a block of at least four nucleotides.

## RESULTS

### MORPHOLOGICAL DATA

Examination of 322 specimens from different localities, habitats, and depths along the Australian coast allowed us to classify them into six more or less discrete morphotypes within *Parasabella* and one belonging to *Sabellomma*. Some of these forms are clearly identifiable by noticeable morphological features such as the presence of a unique type of radiolar eyes (i.e. *Parasabella biocolata* sp. nov.) or the presence of distinctively swollen anterior thoracic segments [i.e. *Parasabella aberrans* (Augener, 1926)]. In other cases, morphotypes were classified according to a unique combination of features that include discrete but also some continuous qualitative or quantitative traits. This can raise issues regarding the establishment of species boundaries, especially when there is overlapping between intra- and interspecific variation, or when little morphological variation can be assigned to disjunct and geographically distant populations. Consequently, the validity of some of the features previously considered as diagnostic is questionable. A summary of the characters used for classifying all accepted *Parasabella* nominal species, compiled from the literature and the present study, is presented in Table 2. Information on the species dealt with in the present study, together with comments regarding the intraspecific variation observed, is included. Additionally, some characters not

considered in previous species descriptions (such as the number of internal rows of vacuolated cells supporting the radioles or measurements from chaetae and uncini) are also included as they provide some useful taxonomic information. With the data currently in hand (species descriptions and examination of some types and additional material), and after taking into account the traditional and new proposed taxonomic features, some of the Australian morphotypes matched with the combination of characters attributed to previously described species: *Parasabella aulacnota* (von Marenzeller, 1884), *Parasabella japonica* (Moore & Bush, 1904), and *Parasabella rugosa* (Moore, 1904). As these species were originally described from different environmental conditions and distant biogeographical regions, and because types of the species or fresh material from the type locality were lacking, it was decided to refer to these specimens as 'comparable with' (cf.) the nominal species. These identifications should be confirmed in the future. A number of small specimens with juvenile appearance, in most cases possessing fewer than eight thoracic chaetigers, low abdominal chaetiger number, and expanded radiolar distal tips resembling flanges were also difficult to identify. They exhibit a mixture of features of different species or what appear to be juvenile structures. Owing to their indeterminate morphology, these specimens are not considered in the Taxonomic account section. Nevertheless, some of them were included in the molecular analyses, demonstrating that there are more species present in Australian waters than the ones described below (see *Parasabella* sp. 1 and sp. 2 in the phylogenetic hypotheses in Fig. 3A–C).

#### MOLECULAR DATA ANALYSES

DNA was successfully sequenced from 26 specimens with Australian origin and four from the USA. The phylogenetic relationships of the *Parasabella* specimens were assessed based on *cox1* sequences (16 terminals), including (Fig. 3A) and excluding third codon positions (not shown), ITS sequences (29 terminals, Fig. 3B), and combined data sets (30 terminals, including integral alignments, Fig. 3C). The best fitting amino acid substitution model for *cox1* was Hasegawa–Kishino–Yano, plus gamma (HKY + G) and Generalised Time Reversible plus gamma (GTR + G) for ITS sequences. *Parasabella* was recovered as monophyletic after analyses of the *cox1* fragments but as paraphyletic after analyses of the ITS sequences. The analyses combining both loci recovered *Parasabella* as monophyletic but with weak support (BS = 62; Fig. 3A–C).

The differences between the complete and reduced (omitting third codon position) *cox1* data sets did not affect the content or delineation of the lineages (i.e. species) herein considered, but their inter-relationships, poorly supported in both cases. When third codon po-

sitions (more susceptible to saturation) were omitted, *Parasabella crassichaetae* sp. nov. was recovered as paraphyletic, with the large clade branching of basally and PS09 sister to *P. cf. aulacnota*; *Sabellomma cupocolata* sp. nov. is nested within *P. aberrans* (not shown).

The phylogenetic hypotheses resulting from different data sets (*cox1*, ITS, and combined) are congruent and the initial identified morphospecies are herein recovered as well supported clades, supporting the current species concept. However, in some of these morphotypes, the intraspecific genetic variability is high (Fig. 3A–C; Tables 3, 4) and has a geographical component, with long branches separating geographically distant terminals in *P. aberrans*, *P. crassichaetae* sp. nov., *P. cf. japonica*, and *S. cupocolata* sp. nov. which may indicate strong geographic population structure or a complex of sibling species. Our analyses also revealed previously unsuspected genetic differentiation between specimens from the same or close localities (e.g. *P. crassichaetae* sp. nov. NSW clade and PS16, Fig. 3B, C), which may indicate the presence of sympatric species. *Parasabella aberrans* and *P. crassichaetae* sp. nov. may represent species complexes with no morphological variation (cryptic species) or if morphological differences have been observed between specimens, these are not congruent with the recovered subclades (see Remarks for each species in the Taxonomic section).

DNA sequences from juveniles with indistinct diagnostic features (radiolar crown appearing underdeveloped, low number of segments, etc.), for example, PS01, PS22, and PS38, were recovered within clades together with of the original proposed morphotypes. Nevertheless, other small specimens formed clade *Parasabella* sp. 1 and terminal *Parasabella* sp. 2 (Fig. 3A–C). *Parasabella* sp. 1 comprises two specimens, one collected in Darwin, Northern Territory, and the other from Hutchinson Island, Florida, showing no differences in the ITS sequences. This could be an indication of an unintentional translocation of members of an Australian population to Florida or in the opposite direction.

#### TAXONOMIC REVISION OF *PARASABELLA* IN AUSTRALIA

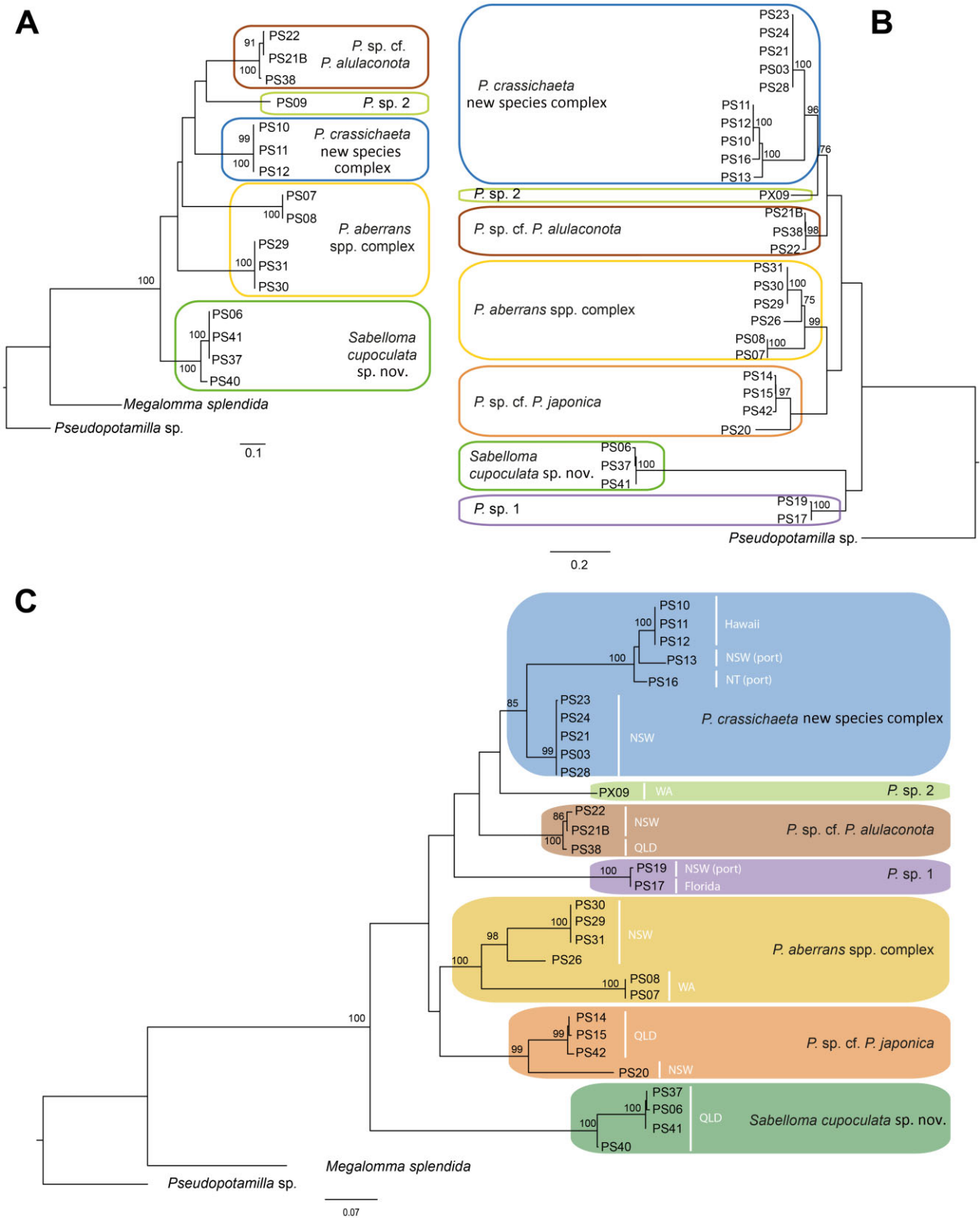
##### GENUS *PARASABELLA* BUSH, 1905, EMEDED

*Demonax* Kinberg, 1867: 354 (not Thomson, 1860); 1910: 72. – Johansson, 1925: 26–27; 1927: 136. – Knight-Jones, 1983: 254. – Perkins, 1984: 292–293. – Knight-Jones & Walker, 1985: 605. – Fitzhugh, 1989: 75–76. – Giangrande, 1994: 229–230.

*Parasabella* Bush, 1905: 191, 199–200. – Johansson, 1927: 136. – Tovar-Hernández & Harris, 2010: 14.

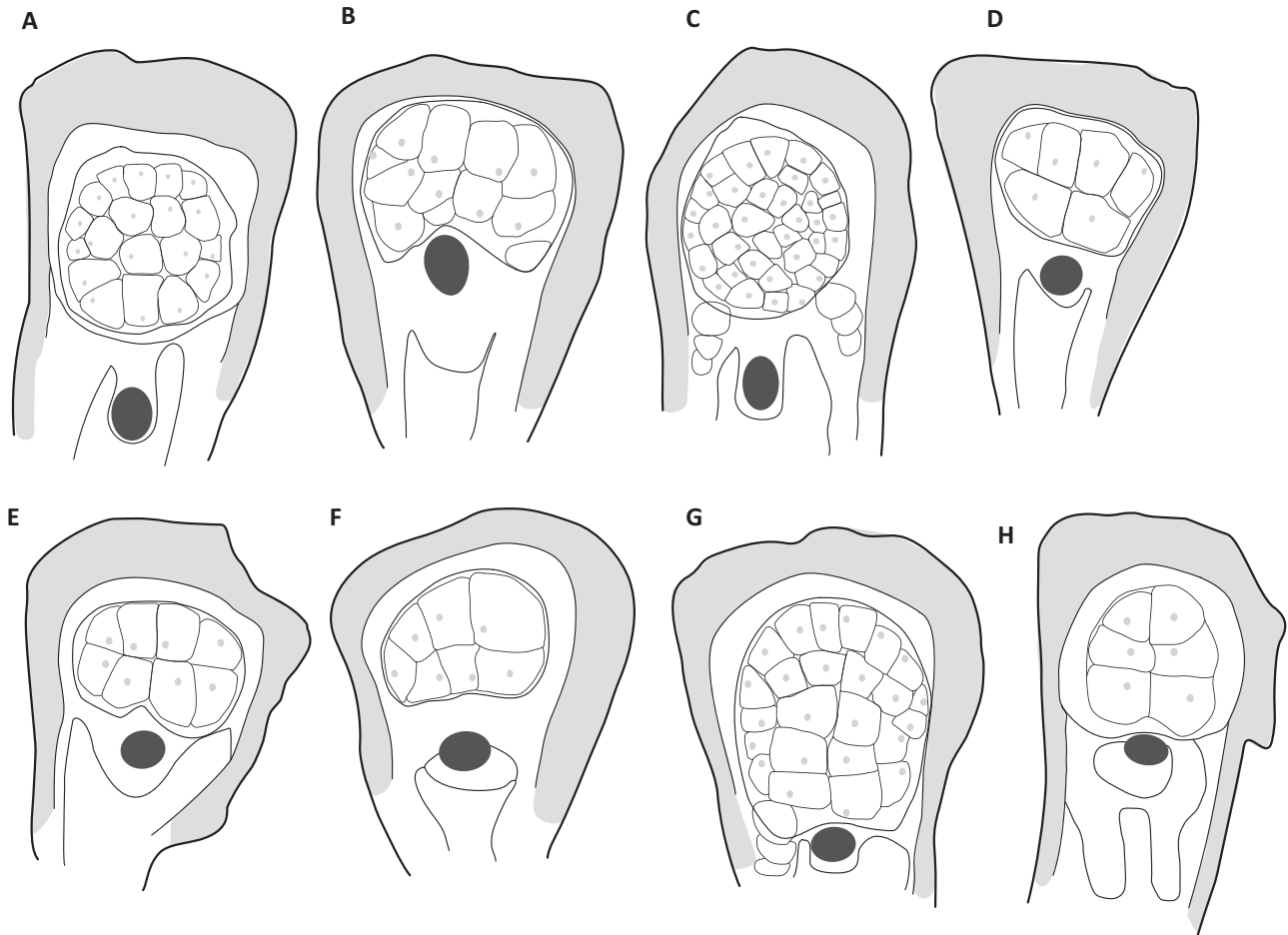
*Distyliidia* Hartman, 1961: 129. – Fauchald, 1977: 138. – Banse, 1979: 870.

*Type species: Parasabella media* Bush, 1905 (see Read, 2010, contrary to Tovar-Hernández & Harris, 2010).



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**Figure 3.** Maximum likelihood topologies. A, cytochrome oxidase 1 fragments. B, internal transcribed spacer fragment. C, combined data set. Bootstrap supports over 75% shown on nodes. Scale bar, average of nucleotide substitutions per site.



**Figure 4.** Cross-sections of radiolar crown near the base showing the supporting cartilaginous vacuolated cells in the rachis (with grey nuclei), surrounded by an extracellular cartilaginous sheath (white) and covered by columnar epithelium (grey). Upper side of drawings are the outer margin of radiolar crown; on the bottom incomplete pinnules are sketched with a blood vessel (black) in between. A, *Parasabella aberrans* spp. complex. B, *Parasabella* sp. cf. *Parasabella aulacnota*. C, *Parasabella fullo*. D, *Parasabella bioculata* sp. nov. E, *Parasabella crassichaetae* sp. nov. complex. F, *Parasabella* sp. cf. *Parasabella japonica*. G, *Parasabella* sp. cf. *Parasabella rugosa*. H, *Sabellomma cupocolata* sp. nov. A, AM W.36947; B, AMW.47009; C, ZMB 5731; D, AM W.46840; E, AM W.47181; F, AM W.36450; G, AM W.36431; H, AM W.47189.

**Diagnosis:** Thoracic neuropodial companion chaetae with subdistal end enlarged, conspicuous microtubercles forming hood, resulting in dentate appearance at base of hood, and with thin distal mucro compressed laterally.

**Description:** Sabellids ranging between 0.5 and 10 cm in length; thorax with four to eight chaetigers, and abdomen with numerous chaetigers. Radiolar crown with six to 60 pairs of radiolar lobes, arranged in one to three concentric semicircles or curling inwards ventrally. Radiolar crown supported basally by four to 40 rows of vacuolated cells in cross-section (Fig. 4A–H). Radiolar crown generally without flanges, but some species (or at least juveniles of some species) with distal flanges along radiolar tips (Fig. 14E, F); stylodes and basal mem-

brane absent. Radiolar eyes absent or present (Fig. 10G–I). Dorsal lips with long and tapering radiolar appendages and 0–3 pinnular appendages. Ventral lips and parallel lamellae present, ventral sacs absent. Peristomial eyespots present, subdermally and below radiolar lobes (Fig. 12C) or absent. Posterior peristomial ring collar with dorsal margins widely separated, not fused to faecal groove; lateral margins entire with no incisions; ventral margins with triangular or rounded ventral lappets and mid ventral incision. Thorax with eight or fewer chaetigers. Collar notochaetae elongate, narrowly hooded (e.g. Figs 7F, 9E, 11E, 13E, 15D). Notopodia of subsequent thoracic chaetigers with elongate, narrowly hooded chaetae in superior group (e.g. Figs 11E, 13F, 17B) and broadly hooded chaetae in inferior group (e.g. Figs 2A–F, 5A–J). Thoracic neuropodial uncini avicular,



**Figure 5.** Drawings of chaetae and uncini. A–H, broadly hooded inferior thoracic chaetae from midthoracic chaetiger. A, idealized chaeta showing the measurements taken for comparison amongst species (A: shaft width, B: hood maximum width, C: hood total length). B, *Parasabella aberrans* spp. complex. C, *Parasabella* sp. cf. *Parasabella aulaconota*. D, *Parasabella bioculata* sp. nov. E, *Parasabella crassichaetae* sp. nov. complex. F, *Parasabella* sp. cf. *Parasabella japonica*. G, *Parasabella* sp. cf. *Parasabella rugosa*. H, *Sabellomma cupocolata* sp. nov. I, idealized uncinus showing the measurements taken for comparison amongst species (A: length of main fang, B: length of neck, C: breast length, D: distance of breast to main fang, E: length of handle). J, K, M, O, P, R, U, W, Y, uncini from midthoracic chaetiger. J, K, *Parasabella aberrans* spp. complex (from specimens with a single and split dorsal swelling respectively). M, *Parasabella* sp. cf. *Parasabella aulaconota*. O, *Parasabella fullo*, P, *Parasabella bioculata* sp. nov. R, *Parasabella crassichaetae* sp. nov. complex. U, *Parasabella* sp. cf. *Parasabella japonica*. W, *Parasabella* sp. cf. *Parasabella rugosa*. Y, *Sabellomma cupocolata* sp. nov. L, N, Q, S, T, V, X, Z, midabdominal uncini. L, *P. aberrans* spp. complex. N, *P.* sp. cf. *P. aulaconota*. Q, *P. bioculata* sp. nov. S, T, *P. crassichaetae* sp. nov. complex. (two different morphotypes as in Table 5). V, *P.* sp. cf. *P. japonica*. X, *P.* sp. cf. *P. rugosa*. Z, *S. cupocolata* sp. nov. B, L, AM W.32586; K, AM W.36947; C, M, N, AM W.22480; D, P, Q, AM W.37054; E, T, AM W.47147; R, AM W.47178; S, AM W.47181; F, AM W.46988; U, V, AM W.36450; G, W, X, AM W.36431; H, Y, AM W.47189; J, W.36953; O, ZMB 5731; Z, AM W.47188. Scale bars = 100 µm.

with similar-sized teeth above main fang, well-developed breast, medium to long handles (at least longer than the distance from main fang to breast), and hood absent (Fig. 5L, M, O, Q, R, T, V, X, Z). Thoracic neuropodial companion chaetae with subdistal end enlarged, conspicuous microtubercles forming hood, resulting in dentate appearance, with thin distal mucro compressed laterally (Figs 7K, L, 9J, 11H, 13I, 15H, 17E, F). Abdominal neurochaetae narrowly hooded in both anterior and posterior groups (Figs 7M, 9L, 13J, 15I, 17G). Abdominal uncini similar to thoracic but with shorter handles (Fig. 5J, K, M, O, P, R, S, U, W, Y). Numerous abdominal chaetigers. Pygidium a rim around ventral anus (Figs 7O, 13L), eyespots present or absent.

*Remarks:* Even though the monophyly of *Parasabella* has not herein been assessed, members of this genus are characterised and distinguished from other sabellids by the subdistal dentate condition of the companion chaetae (after Fitzhugh, 1989). *Parasabella* species are also unique because of the shape of the distal mucro of the companion chaetae as it is compressed laterally. By contrast, all other sabellids including other closely related genera such as *Sabellomma* and *Megalomma* Johansson, 1927 show a distal enlargement of the chaetae (often referred to as a hyaline membrane) that is flattened transversely and has a more or less symmetrical shape. The present study is the first report of radiolar flanges in members of this genus. This feature was observed in small specimens of juvenile appearance (Fig. 14E, F) whose identification to species was often not possible, indicating that it could be a developmental feature not present in adults. The emendation of the genus is also justified by the greater variety of types and arrangements of eyespots than previously documented. Perkins (1984: 304) described *Parasabella microphthalma* (Verrill, 1873) as possessing a pair of prostomial eyes, which could refer to the peristomial eyes mentioned herein. They appear to be present in

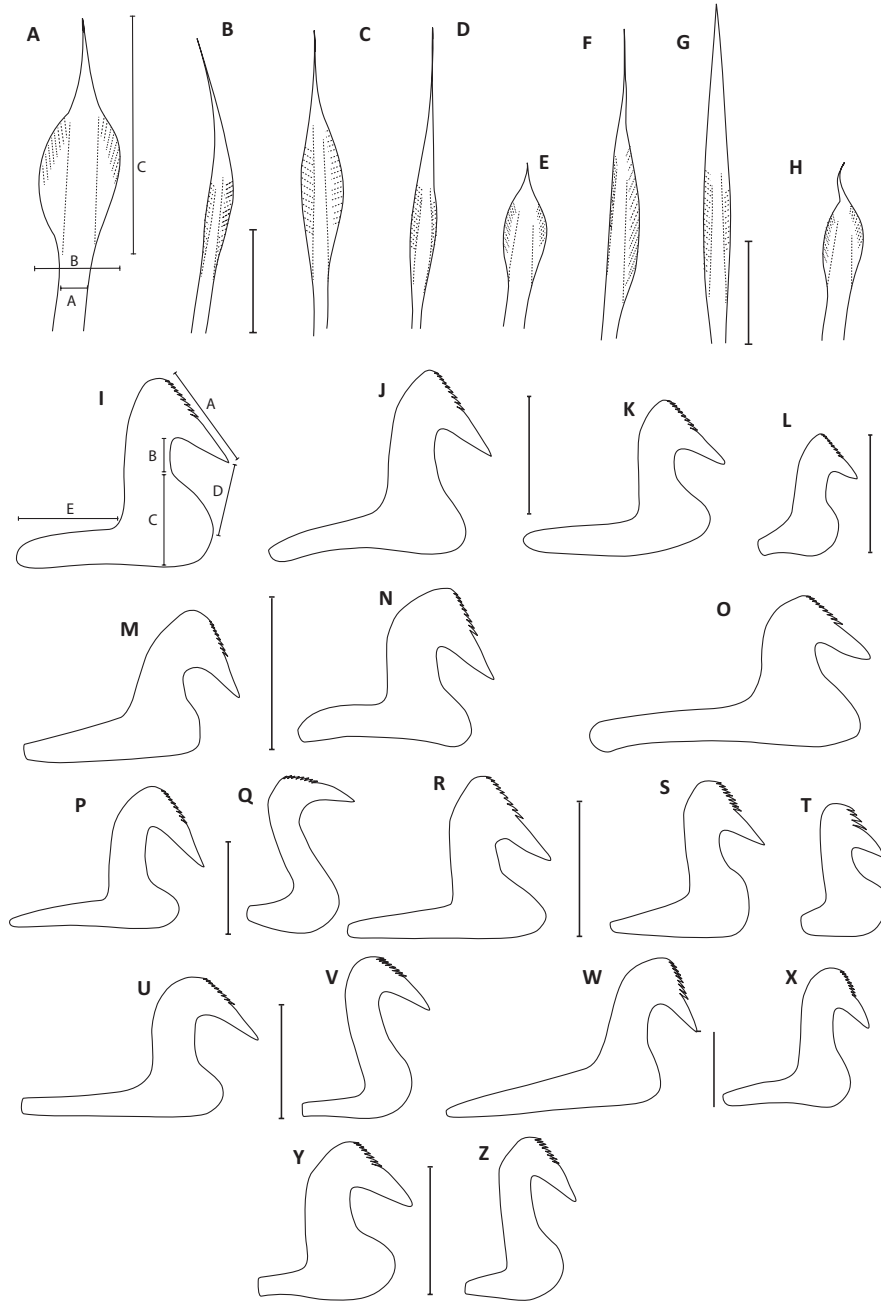
all specimens examined for this paper, being embedded, mid-lateral on the peristomium, near the bases of the dorsal lips (see Fig. 12C) and need to be re-examined in other species in the genus. Eyespots have also been reported in the ventral lappets in *Parasabella oculus* (Pillai, 1965), although confirmation of the nature of these spots is needed as this is a unique feature amongst sabellids. Radiolar eyes have previously been described in *P. microphthalma* as ‘simple eyespots’ (Perkins, 1984: 303–304, Fig. 6A–C) and in *Parasabella tommasi* (Giangrande, 1994) as ‘large lenticular eyes irregularly arranged’ (Giangrande, 1994: 230). Specimens collected from the type locality of *P. microphthalma*, which share other diagnostic features, lack eyespots and instead possess pigment spots, raising questions about the true nature of the spots described in the original description (Nogueira *et al.*, 2010: 5). However, Perkins (1984) drew the detailed structures of these, which appear to resemble closely the eyes described for *Sabellomma*. Further detailed examination has confirmed that the voluminous spots in the radioles of *P. tommasi* are just pigmented epithelial cells and not lenticular eyes (Giangrande, pers. comm.). Radiolar eyes were also reported to be present in *Parasabella flecata* Hoagland, 1919, and in *P. fullo* (according to A. Giangrande, 1994: 230). Examination of syntypes of *P. fullo* for the present study confirmed the lack of radiolar eyes. Similarly, radiolar eyes can be presumed to be absent from *P. flecata* as they were not mentioned in the original or further descriptions (Hoagland, 1919; Knight-Jones, 1983; Buzhinskaja, 1985).

*PARASABELLA ABERRANS* (AUGENER, 1926) SPP.  
COMPLEX (FIGS 2C, 4A, 5B, J–L, 6, 7)

*Sabella aberrans* Augener, 1926: 245–253, fig. 18.

*Sabella porifera* – Augener, 1914: 106–109 (in part).

*Demonax aberrans* – Knight-Jones & Perkins, 1998: 404.



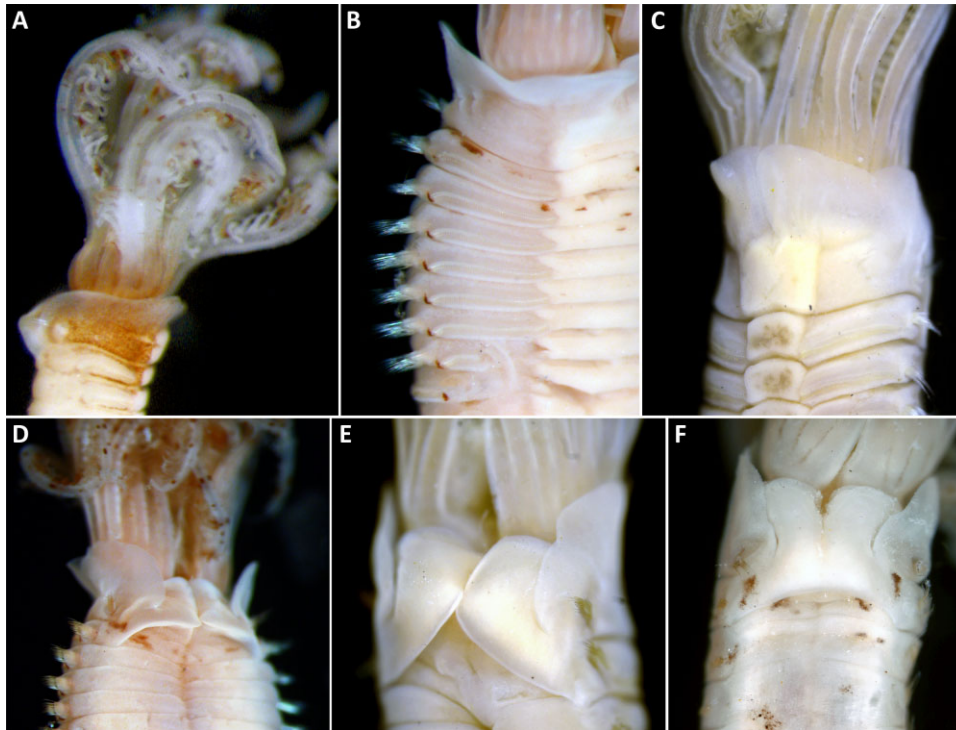
*Parasabella aberrans* – Tovar-Hernández & Harris, 2010: 14.

*Holotype*: ZMUC-POL-2115, Little Barrier Island, New Zealand, 55 m depth, 29.xii.1914, Dr Th. Mortensen Pacific Expedition.

*Additional material examined* (see Appendix for details): Western Australia: Bunbury (one); Ningaloo reef (three); Northern Territory: Darwin Harbour (one); Queensland: Lizard Island (three); New South Wales: Coffs

Harbour (one), Port Stephens (eight), Newcastle (four), Malabar (one), Botany Bay (12), Port Kembla (one), Bass Point (one), Jervis Bay (two), Ulladulla (two), Tathra (three), Batemans Bay (one), Point Upright (one), Eden (eight), Twofold Bay (eight); South Australia: Kangaroo Island (nine), Port Hughes (two).

*Diagnosis*: Stiff, fleshy swelling occupying dorsum of first two chaetigers, with transverse ridge and forming posterior-facing pocket(s), either continuous across dorsum or separated by faecal groove (synapomorphy



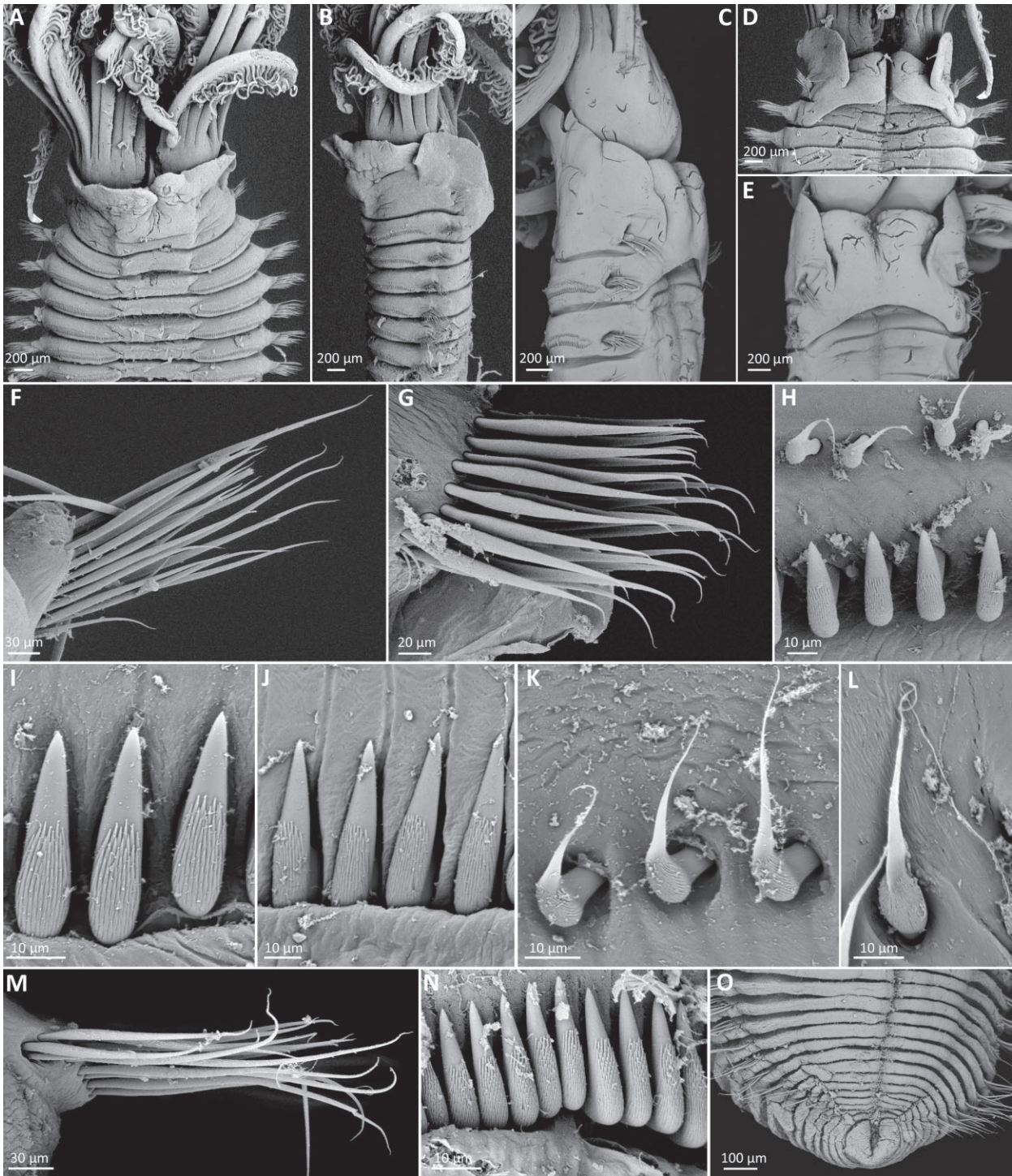
**Figure 6.** *Parasabella aberrans* spp. complex, colour micrographs. A, crown and anterior thoracic segments, lateral view. B, thoracic chaetigers showing ventral shields in contact with neuropodial tori. C, anterior thoracic chaetigers and base of crown, showing collar ventral lappets and shape of ventral shields. D, anterior thoracic segments in dorsal view, showing the stiff fleshy swelling separated by the faecal groove. E, same. F, fleshy swelling continuous across dorsum. A, AM W.36946; B, D, AM W.36935; C, E, AM W.36430; F, AM W.32018.

for this species complex). Radiolar eyes absent. Radioles supported basally by 14–20 rows of vacuolated cells in cross-section. Thoracic ventral shields in contact with neuropodial tori. Inferior thoracic notochaetae broadly hooded, of type B; hoods 1.5 times the width of shaft, and as long as four to five times maximum width. Thoracic uncini with medium-length handles.

*Description of Australian specimens:* 2.3 to 35 mm long, 0.5 to 3 mm wide, 5–8 thoracic chaetigers, 20 to > 60 abdominal chaetigers. Radiolar crown with long basal lobes (~ two thoracic segments), radioles arranged in two semicircles, curling inward in larger specimens. Six to 14 pairs of radioles, each supported basally by 14–20 rows of vacuolated cells in cross-section (Fig. 4A). Radioles with wide, tapering tips, bare for the length of two thoracic segments. Radiolar flanges and eyes absent. Dorsal lips with radiolar appendages as long as 4–6 thoracic segments; 0–2 dorsal pinnular appendages. Posterior peristomial ring collar of even length all way round (Figs 6B, 7A, B) or oblique laterally (Fig. 7C), reaching junction of crown and thorax (Figs 6A, 7C), with midventral incision and broad ventral lappets with rounded anterior margins (Figs 6C, 7A); dorsal margins subquadrate (Figs 6D–F, 7D, E). Peristomial

eyes shallowly embedded under base of radiolar crown. Fleshy swelling with transverse ridge, occupying dorsum of first two chaetigers, forming either two posterior-facing sinuses or pockets separated by faecal groove (Figs 6D, E, 7D), or continuous across faecal groove forming one large posterior-facing pocket (Figs 6F, 7E). Ventral glandular shields similar in width to each other, in contact with tori (Figs 6B, C, 7A); first ventral shield one to two times length of following, with anterior margin m-shaped (Fig. 6C). Collar chaetae elongate, narrowly hooded (Fig. 7F). Superior thoracic notochaetae elongate, narrowly hooded, inferior group with two rows of shorter broadly hooded chaetae of type B (Figs 2C, 5B, 6G), with hoods as long as 4–5 times maximum width and maximum width 1.5 times width of shaft. Thoracic neuropodial tori slightly diminishing in width posteriorly (Figs 6B, 7A, B). Uncini with about 10 rows of similar-sized teeth above main fang, covering more than half length of main fang (Fig. 7I, J), neck as long as breast, well-developed breast and medium-length handles (~1.5 times distance from main fang to breast) (Fig. 5J, K). Companion chaetae with enlarged subdistal end, conspicuous microtubercles forming hood, resulting in dentate appearance, with thin distal mucro compressed laterally (Fig. 7K, L). Abdominal neuropodial





**Figure 7.** *Parasabella aberrans* spp. complex, scanning electron microscope photographs. A, anterior thoracic chaetigers and base of radiolar crown, ventral view. B, same, showing collar, lateral view. C, collar dorsal margins, lateral view. D, collar dorsal margins and fleshy swelling divided in two by faecal groove, dorsal view. E, fleshy swelling continuous across dorsum. F, elongate, narrowly hooded collar chaetae. G, inferior thoracic notochaetae (broadly hooded, type B). H, thoracic uncini and companion chaetae. I, J, thoracic uncini from specimens with continuous and divided dorsal swellings, respectively. K, L, companion chaetae from specimens with continuous and divided dorsal swelling, respectively. M, midabdominal, narrowly hooded neurochaetae. N, abdominal uncini. O, posterior abdominal chaetigers and pygidium, ventral view. A, B, D, F, G, H, M, N, AM W.36935; C, E, J, L, O, AM W.32018; I, K, AM W.36430.



chaetae narrowly hooded in both anterior and posterior rows (Fig. 7M). Abdominal uncini with about 10 rows of similar-sized teeth above main fang covering more than half length of main fang (Fig. 7N), neck shorter than breast, well-developed breast and short handles (0.5 times distance between breast and main fang, Fig. 5L). Pygidium as rounded rim around ventral anus (Fig. 7O), with scattered eyespots present on both sides, only visible in some specimens.

*Colour pattern:* Brown pigmentation on bases of radioles and on groups of pigmented pinnules (Fig. 6A, D) in some specimens. Scattered pigment spots present along longitudinal axis of radioles (Fig. 6A, D). Some specimens with brown pigment on thorax, absent from ventral shields and tori (Fig. 6A–C). Spots present between neuro- and notopodial rami, superficially resembling interramal eyespots (Fig. 6B), faded in some specimens.

*Reproductive features:* Gravid specimens with body lengths of 10–35 mm were found, with eggs in last thoracic and in abdominal segments.

*Genetic data:* Sequences from two specimens from Western Australia and four from New South Wales show wide genetic variation, congruent with their geographical distribution, with the physically most distant specimens showing the largest genetic divergence (of up to 23.6% in *cox1* and 10.2% in ITS sequences). Genetic distance in *cox1* sequences to the other *Parasabella* species is 29.6–31.5% (Table 3) and 20.9–28.4% in ITS (Table 4). All members of this clade exclusively show the nucleotide sequence TGGGA in positions 173–176 of the ITS alignment, amongst several scattered one-nucleotide synapomorphies along the nuclear and mitochondrial fragments.

*Remarks:* This species is easily distinguished from other congeners by the fleshy swellings on the dorsum of the first two chaetigers. Augener (1926: 247, fig. 18A, B) illustrated this very distinctive feature in his original description. However, variations have been found amongst Australian specimens, as some show the swelling as a continuous transverse ridge with a single large posterior-facing sinus and without the faecal groove and cilia running longitudinally across this structure. The two morphological conditions (continuous, or dual dorsal swelling across anterior thoracic segments) are not congruent with the two subclades that show maximum genetic divergence. PS26 (from New South Wales) is the only specimen included in the genetic analyses with a continuous transverse dorsal swelling whereas the rest of specimens (New South Wales and Western Australia) present the dual split structure across the dorsum.

*Parasabella aberrans* was recorded in Australia, albeit as part of the material of *Sabella porifera* Grube, 1878, by Augener (1914) from Shark Bay in Western Australia, before he subsequently described it from Little Barrier Island in New Zealand (see Augener, 1926). Further collecting within the distribution range will determine if this species is broadly distributed but with great genetic population structure, or whether there has been a lack of gene flow between two populations from distant localities that can be interpreted as an indication of separate, closely related species that show no morphological variation (cryptic species).

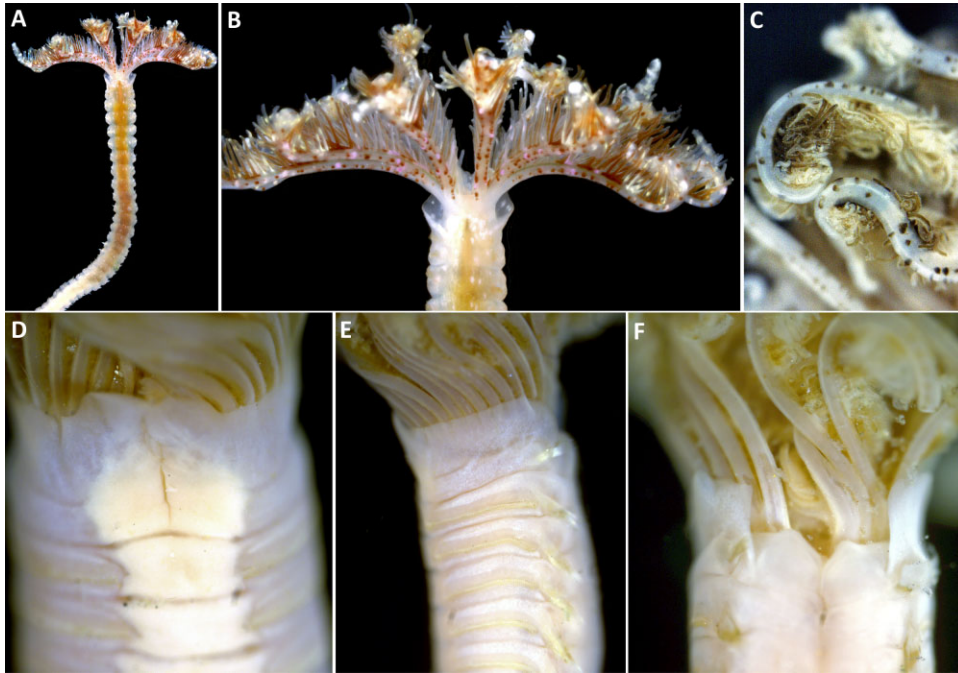
*Type locality:* Little Barrier Island, New Zealand, 55 m depth.

*Distribution:* New Zealand, Australia (Queensland, New South Wales, South Australia, Western Australia; Fig. 1A).

*Ecological notes:* The species is widespread in New Zealand but usually occurs as single individuals on wharf piles (G. Read, pers. comm.). It was reported in New Zealand Port surveys from 2005–2008 (Inglis *et al.*, 2005, 2006, 2008). In Australia, it has been recorded not only in the fouling communities from wharf piles in port areas (Port Kembla, Eden, Botany Bay and Bunbury Harbour, see Appendix), but has also been collected from more pristine coastal and offshore environments such as Lizard Island in Queensland, Kangaroo Island in South Australia, and south of Jervis Bay, New South Wales, from the intertidal to 80 m depth. In future, genetic studies of New Zealand populations should also be included to evaluate the broad distribution range reported for the species to determine if this can be explained through natural means or if unintentional translocations could be responsible for such a wide distribution (not detected in this study).

*PARASABELLA* SP. CF. *P. AULACONOTA* (VON MARENZELLER, 1884) (FIGS 2B, 4B, 5C, M, N, 8, 9)  
*Sabella aulacnota* von Marenzeller, 1884: 210, pl. 2, fig. 8. – Johansson, 1927: 124–125. – Fauvel, 1936: 84. – Okuda, 1939, 241, textfig. 13.  
*Demonax aulacnota* – Imajima & Hartman, 1964: 356.  
*Demonax aulacnotus* – Perkins, 1984: 294.  
*Parasabella aulacnota* – Tovar-Hernández & Harris, 2010: 15.

*Material examined (see Appendix for details):* Western Australia: Outer Bunbury Harbour, [four, including one by scanning electron microscopy (SEM)]; Northern Territory: Darwin Harbour (five); Queensland:



**Figure 8.** *Parasabella* sp. cf. *Parasabella aulacnota* colour micrographs. A, B, live specimen, anterior end, dorsal view. C–F, preserved specimen. C, detail of remaining pigmentation on radioles. D, anterior end showing collar margins, ventral lappets, ventral shields, and neuropodial tori. E, anterior end, lateral view. F, anterior end, dorsal view, showing dorsal collar margins. A, B, AM W.35612; C, AM W.47006; D–F, AM W.22480.

Townsville (> 100); Heron Island (one = PS38); New South Wales: Port Stephens (one); Newcastle, (14); Port Jackson (43, including one by SEM); Botany Bay area (five, including PS01, PS22); Port Kembla (32).

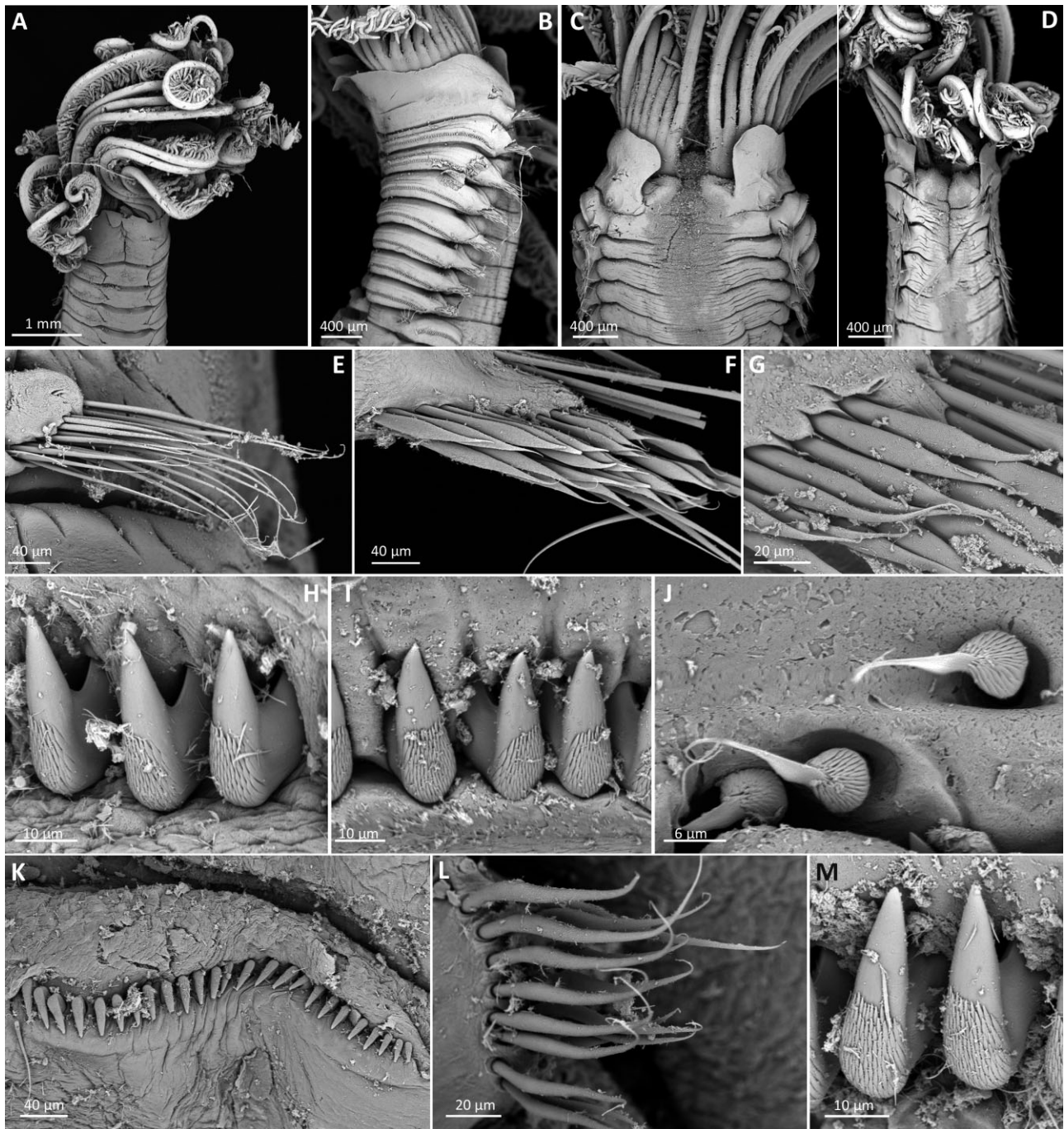
*Comparative material examined:* Holotype of *Demonax leucaspis* Kinberg, 1867, SMNH 575, Peru, east of Lima, San Lorenzo Island, 12°00'S, 077°00'W, collected by Eugenie Expedition 1851–1853 station 568–9. Holotype of *Sabella albicans* Johansson, 1922, UPSZTY 2304, Japan, Misaki, 'Diver' from *Laminaria*, S. Bock collection. Syntypes of *Demonax fullo* (Grube, 1878) ZMB 5731, five complete specimens plus one detached crown. *Parasabella aulacnota*, AM W.37073 (one), Japan, Sagami Bay, Koshigoe near Fujisawa, 35°18'20"N, 129°29'40"E, collected and identified by E. Nishi, 2004.

*Diagnosis:* Radiolar eyes absent. Radioles supported by eight to ten rows of axial cells near the base. Thoracic ventral shields in contact with neuropodial tori, inferior thoracic notochaetae broadly hooded with progressively tapered tips (type B), hood width 2.5 times width of shaft, and as long as five times maximum width. Thoracic uncini with medium-length handles, and neck as long as breast or slightly shorter.

*Description of Australian specimens:* Four to 30 mm long, 0.8–4 mm wide, and 35 to > 60 abdominal

chaetigers. Radiolar crown with basal lobes as long as two thoracic segments, arranged in two semicircles, involute ventrally in larger specimens. Seven to 22 pairs of radioles, with vacuolated cells supporting the radioles numbering eight to ten in cross-section near base (Fig. 4B); radiolar tips wide, tapering, bare for length of approximately 1.5 thoracic segments. Radiolar flanges and eyes absent. Dorsal lips with radiolar appendages as long as four thoracic segments, 1–2 pairs of pinnular appendages. Posterior peristomial ring collar reaching almost to level of base of radioles, of even height all around except for narrow and elongate ventral lappets with rounded anterior margins (Figs 8D, 9A, B); collar dorsal margins subquadrate, or convex and flap-like in larger specimens (Figs 8F, 9C, D). Peristomial eyes present, subdermal. Anterodorsal fleshy swelling absent. Thoracic ventral shields similar in size, 1.5 to two times wider than long, in contact and indented by adjacent neuropodial tori, first shield anterior margin m-shaped. Collar chaetae elongate, narrowly hooded (Fig. 9E). Superior thoracic notochaetae elongate, narrowly hooded; inferior group with two rows of shorter, broadly hooded chaetae of type B, with hoods two to three times width of shaft, and five times as long as maximum width (Figs 2B, 5C, 9F, G). Thoracic neuropodial uncini with about eight to ten rows of similar-sized teeth above main fang, covering half length of main fang (Fig. 9H, I), neck shorter than





**Figure 9.** *Parasabella* sp. cf. *Parasabella aulaconota* scanning electron microscope photographs. A, anterior thoracic chaetigers and base of radiolar crown, ventral view, with ventral shields in contact with neuropodial tori. B, same, showing the collar, lateral view. C, collar dorsal margins, lateral view. D, anterior thoracic chaetigers and base of radiolar crown, showing collar dorsal margins, dorsal view. E, collar chaetae, elongate, narrowly hooded. F, thoracic elongate, narrowly hooded superior notochaetae and inferior, broadly hooded (type B) chaetae. G, detail of inferior thoracic chaetae. H, I, thoracic uncini from specimens collected in temperate and tropical sites, respectively. J, companion chaetae. K, complete row of uncini in abdominal notopodia, showing the range in size from dorsal- to ventral-most uncini. L, midabdominal narrowly hooded neurochaetae. M, abdominal uncini. B, C, F, H, K–M, AM W.22017; A, D, E, G, I, J, AM W.22480.

breast, well-developed breast and medium-length handles (one to 1.5 times the distance from main fang to breast; Fig. 5M). Thoracic neuropodial companion chaetae with subdistal end enlarged, conspicuous microtubercles forming hood, resulting in dentate appearance, and thin distal mucro compressed laterally (Fig. 9J). Abdominal chaetae narrowly hooded in both anterior and posterior rows (Fig. 9L), uncini with around ten to 11 rows of similar-sized teeth above main fang covering about half length of main fang (Fig. 9M), neck as long as breast, breast well-developed and medium-size handle (one to 1.5 times the length of the distance between breast and main fang, Fig. 5N). Pygidium a rounded lobe, with groups of discrete dark pigment eyespots.

*Colour pattern:* Radiolar crown with highly variable pigment pattern. Some specimens possess pigmented groups of pinnules with some also having discrete spots along longitudinal axes on some radioles; others have faded pigment spots on only a few radioles (Fig. 8C). Pigment absent on body or light brown pigment on dorsum of body present in some preserved specimens (Fig. 8D, E, F). White spots in live specimens (Fig. 8A, B).

*Reproductive features:* Gravid females were found, measuring 7–30 mm long (excluding crowns), with eggs in abdominal segments.

*Genetic data:* Sequences were obtained from juvenile specimens (PS01, PS22, with short collars, and only five to six thoracic segments) that were assigned with some uncertainty to this species (the number of vacuolated cells in the radioles was not verifiable, but the remaining features were similar to other specimens identified as members of this species, e.g. PS38). Little intraspecific variation was found among the *cox1* and ITS sequences (1.5 and 0.6%, respectively; Tables 3, 4) of three specimens from two sites in New South Wales and one in Queensland. The genetic distances to other lineages were 27.5–31.5% if comparing mitochondrial and 12.6–22.3% if comparing nuclear sequences. These three specimens are characterized by sharing 23 unique nucleotides scattered along the *cox1* fragment and diagnostic blocks such as AACATT (221–226 nucleotide positions), AACCGCACTTGTGCGGTTAAAGCACT (375–400 nucleotide positions), and AAGACCAGTCCACAC CACCAGCCTATGAA (551–579 nucleotide positions) in the ITS alignment.

*Remarks:* Examined Australian specimens resemble *P. aulacnota* (von Marenzeller, 1884), described from Japanese waters. The original illustrations by von Marenzeller (1884) (plate 2, fig. 8A–D) show thoracic uncini with handles approximately 1.5 times the distance from the breast to main fang, and the thoracic

inferior notochaetae appear to be of type B, with hoods about six times their maximum width, similar to the specimens from Australia described herein. Even though the species was originally described as lacking pigmentation, examination of a specimen from Sagami Bay, Japan (6.5 mm long excluding crown, 0.6 mm wide, 46 abdominal segments, with nine pairs of radioles, and matching the diagnosis of *P. aulacnota* in the number of vacuolated cells supporting the radioles and the morphology of chaetae and uncini), revealed two faded pale brown transverse pigment bands in the radiolar crown. The body was without obvious pigmentation except for some residual pigment present in the first ventral shield. This Japanese specimen also resembles the Australian specimens as it has a collar reaching to the base of the radioles, with ventral margins forming elongate lappets covering the base of the radioles. However, the geographical distance between the reported distribution range of *P. aulacnota* and the Australian specimens and some overlapping features with other *Parasabella* species justify the need to confirm the true identification of the Australian specimens. Synonymies of this species with *Parasabella leucaspis* and *P. media* (Perkins, 1984) have been suggested in the past (Johansson, 1927; Monro, 1933). However, the number of vacuolated cells supporting their radioles seems to be a conspicuous difference between them (Table 2). Moreover, both *P. leucaspis* and *P. media* possess type A inferior thoracic chaetae, in contrast to these Australian specimens, which possess only type B chaetae.

Other *Parasabella* species reported from the Pacific Ocean that possess thoracic ventral shields in contact with the neuropodial tori and type B inferior thoracic notochaetae are *Parasabella albicans* (Johansson, 1922), *P. fullo*, and *P. rufovittata*. *Parasabella rufovittata* has only been reported once, from Singapore, with a brief description lacking illustrations and so comparisons are of limited use. Similarly, the original description of *P. albicans* from Japan, with holotype measuring 13.5 mm long excluding crown, and 1.2 mm wide, is brief and lacks information about some of the specific diagnostic features herein considered important (see Table 2). The poor condition of the examined holotype did not allow dissections of radioles, and chaetae were broken or missing. Differences between *P. albicans* and *P. aulacnota*, from the literature, rely on features that are presumed to vary with size and fixation processes such as the collar length (short dorsally and only reaching to the junction of the crown base and the peristomium in *P. albicans* and as long as the radiolar base in *P. aulacnota*) and the maximum number of radioles (nine pairs of radioles in *P. albicans* and up to 33 in *P. aulacnota*) (von Marenzeller, 1884; Johansson, 1922, 1927; Okuda, 1939; Uchida, 1968). Therefore, although the separation of these two species is not evident, the similarities based on these probably unreliable



features justify the need to confirm the identification of the Australian specimens as *P. aulacnota*. *Parasabella fullo* was mistakenly omitted from a recent list of valid species of *Parasabella* (Tovar-Hernández & Harris, 2010). After examination of Grube's syntypes of *Sabella fullo* (which comprised five complete but damaged specimens ranging from 17–52 mm in body length excluding crown, with 14–27 pairs of radioles, plus an extra detached crown, and a sixth specimen that had previously been re-identified, by an unknown person, as a specimen of *Bispira*), differences are apparent. *Parasabella fullo* has numerous rows of axial cells supporting the radioles at their base (> 30 cells, Fig. 4C) and long-handled thoracic uncini (2.5 times the distance between the fang and the breast, Fig. 5Q), unlike *P. aulacnota*, which has handles 1–1.5 times the distance between the fang and the breast and 8–10 rows of cells supporting the radioles. *Parasabella flecata* described from Puerto Rico resembles *P. aulacnota* in the morphology of the inferior thoracic chaetae and number of axial cells supporting the radioles. However, *P. flecata* seems to have thoracic uncini with a broader breast and shorter neck when compared with those of *P. aulacnota* (Table 2).

*Type locality:* Nagasaki, Japan.

*Distribution:* Japan and (Western Australia, Northern Territory, Queensland, and New South Wales) (Fig. 1A).

*Ecological notes:* This species is found on hard substrates. In Australia, it inhabits mainly harbour and port environments (e.g. on pier pylons) but it has also been collected from hard substrates from the inter-tidal to 20 m depth in a few natural environments (Appendix).

***PARASABELLA BIOCULATA* SP. NOV.** (FIGS 2D, 4D, 5D, P, Q, 10, 11)

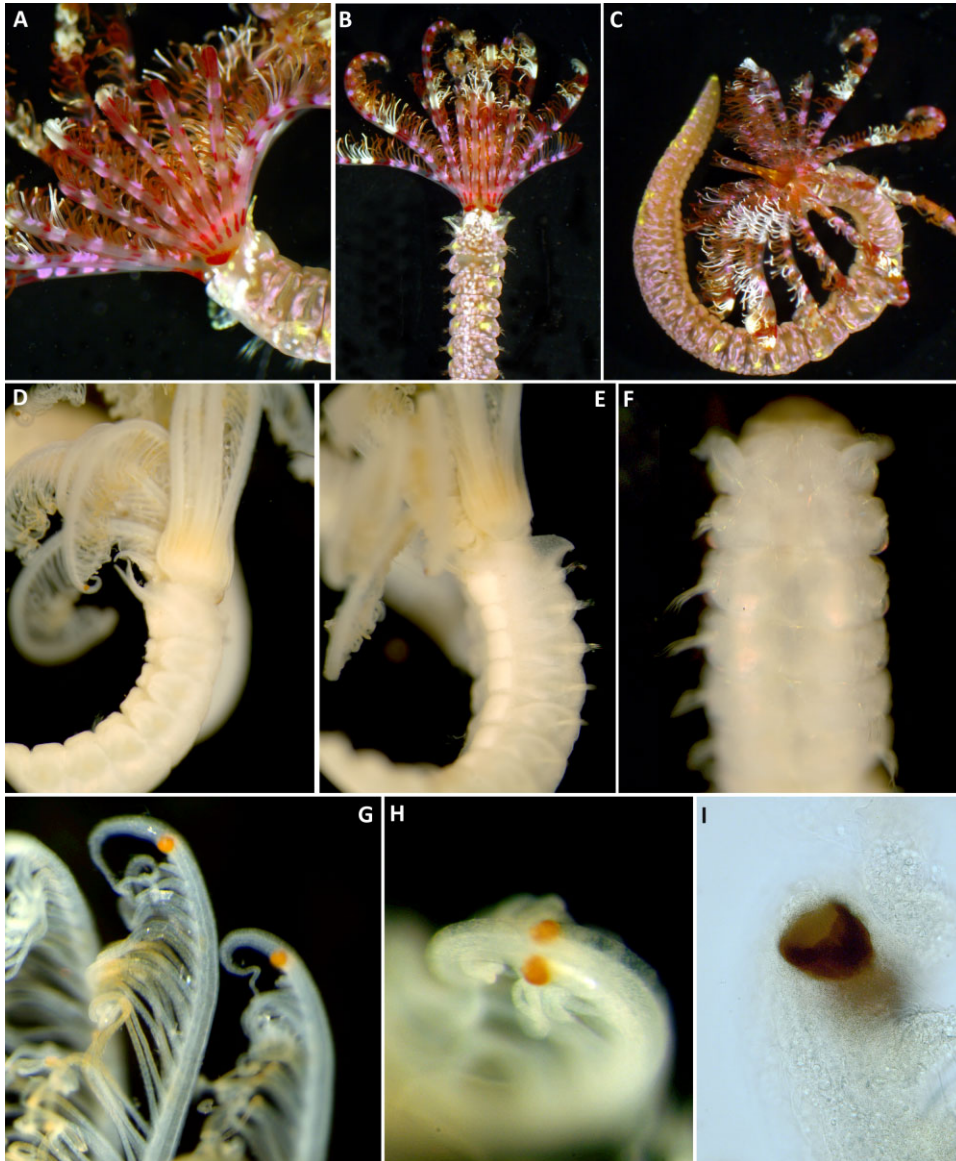
*Holotype:* Australia. Queensland, AM W.37054 (1), Heron Island, Lamont Reef, 23°35'56"S, 152°03'02"E, coral rubble, 30 m depth, xi.2009.

*Paratypes:* Queensland, AM W.37055 (one), AM W.37056 (one), Heron Island, Sykes Reef, 23°25'56"S, 152°02'02"E, coral rubble, 15 m, xi.2009, CReefs Heron Island Expedition 2009, MI QLD 2102; AM W.37053 (one, live photo), AM W.36449 (one, by SEM), same locality, coarse coral rubble, 30 m, 14–16.xi.2009, CReefs Heron Island Expedition 2009, MI QLD 2073.

*Additional material examined (see Appendix for details):* Australia. Western Australia: Ningaloo Reef (one). New South Wales: Port Stephens (one). Timor-Leste: Atauro Island (one).

*Diagnosis:* Paired radiolar eyes on tips of radioles (autapomorphy). Radioles supported by six rows of axial cells near base. Thoracic ventral shields separated from neuropodial tori by wide gap. Inferior thoracic notochaetae type B, with hoods 2–3 times width of shaft, and 8–9 times as long as maximum width. Thoracic uncini with medium-length handles, and neck longer than breast.

*Description:* Holotype 10 mm long, 1.5 mm wide, radiolar crown length 5 mm. Thorax with eight chaetigers, abdomen with 46, posterior end regenerating. Preserved body colourless, a few longitudinal brown streaks on radiolar base, dorsal lips and radiolar appendages with brown pigment, and crown with about three transverse bands with pigmented pinnules. Radiolar crown with short basal lobes as long as one thoracic segment, arranged in two semicircles (Figs 10A–C, 11A–D). Six pairs of radioles with rounded edges, flanges absent, with six rows of vacuolated cells supporting each radiole near base (Fig. 4D). Radiolar tips short, thin, and bare distal to eyes (approximately the length of one thoracic segment). Radiolar flanges absent. Paired, distal, apparently simple radiolar eyes present in most radioles except for ventral-most (developing) and several dorsal-most (regenerating). Radiolar eyes spherical, bright red, and located at base of dorsal-most pinnule on inner side of radiole (Fig. 10G–I). Dorsal lips with radiolar appendages as long as four thoracic segments (Fig. 11D); pinnular appendages not seen. Posterior peristomial collar of similar length all around, slightly longer ventrally, forming low, narrow ventral lappets similar in length to one thoracic segment, with rounded anterior margins (Figs 10A, D, 11A, B); collar dorsal margins rounded. Peristomial eyes present subdermally. Anterodorsal fleshy swelling absent. Thoracic ventral shields all similar in width and separated from adjacent neuropodial tori (Figs 10D, E, 11A, B); first shield as wide as long, with anterior margin m-shaped (Fig. 11A); second and remaining shields similar in length and width. Collar chaetae elongate, narrowly hooded (Fig. 11E). Superior thoracic notochaetae elongate, broadly hooded; inferior chaetae broadly hooded with progressively tapering distal tips (type B), with hoods 1.5–2 times as wide as shaft (Figs 2D, 5D, 11F). Thoracic neuropodia with uncini with about eight rows of similar-sized teeth above main fang, covering just over half length of main fang (Fig. 11G), with well-developed breast, neck longer than breast, and handle of medium size (slightly longer than the length of the distance between breast and main fang; Fig. 5P). Thoracic neuropodial companion chaetae with subdistal end enlarged, conspicuous microtubercles forming hood resulting in dentate appearance, with thin distal mucro compressed laterally (twisted over top of itself in SEM, Fig. 11H).

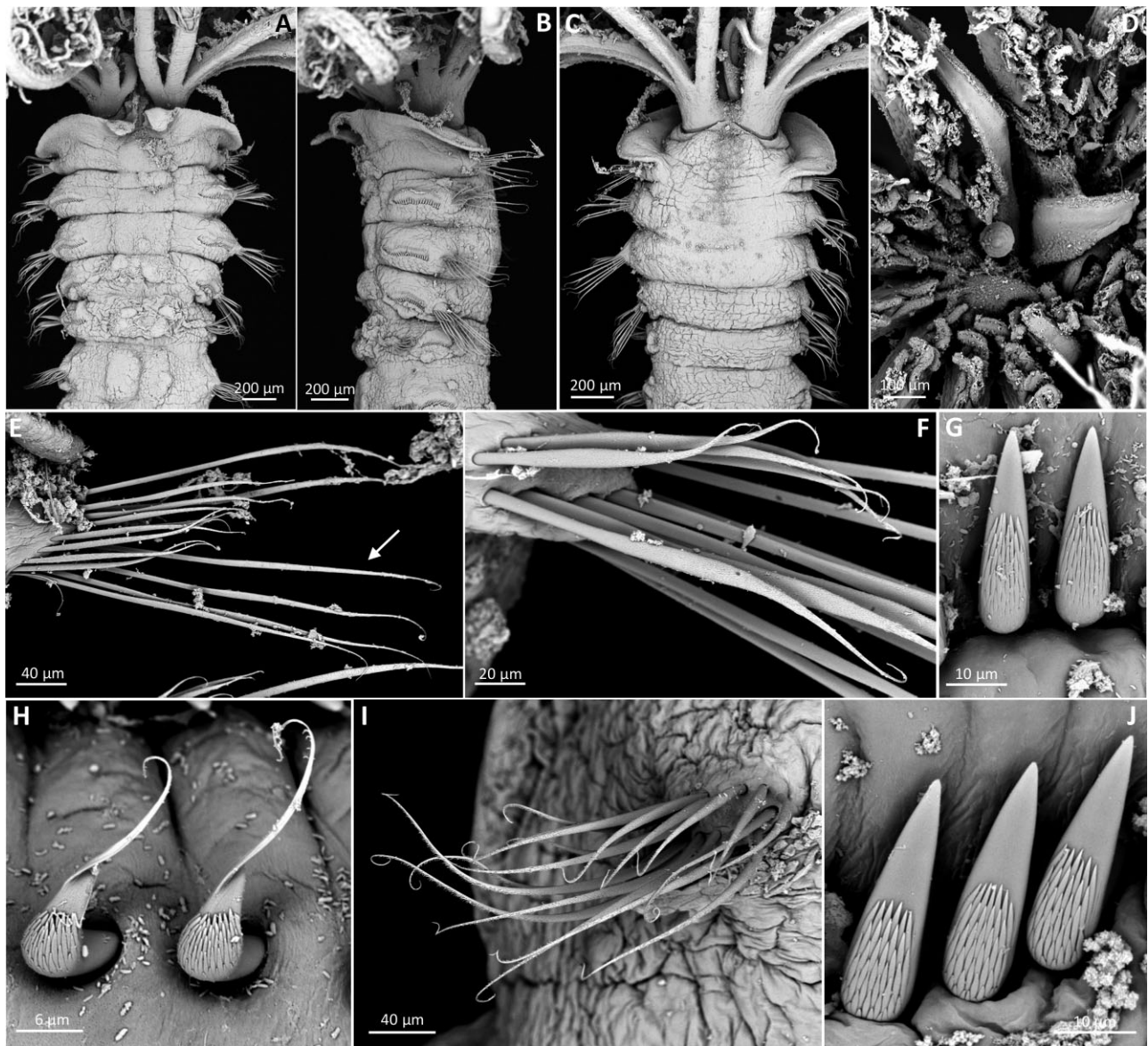


**Figure 10.** *Parasabella bioculata* sp. nov. colour micrographs. A–C, live specimen. A, radiolar crown and anterior thoracic chaetigers, lateral view. B, same, dorsal view. C, whole specimens with opened radiolar crown. D–I, preserved specimens. D, anterior thoracic chaetigers and base of radiolar crown, lateral view. E, same, ventrolateral view. F, specimen with detached crown, dorsal view. G, tip of lateral radioles showing the subdistal radiolar eyes. H, arrangement of radiolar eyes on lateral radiole. I, magnified detail showing cup-shaped radiolar eye. A–C, AM W.37053; D, E, G, H, AM W.46997; F, I, AM W.37056.

Abdominal neurochaetae narrowly hooded (Fig. 11I). Abdominal uncini with about 7–8 rows of similar-sized teeth above main fang, covering half length of main fang (Fig. 11J), neck longer than breast, with an ill-defined breast and handle shorter than distance between breast and main fang (Fig. 5Q). Size of thoracic and abdominal uncini variable in size within same torus. Pygidium somewhat damaged, present as a rim around ventral anus, eyespots not observed.

*Variation:* Holotype and paratypes show some deformation and shrinkage as a result of their fixation in 95% ethanol. Largest specimen was collected in Timor-Leste, measuring 30 mm body length, plus 10 mm crown length with 12 pairs of radioles, seven thoracic segments, and 55 abdominal segments (also fixed in 95% ethanol). All specimens examined possess paired subdistal eyes in all radioles except ventral-most pair with the exception of a specimen from Western Australia, and the specimen





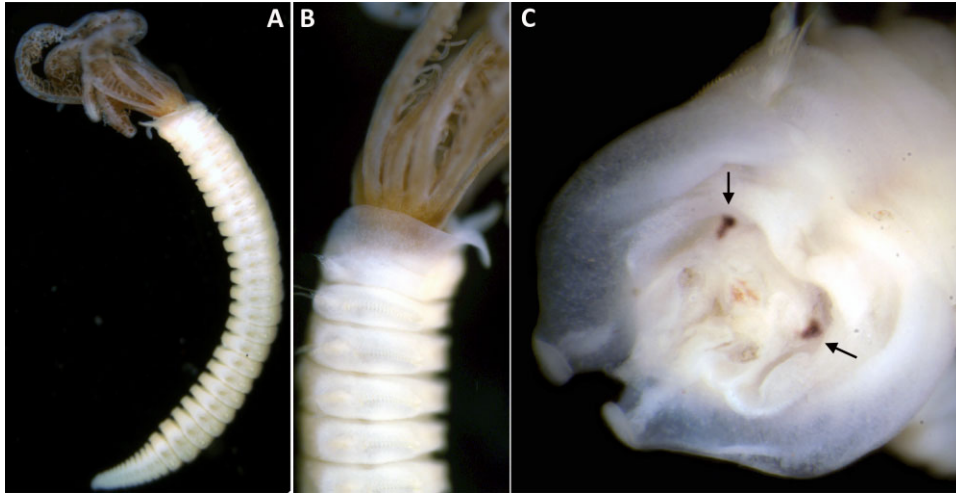
**Figure 11.** *Parasabella bioculata* sp. nov. scanning electron microscope photographs. A, anterior thoracic chaetigers and base of radiolar crown, ventral view, showing ventral shields separated from neuropodial tori. B, same, lateral view. C, same, dorsal view. D, inside of radiolar crown, frontal view, showing dorsal lips and long radiolar appendages. E, elongate, narrowly hooded collar chaetae. F, midthoracic chaetiger, elongate, narrowly hooded superior thoracic chaetae, and inferior, broadly hooded type B chaetae. G, thoracic uncini. H, companion chaetae. I, midabdominal, narrowly hooded neurochaetae. J, abdominal uncini. A–J, AM W.36449.

from Timor-Leste, which have them missing only from the dorsal-most pair. The specimen from New South Wales possesses eyes on all of its nine pairs of radioles. Pygidial eyespots were observed in some paratypes (e.g. AM W.37055). Ventral lappets are more elongated (as long as two thoracic chaetigers) in specimen from Western Australia (AM W.46997). Dorsal lips are long in most specimens (as long as four to five thoracic chaetigers) and have a single pinnular appendage.

Colour pattern in live specimens consists of yellow, white, and pink specks on body and crown with transverse red and white bands on radioles, alternating with pink patches or paired pink spots (Fig. 10A–C). Colour fades in fixed specimens, and only brownish pigment stays in crown of some specimens (Fig. 10D–F).

*Reproductive features:* Some specimens (e.g. paratype AM W.37055) have eggs filling most abdominal segments.





**Figure 12.** *Parasabella crassichaetae* sp. nov. complex, colour micrographs of preserved specimens. A, whole specimen, lateral view. B, anterior chaetigers, showing the base of crown and the collar margins. C, specimens with detached crown showing the peristomial eyes (arrows) near the insertion site of the radiolar lobes. A–B, AM W.31103; C, AM W.37028.

*Genetic data:* No sequences were obtained from members of this species.

*Remarks:* Although DNA sequencing failed for the specimens now assigned to this species (i.e. all those possessing distal paired radiolar eyes), the description of the nonsequenced specimens as a new species is justified by the presence of (probably simple) paired distal eyes on radioles, an autapomorphy for this species. This is the first time that this feature has been described in *Parasabella* and also in Sabellidae. Distal radiolar eyes have been described in other sabellids but they are always single distal compound eyes, as in *Megalomma* spp. and *Stylomma palmatum* (de Quatrefages, 1866). An incomplete sabellid bearing paired compound distal radiolar eyes was partially described (Fitzhugh, 2002: 419) but not assigned to any genus. Other sabellids with paired radiolar eyes (*Bispira* spp. *Branchiomma* spp., or *Stylomma juani* Capa, 2008) present more than one pair. Other species in the genus bearing radiolar eyes include *P. microphthalmia* (Verrill, 1873), from Puerto Rico (although the presence of eyes is disputed – see remarks by Nogueira *et al.*, 2010: 5); see also Remarks herein under the *Parasabella* diagnosis for information on other species reported as having radiolar eyes in the genus. *Parasabella microphthalmia* possesses numerous eyes randomly arranged along radioles and not exclusively at the tips. Besides the presence of these atypical radiolar eyes, *P. bioculata* sp. nov. is characterized by the combination of a unique set of characters: radioles supported by six rows of axial cells near the base, thoracic ventral shields separated from neuropodial tori by a wide gap, inferior thoracic notochaetae type B, with hoods two to three times as wide as the width of the shaft and as long as eight

to nine times its maximum width, thoracic uncini with medium-length handles, and neck longer than breast. The most similar species of *Parasabella* described to date is *P. japonica* (Table 2), with the only apparent difference being the presence of radiolar eyes in the new species.

*Etymology:* The name of the species refers to the arrangement of radiolar eyes, in pairs, in the distal tips of the radioles.

*Type locality:* Heron Island, Queensland, Australia.

*Distribution:* Northern tropical Australia, and New South Wales, Australia (Fig. 1A); Timor-Leste.

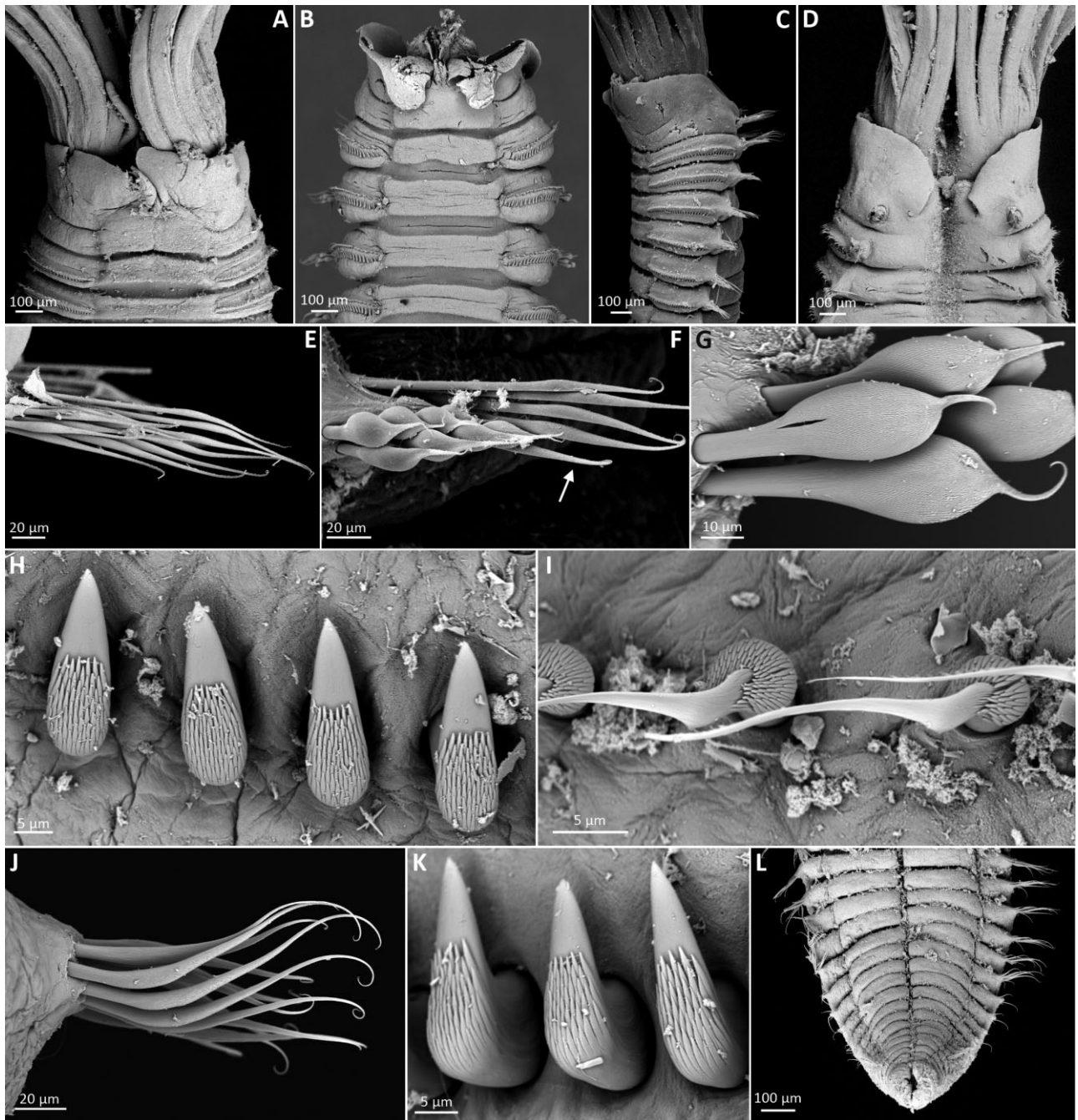
*Ecological notes:* Specimens were found in dead coral rubble or associated with soft coral or algae in tropical waters, between 3 and 15 m depth.

***PARASABELLA CRASSICHAETAE* SP. NOV. COMPLEX**  
(FIGS 4E, 5E, R–T, 12, 13)

*Holotype:* AM W.47145, New South Wales, Shellharbour, north-east of Bass Point, ‘The Humps’, 34°35’35”S, 150°54’22”E, from orange sponge, 22.4 m depth, 4.v.2010, coll. R.T. Springthorpe, MI NSW 3956.

*Paratypes:* AM W.47146 (6), same collection details as holotype.

*Additional material examined (see Appendix for details):* Australia. Western Australia: Esperance (three), Albany (four), Outer Bunbury Harbour (two), Ningaloo Reef (many), Dampier Archipelago (nine); Northern Territory: Darwin Harbour (two); Queensland: Weipa (six), Cairns (six); New South Wales: Cook Islands (four),



**Figure 13.** *Parasabella crassichaetae* sp. nov. complex, scanning electron microscope photographs. A, anterior thoracic chaetigers and base of radiolar crown, ventral view, showing ventral shields in contact with neuropodial tori, and ventral lappets. B, anterior chaetigers, ventral view, of specimens with crown removed. C, anterior body, lateral view. D, same, dorsal view. E, elongate narrowly hooded collar chaetae. F, midthoracic parapodium, elongate, narrowly hooded superior chaetae (arrow) and broadly hooded type A chaetae in inferior group. G, detail of inferior, broadly hooded type A chaetae. H, thoracic uncini. I, companion chaetae. J, midabdominal, narrowly hooded neurochaetae. K, abdominal uncini. L, posterior abdominal chaetigers and rim-like pygidium. A, C, D, E, L, AM W.36298; B, F–K, AM W.31103.



Byron Bay (two), Solitary Islands (eight), Coffs Harbour (two), Port Stephens (11), Port Jackson (12), Botany Bay area (16, including PS21, PS23, PS24, PS28), Shellharbour (one = PS03), Jervis Bay (one), Batemans Bay (six). USA. Hawaii: Oahu, Coconut Island (eight, including PS10, PS11, PS12).

*Comparative material examined:* Holotype of *Demonax leucaspis* Kinberg, 1867, SMNH 575, Peru, east of Lima, San Lorenzo Island, 12°00'S, 077°00'W, collected by Eugenie Expedition 1851–1853, station 568–9. Holotype of *Sabella albicans* Johansson, 1922, UPSZTY 2304, Japan, Misaki, 'Diver' from *Laminaria*, S. Bock collection.

*Diagnosis:* Radiolar eyes absent. Radioles supported by 6–10 rows of vacuolated cells near base. Thoracic ventral shields in contact with neuropodial tori. Inferior thoracic notochaetae type A, with hoods three times as wide as shaft, and up to three times as long as its maximum width. Thoracic uncini with medium-length handles, and neck half of breast length.

*Description:* Body 12.5 mm long, 1.7 mm wide; crown 4 mm long; Thorax with six chaetigers, and abdomen with 63, posterior end regenerating. Preserved holotype lacks colour on trunk, but diffuse brown pigmentation is present on collar, and crown has four pigment bands with radiolar pinnules also pigmented, as well as brown pigment spots groups of bars along radioles. Radiolar crown basal lobes as long as 1.5 times thoracic chaetigers, with nine pairs of radioles arranged in two semicircles. Radioles with outer margins quadrangular to round in cross-section (Fig. 13A, D) and each supported basally by eight vacuolated cells (Fig. 4E). Radiolar tips wide, tapering, bare for approximately twice length of longest pinnules (or equal to length of four thoracic segments). Radiolar flanges and eyes absent. Dorsal lips with radiolar appendages as long as five thoracic segments, each with single pinnular appendage. Posterior peristomial ring collar similar in length all around, completely covering base of crown, with rounded ventral lappets shorter than one thoracic segment (Fig. 13A, B) and rounded dorsal margins. Peristomial eyes present subdermally. Anterodorsal fleshy swelling absent. Thoracic ventral shields similar in length, twice as wide as long, in contact with thoracic tori. First ventral shield with slight incision in anterior margin and m-shaped. Collar chaetae elongate, narrowly hooded (Fig. 13E). Superior thoracic notochaetae elongate narrowly hooded (Fig. 13F); inferior thoracic chaetae broadly hooded (type A), and hood three times width of shaft and about three times as long as its maximum width (Figs 5E, 13F, G). Thoracic uncini with eight to ten rows of teeth over main fang, covering slightly over half length of main fang (Fig. 13H), with well-developed breast, reaching to the

tip of main fang, neck half length of breast, and handle 1.5–2 times length of the distance between breast and main fang (Fig. 5R). Thoracic neuropodial companion chaetae with subdistal end enlarged, conspicuous microtubercles forming hood resulting in dentate appearance, and with thin distal mucro, compressed laterally (Fig. 13I). Abdominal neurochaetae narrowly hooded (Fig. 13J). Abdominal uncini with about eight rows of teeth over main fang, covering half length of main fang (Fig. 13K), neck shorter than breast, breast well developed and with medium-length handle, 1.5 times length of the distance between main fang and breast (Fig. 5S). Pygidium a rim with a ventral anus (Fig. 13L), several red eyespots on both sides.

*Variation:* Specimens display variability for many features: size (4–22 mm length, 0.5–1.8 mm width), numbers of thoracic chaetigers (4–8), abdominal segments (ten to 63), number of radioles (5–12), and numbers of rows of vacuolated cells supporting radioles basally (six to ten). Dorsal radiolar appendages vary from 4–8 thoracic segments in length; pinnular appendages vary from 0–2 pairs. Collar completely covers base of crown in some specimens, but junction of peristomium and crown is laterally visible in some small specimens. Thoracic uncini vary in shape with handles one to two times length of the distance between breast and main fang, and 8–10 rows of teeth over main fang. Abdominal uncini have 6–10 rows of teeth over main fang and short- to medium-length handles (0.5–1.5 times length of the distance between main fang and breast; Fig. 5S, T). There is not much variability, however, in the shape of inferior thoracic chaetae – their width varies from 2–3 times width of shaft and three times as long as its maximum width. Some of this morphological variability is summarized in Table 5. Preserved specimens vary from possessing little colour pigment in radioles (a few spots) to three to four pigment bands in crown, with pigmented radiolar pinnules, and longitudinal bars of pigment embedded in rachis of radioles (Fig. 12A–C). Pygidial eyespots faded in some specimens. Tubes are tough and chitinous, with adherent sand particles, shell, and bryozoans.

*Reproductive features:* Some specimens as small as 8 mm in body length contain eggs in abdominal segments.

*Genetic data:* Within the definition of *P. crassichaetae* sp. nov. two subclades, well supported and significantly different, were recovered (Fig. 3B, C). The same haplotype was found for Australian specimens and a single mitochondrial sequence obtained from Hawaiian populations. Comparisons of nuclear fragments showed that divergence between clades is up to 10.6% (Table 4). One clade comprises specimens from Hawaii,



**Table 5.** Comparison of some morphological features amongst specimens of *Parasabella crassichaetae* sp. nov.

Morphological features	Distribution	Specimens (Registration numbers)
Abdominal uncini with medium handle and around ten rows of small teeth above main fang	WA	NMVF108905*, NMVF108908*, AM W.21996, AM W.47144*, AM W.47148–9
	QLD	AM W.36448*, AM W.4392, AM W.47178–80, AM W.47151
	NSW	AM W.47181*, AM W.31102, AM W.46677, AM W.31103 AM W.37028 (PS03), AM W.37044 (PS21), W.37046 (PS23), W.37047 (PS24), W.37049 (PS28)
	Hawaii	AM W.37036 (PS12), AM W.47183
Abdominal uncini with short handle and six to seven rows of larger teeth above main fang	WA	NMVF108906, AM W.36447, AM W.47150
	NT	AM W.32579 (PS16), AM W.47147
	Hawaii	AM W.37034 (PS10), AM W.37035 (PS11), AM W.37037 (PS13)

\*Specimens with six to eight rows of vacuolated cells supporting the radioles basally. NSW, New South Wales; QLD, Queensland; NT, Northern Territory; WA, Western Australia.

New South Wales, and the Northern Territory that differ by a maximum of 6.0% of their ITS sequences (New South Wales and Northern Territory specimens, not shown). Specimens belonging to this clade are characterized by sharing several diagnostic nucleotide blocks such as CTACCCCTGT in the 334–344 nucleotide positions and the ATCTGCTCTGGCGGTCCT in the 586–584 nucleotide positions of the ITS alignment. The second clade, consisting of five specimens from three close localities in New South Wales, with only ITS fragments successfully sequenced, had the same haplotype with unique blocks, such as CTTCACTCTACCCCTGT in the 327–377 nucleotide positions, ACGTCTGCCGAC in the 356–368 nucleotide positions, and TGCAAGGAC CCGCCCCACATCTGCTCTGGCGGTCCTCCTT in the 548–588 nucleotide positions in the ITS alignment.

*Remarks:* *Parasabella crassichaetae* sp. nov. complex is characterized by exceptionally broad and short inferior thoracic chaetae with a thin distal tip, almost resembling paleae externally but with a shaft continuing through the hood and into the distal tip, a character that defines broadly hooded chaetae. This attribute is also shared by other congeneric species such as *P. albicans*, *P. leucaspis*, *Parasabella langerhansi*, *Parasabella brevithoracica* (Pillai, 1961), *Parasabella pallida* Moore, 1923, *Parasabella saxicola* (Grube, 1861), *P. media*, *Parasabella tenuicollaris*, *P. tommasi*, and *Parasabella torulis* (Table 2). *Parasabella torulis* is distinguished from the others by possessing thoracic ventral shields separated from neuropodial tori. All the other species have ventral shields in contact with neuropodial uncinal tori. Some of these species, such as *P. media* and *P. leucaspis* (Claparède, 1870; Knight-Jones, 1983; Perkins, 1984; Giangrande, 1994), differ from *P. crassichaetae* sp. nov. by the presence of radioles with

more than 20 vacuolated cells in the bases of radioles. *Parasabella leucaspis* also possesses much shorter dorsal lips, only as long as one thoracic chaetiger compared with lengths more than four chaetigers in *P. crassichaetae* sp. nov. Both *P. media* and *P. leucaspis* also display variability in the shape of the inferior thoracic chaetae (Perkins, 1984), unlike *P. crassichaetae* sp. nov., which possesses only wide and short type A inferior thoracic chaetae.

*Parasabella langerhansi* is distinguished from *P. crassichaetae* sp. nov. by having only four rows of vacuolated cells supporting the radioles (Knight-Jones, 1983). Of the remaining species having a similar number of vacuolated cells, *P. tommasi* possesses thoracic uncini with necks longer than breast and handles up to twice the length of distance between breast and main fang (Giangrande, 1994), while in *P. crassichaetae* sp. nov. necks are half the length of the breast, and handle is as long as the distance between breast and main fang or slightly longer. *Parasabella brevithoracica* has thoracic uncini with both necks and handles shorter than the new species (Knight-Jones, 1983; Table 2). *Parasabella saxicola* has longer inferior thoracic chaetae, and the thoracic uncini have shorter necks compared with *P. crassichaetae* sp. nov. (Knight-Jones, 1983). *Parasabella albicans* differs from *P. crassichaetae* sp. nov. in the relative length of the neck and breast of the thoracic uncini (Table 2; Johansson, 1922; Uchida, 1968) and a much shorter peristomial collar. Additionally, although we were unable to dissect thoracic inferior chaetae from the type specimen of *P. albicans*, these were reported by Imajima & Hartman (1964) as being ‘non-spatulate’, and ‘short, broadly limbate’ by Uchida (1968: 608, Fig. 11), suggesting that they are dissimilar to the very broad type A chaetae of *P. crassichaetae* sp. nov. The species sharing the most

features with *P. crassichaetae* sp. nov. is therefore *P. pallida* (Table 2). The differences between these species are the lengths of dorsal radiolar appendages, which are short in *P. pallida* (Perkins, 1984: 313; Fig. 15F) but as long as 4–8 thoracic chaetigers in *P. crassichaetae* sp. nov., as well as the apparent pigmentation pattern. *Parasabella pallida* was described without any pigment (Moore, 1923), although Perkins (1984) described nontype material of *P. pallida* as having ‘faint, light brown color spots on radioles’ – a distinct difference compared with specimens of *P. crassichaetae* sp. nov., which typically show pigment in the radioles (either transverse bands, spots, or longitudinal bars).

*Etymology:* The name of the species refers to the broad inferior thoracic chaetae, a distinct trait when compared with other Australian congeners.

*Type locality:* Shellharbour, New South Wales, Australia.

*Distribution:* Around Australian coasts except Victoria and South Australia (Fig. 1B); Hawaii.

*Ecological notes:* Specimens have been found in tropical and temperate environments in dead coral rubble, sponges, algae, and artificial surfaces in ports and harbours, from the intertidal to 25 m depth.

PARASABELLA SP. CF. *P. JAPONICA* (MOORE & BUSH, 1904) (FIGS 4F, 5F, U, V, 14, 15)

*Sabella japonica* Moore & Bush, 1904: 157–159, pl. XL, figures 1, 2, pl. XII, figures 39, 40. – Imajima & Hartman, 1964: 363.

*Parasabella japonica* – Tovar-Hernández & Harris, 2010: 15.

*Australian material examined (see Appendix):* Australia. Western Australia, Kimberley region (three). Northern Territory. Darwin Harbour, (two, including one by SEM); Queensland: Heron Island (five); Lizard Island (one). New South Wales: Burrewarra Point (five, including one by SEM); Jolong Reef (one). Tasmania. Port Davey (one); South Australia. Kangaroo Island (one).

*Diagnosis:* Radiolar eyes absent. Radioles supported by 6–8 rows of vacuolated cells near bases. Thoracic ventral shields separated from neuropodial tori by wide gap. Inferior thoracic notochaetae type B, hoods width 1.5 times width of shaft, as long as 9–10 times maximum width. Thoracic uncini with medium-length handles, neck slightly longer than breast.

*Description of Australian specimens:* Largest specimen (SAM TE 14511) 13 mm long excluding crown, crown 7 mm; eight thoracic and 41 abdominal chaetigers. Radiolar crown basal lobes as long as one thoracic chaetiger, with 12–14 pairs of radioles arranged in semicircles (Fig. 14A–C, G–I). Radioles supported basally by six to eight rows of vacuolated cells at bases (Fig. 4F). Radiolar tips wide, tapering, bare for approximately length of single pinnule. Radiolar flanges and eyes absent in large specimens. Smaller (juvenile) specimens (5–8 mm long with 5–7 pairs of radioles, e.g. AM W.31101, AM W.46989) show wide flanges along radioles that end subdistally in a scoop-like formation (Fig. 14E, F). Dorsal lips with radiolar appendages as long as eight thoracic chaetigers (SAM TE 14511), each with single pinnular appendage. Posterior peristomial ring collar up to base of radiolar crown, with lateral margins oblique, increasing in length ventrally, with ventral lappets as long as one thoracic segment, subtriangular (Figs 14D, E, 15A); with rounded dorsal margins. Peristomial eyes present subdermally. Anterodorsal fleshy swelling absent. Thoracic ventral shields almost square or slightly wider than long, separated from thoracic tori by wide gap. Collar chaetae elongate, narrowly hooded. Superior thoracic notochaetae elongate narrowly hooded (Fig. 15D); inferior thoracic notochaetae broadly hooded with slender and progressively tapering hoods (type B; Figs 5F, 15E) 1.5 times the width of shaft, 9–10 times as long as its maximum width. Thoracic uncini with 8–10 rows of teeth over main fang, covering slightly over half length of main fang (Fig. 15G), well-developed breast, neck slightly longer than breast, and handle twice length of the distance between breast and main fang (Fig. 5U). Thoracic neuropodial companion chaetae with subdistal end enlarged, conspicuous microtubercles forming hood resulting in dentate appearance, thin distal mucro compressed laterally (Fig. 15H). Abdominal neurochaetae narrowly hooded (Fig. 15I). Abdominal uncini with about seven rows of teeth over main fang covering half length of main fang (Fig. 15J), neck as long as breast, breast well developed, and short handle (< 1 the length of the distance from main fang to breast). Pygidium a rim with ventral anus and several red eyespots present on both sides.

*Colour pattern:* Live specimens show a broad variation of pigments. Specimens examined have red, pink, yellow, and white bands and spots on radiolar crown, but in some, the dominant colour is red (Fig. 14A, B), whereas in others it is white (Fig. 14C, D); white and yellow spots scattered along the trunk, especially in thoracic segments (Fig. 14A–D). Preserved specimens with no pigmentation or only a few reddish spots on radiolar crown (Fig. 14E, G–I).

*Reproductive features:* Some specimens are gravid females with eggs in abdomen.



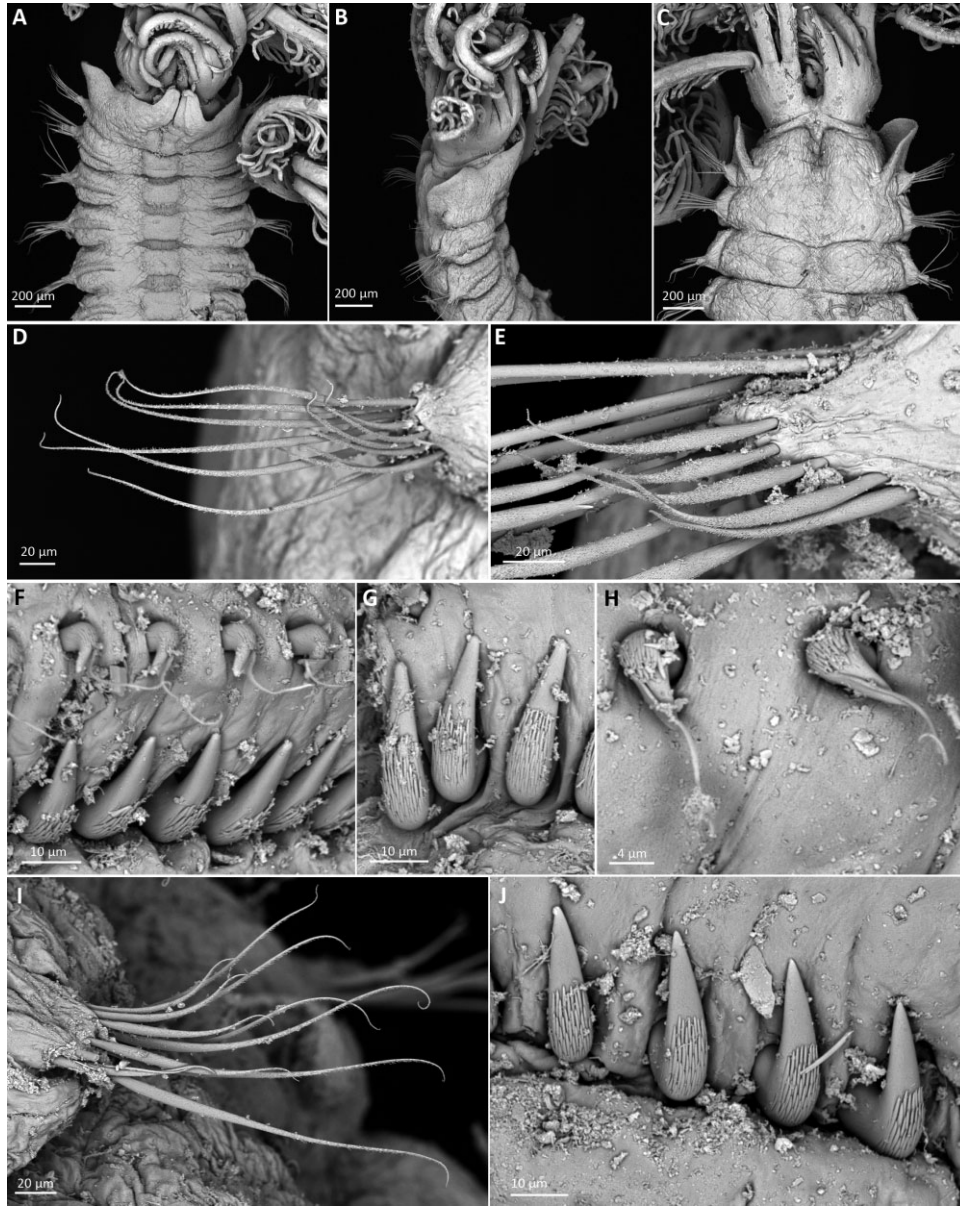
**Figure 14.** *Parasabella* sp. cf. *Parasabella japonica*, colour micrographs. A–D, live specimens. A, anterior end, lateral view. B, radiolar crown and anterior thoracic chaetigers, lateral view. C, same, frontal view. D, colour pattern on lateral radioles. E–I, preserved specimens. E, distal end of radioles with well-developed radiolar flanges forming a ‘scoop’. F, scanning electron micrograph, radiolar crown, showing ‘flanged’ distal radioles. G, complete specimen, lateral view. H, posterior peristomial ring collar with enlarged ventral lappets, lateral view. I, same, dorsolateral view. A, B, AM W.37062; C, D, AM W.36451; E, F, AM W.31101; G–I, AM W.36451.

*Genetic data:* The maximum genetic divergence amongst the four ITS fragment sequences obtained from specimens collected in New South Wales and Queensland was 7.1%. The genetic distance to other species was 17.1–23.7%. The four specimens analysed are characterized by several one-nucleotide

synapomorphies and a short and unique block, ACTTG, in the 172–176 nucleotide positions of the alignment.

*Remarks:* The specimens collected in Australia share diagnostic features with the original description of

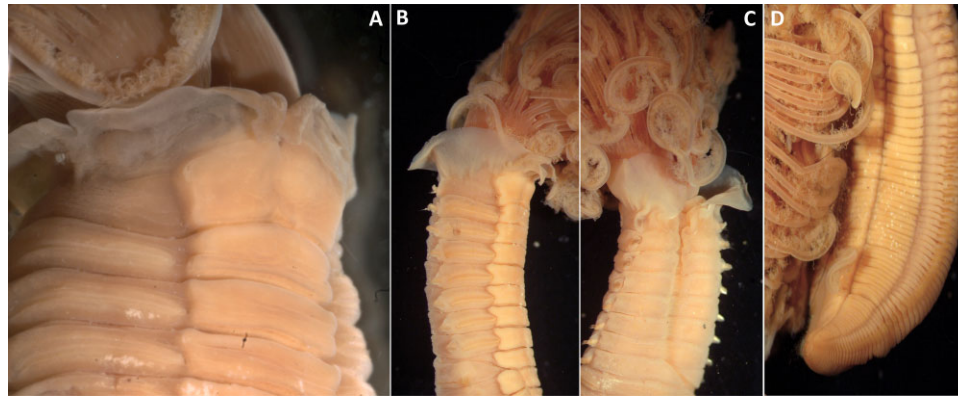




**Figure 15.** *Parasabella* sp. cf. *Parasabella japonica*, scanning electron microscope photographs. A, anterior thoracic chaetigers and base of radiolar crown, ventral view, showing ventral shields separated from neuropodial tori, and ventral lappets. B, anterior chaetigers, lateral view. C, same, dorsal view. D, midthoracic parapodium, elongate, narrowly hooded superior chaetae and broadly hooded type B chaetae in inferior group. E, detail of inferior, broadly hooded type B chaeta. F, thoracic uncini and companion chaetae. G, thoracic uncini, detail. H, companion chaetae showing the laterally compressed hood. I, midabdominal narrowly hooded neurochaetae. J, abdominal uncini. A–J, AM W.36450.

*P. japonica* from Suraga Bay (Japan), such as ventral shields separated from tori by a wide gap, long and slender inferior thoracic chaetae (type B), thoracic uncini with long to medium-length handles (Moore & Bush, 1904: plate XII, fig. 39), and a collar with conspicuous pointed ventral lappets. The specimens described from Japan are bigger (up to 33 mm in length) than Australian specimens, which are not longer than 15 mm.

It was not possible to compare certain features between populations such as length of dorsal lips (almost as long as the thorax in Australian specimens) and number of cells basally supporting radioles (6–8 cells in the Australian specimens), as these were not specified in the original description of *P. japonica* and are impossible to confirm in the type material of this species because the only two types (deposited in Academy of



**Figure 16.** *Parasabella* sp. cf. *Parasabella rugosa*, colour micrographs of preserved specimens. A, anterior thoracic chaetigers, ventral view, showing posterior peristomial ring collar, and ventral shields in contact with neuropodial tori. B, complete thorax, lateral view. C, same, dorsal view. D, posterior abdominal chaetigers and pygidium, ventral view. A, NMV F.108844; B–D, AM W.36431.

Natural Sciences Philadelphia, and the Smithsonian Institution) have lost their crowns (Loi, 1980).

Other species in the genus possessing thoracic ventral shields separated from neuropodial tori are *Parasabella lacunosa*, *P. torulis*, and *Parasabella polarsterni*. Of these *P. torulis* is distinguished from the others by the presence of broad and short inferior thoracic notochaetae (type A) as well as thoracic uncini with short handles (Table 2), whereas the rest of the species have inferior thoracic notochaetae of type B and longer uncini handles. *Parasabella lacunosa* has radioles basally supported by about ten vacuolated cells whereas *P. sp. cf. P. japonica* and *P. polarsterni* have six to eight. These latter two species can be separated by uncinal morphology. Thoracic uncini of *P. polarsterni* have necks shorter than breasts and handles three times longer than the distance between breast and main fang, whereas in *P. japonica* the uncini are longer than wide, with long necks and breasts of similar length and handle lengths that are up to twice the distance from breast to main fang.

In small specimens with few radioles (e.g. AM W.31101, Fig. 14E, F) these radioles appear to be widened into distal ‘scoops’, or along their longitudinal axes forming flanges, features that suggest a specialized juvenile function, perhaps to increase the surface area available for feeding.

*Type locality:* Suruga Bay, Japan, 115–137 m depth, sand and gravel.

*Distribution:* Japan, Australia (in both tropical and temperate waters; Fig. 1B); and ?New Zealand. *Parasabella japonica* was reported from New Zealand by Glasby *et al.* (2009) as *Demonax japonicus*, but this record was based on a single specimen (identified by P. Knight-Jones) that is now misplaced. Further extensive sam-

pling in New Zealand has failed to provide additional specimens of *P. japonica* since that record (G. Read, pers. comm.) and so its presence in New Zealand is herein regarded as dubious.

*Ecological notes:* Specimens from Australia have been collected from 1–30 m depth, in dead coral rubble, associated with sponges, bryozoa, and algae, and also in coarse sand.

*PARASABELLA* SP. CF. *P. RUGOSA* (MOORE, 1904)  
(FIGS 4G, 5G, W, X, 16, 17)

*Distylia rugosa* Moore, 1904: 499–501, pl. 38, figures 8–41; 1909: 289. – Loi, 1980: 143, 144.

*Demonax medius* – Berkeley & Berkeley, 1952: 115.

*Distylidia rugosa* – Hartman, 1961: 129; 1969: 667, in part. – Banse, 1979: 870.

*Sabella (Demonax) media* – Banse, 1979: 878–880. – Hobson & Banse, 1981: 107, in part.

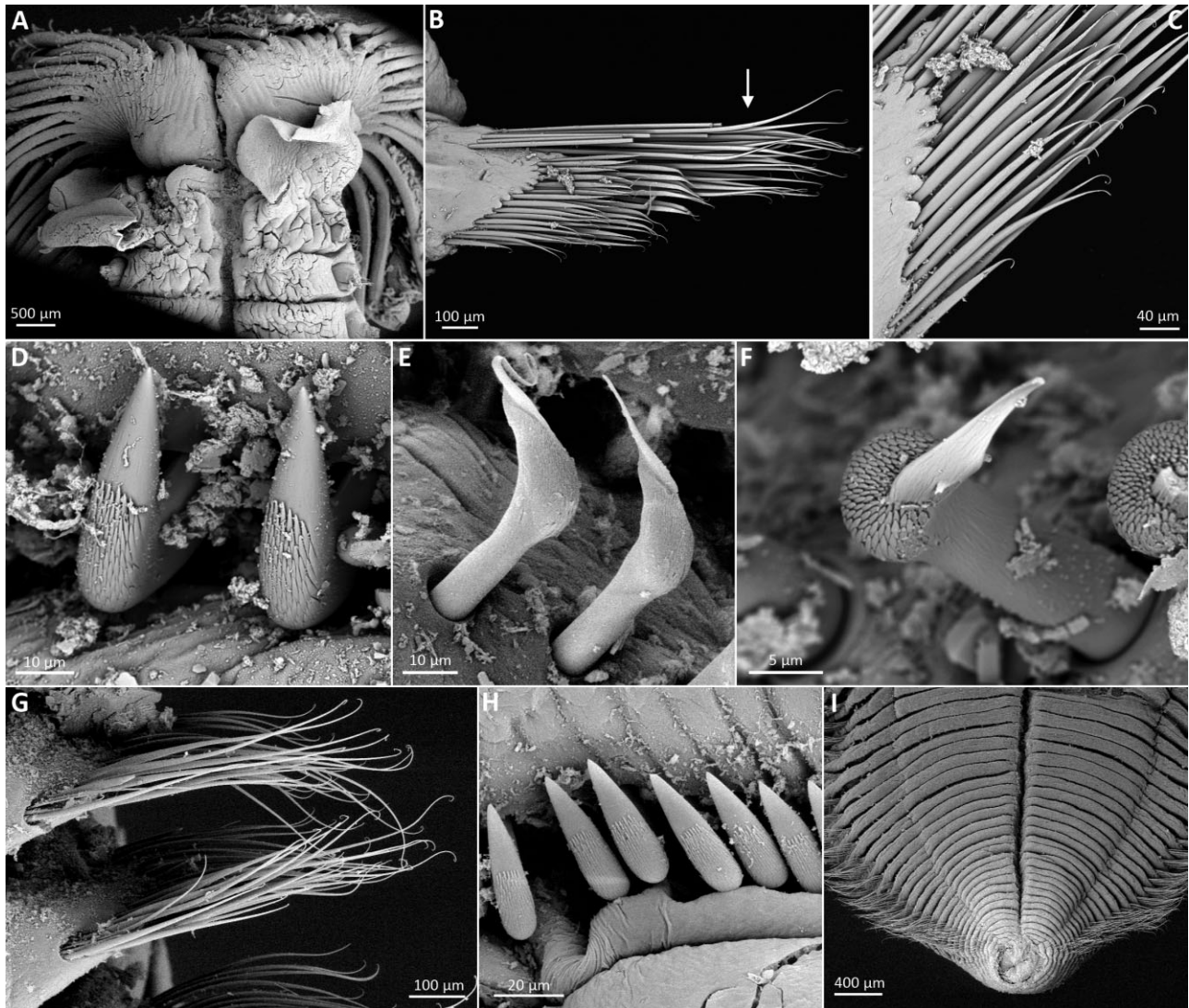
*Demonax rugosus* – Perkins, 1984: 304–307, figures 9, 10.

*Parasabella rugosa* – Tovar-Hernández & Harris, 2010: 15.

*Material examined (see Appendix for details):* Australia. Victoria: Port Phillip Bay (three).

*Diagnosis:* Radiolar eyes absent. Radiolar lobes as two semicircles curling midventrally, with radioles arranged in two or more rows. Radioles with over 20 rows of vacuolated cells supporting radioles near bases. Inferior thoracic notochaetae elongate, slender (type B), hoods up to 1.5 times as wide as shafts and as long as ten to 12 times maximum width. Thoracic uncini with long handles, neck half length of breast.





**Figure 17.** *Parasabella* sp. cf. *Parasabella rugosa*, scanning electron microscope photographs. A, anterior thoracic chaetigers and base of radiolar crown, dorsal view, showing large collar dorsal margins. B, midthoracic parapodium with elongate, narrowly hooded (arrow) superior chaetae and broadly hooded (type B) in inferior group. C, detail of inferior thoracic broadly hooded chaetae of type B. D, thoracic uncini. E, companion chaetae, lateral view. F, companion chaetae, frontal view. G, midabdominal neurochaetae narrowly hooded. H, abdominal uncini. I, posterior abdominal chaetigers and (damaged) pygidium. A–I, AM W.36431.

*Description of Australian specimens:* Largest specimen about 55 mm long (excluding crown), crown 25 mm long, 8 mm wide, with eight thoracic and more than 100 abdominal segments. Radiolar crown basal lobes as long as one thoracic chaetiger, over 40 pairs of radioles arranged in alternating double rows forming semicircles in each branchial lobe, curling inwards ventrally. Radioles quadrangular in cross-section, each supported basally by more than 20 vacuolated cells in radiolar cross-section near bases (Fig. 4G). Radiolar tips thin and even width, bare for approximately length of one pinnule or 1.5 times length of a thoracic segment. Radiolar

flanges and eyes absent. Dorsal lips as long as 5–8 thoracic segments, with one to three pairs of pinnular appendages. Posterior peristomial ring collar of even height all around or slightly longer dorsally, covering junction of crown and peristomium; with lateral notches, rounded ventral lappets, and dorsal margins rounded to flap-like (Figs 16A–C, 17A). Peristomial eyes not seen. Anterodorsal fleshy swelling absent. Thoracic ventral shields almost three times longer than wide, in contact with thoracic neuropodial tori (Fig. 16A). First ventral shield 1.5 times longer than following and with m-shaped anterior margin (Fig. 16A). Collar chaetae



elongate, narrowly hooded. Superior thoracic notochaetae elongate, narrowly hooded (Fig. 17B); inferior thoracic notochaetae type B, slender, with hoods up to 1.5 times as wide as shafts (type B) and 10–12 times maximum width (Figs 5G, 17B, C). Thoracic uncini with 8–10 rows of teeth over main fang, covering half length of main fang (Fig. 17D), with a narrow breast, neck as long as breast, and long handle, over twice length of the distance between breast and main fang (Fig. 5W). Thoracic neuropodial companion chaetae with subdistal end enlarged, conspicuous microtubercles forming hood resulting in dentate appearance, thin distal mucro, at right angle to shaft, compressed laterally (Fig. 17E, F). Abdomen with rugose epithelium in posterior chaetigers. Abdominal neurochaetae narrowly hooded (Fig. 17G, I). Abdominal uncini with minute rows of teeth over main fang covering half length of main fang (Fig. 17H), neck as long as breast, breast well developed, and short handle (shorter than the length of the distance between main fang and breast; Fig. 5X). Pygidium a rim with a ventral anus and several red eyespots present on both sides. Tube thick, chitinous, translucent, with sand grains, shell grit, and other tubes embedded into the tube mucous matrix.

*Colour pattern:* Preserved specimens with radiolar crown with faded transverse brown bands and pigmented pinnule bases, no spots along radiolar axes (Fig. 16B, C). Body unpigmented (Fig. 16A–D).

*Genetic data:* No specimens available for DNA sequencing.

*Remarks:* *Parasabella rugosa*, originally described from California and reported along the American Pacific coast up to British Columbia (Perkins, 1984), is distinguished from other congeners by the presence of radiolar crowns with radiolar lobes partially spiralled, radioles arranged in double rows in large specimens, and slender inferior thoracic chaetae (Perkins, 1984). The specimens collected in Port Phillip Bay, Australia, share all these features with specimens from the eastern Pacific coast, but also share the presence of a large number of rows of vacuolated cells supporting the radioles (20 or more at the base), long dorsal lips (as long as five to eight thoracic segments), the extremely slender form of the inferior thoracic chaetae, long-handled thoracic uncini, and rugose posterior abdomen (Moore, 1904; Perkins, 1984). Besides the barriers and distance separating the Australian specimens from other eastern Pacific populations, the only feature that distinguishes these specimens is the length of the posterior peristomial ring collar, longer in the herein-described material than reported in the paratypes (Perkins, 1984). This feature is probably not enough to consider these as a separate species. As only three specimens of this large *Parasabella*

have been found in Australia, near an international port, translocation of the Australian population could explain the present distribution range of this species. Nevertheless, further investigations to identify any differences between these widely geographically separated populations should be performed when ethanol-fixed specimens become available for examination and analysis.

*Type locality:* California, USA.

*Distribution:* East coast of North America (USA and Canada); Port Phillip Bay, Australia (Fig. 1B).

*Ecological notes:* Species reported from 20–72 m (Perkins, 1984). In Australia, it has been collected from fine shelly sand at 6 m depth.

GENUS *SABELLOMMA* NOGUEIRA *ET AL.*,  
2010, EMEDED

*Sabelloma* Nogueira *et al.*, 2010: 4.

*Type species:* *Parasabella minuta* Treadwell, 1941.

*Diagnosis:* Radiolar eyes irregularly distributed along outer margins, more numerous in areas with pigmented bands across radioles. Thoracic neuropodial companion chaetae with subdistal end enlarged, conspicuous microtubercles forming hood, resulting in dentate appearance, with thin distal mucro, generally flattened transversely.

*Description:* Sabellids ranging in length from 3–30 mm (including crown); thorax with 4–8 chaetigers and abdomen with numerous chaetigers. Radiolar crown with four to 22 pairs of radioles arranged in two semi-circular radiolar lobes, may be involuted dorsally. Radioles without basal membrane, stylodes, or radiolar flanges; outer margins with numerous, irregularly distributed eyespots, usually more numerous in areas with pigmented bands across radioles. Radioles supported by four to six rows of vacuolated cells at bases. Dorsal lips with radiolar appendages; pinnular appendages absent or present, one to two pairs when present, may be fused partially to dorsal lip; distally rounded ventral lips, continuing ventrally as parallel lamellae; ventral sacs present or absent. Peristomial eyespots present subdermally. Posterior peristomial ring collar only just covering branchial lobes; dorsal margins well separated from faecal groove; one pair of triangular, non-overlapping ventral lappets. Inter-ramal eyespots present, especially evident in abdomen, but may be faded or absent. Collar chaetae elongate, narrowly hooded, arranged in two oblique rows, ventral row chaetae shorter than dorsal; remaining thoracic notopodia with

superior arc of elongate, narrowly hooded chaetae, inferior chaetae as two rows of broadly hooded chaetae of type A. Thoracic neuropodia with avicular uncini about as long as high, 4–5 irregular rows of teeth above main fang, extending less than half the length of main fang, well-developed breast, and medium handles (as long as distance from breast to main fang). Thoracic neuropodial companion chaetae with subdistal end enlarged, conspicuous microtubercles forming hood, resulting in dentate appearance, and with thin distal mucro at right angles to shaft and flattened transversely. Abdominal neurochaetae narrowly hooded in both anterior and posterior rows. Abdominal notopodia with avicular uncini similar to thoracic or with shorter handles. Pygidium triangular, distally blunt; eyespots present.

*Remarks:* The description of *Sabellomma* is here emended to incorporate the morphological differences observed in the new species and changes in the interpretation of the shape of the inferior thoracic chaetae. *Sabellomma cupocolata* sp. nov. lacks inter-ramal eyes, the dorsal margins of branchial lobes do not possess thickened ridges but instead radiolar lobes are involuted dorsally, peristomial eyes are present, companion chaetae with a very thin distal mucro are present, radioles are supported by six rows of vacuolated cells, and specimens with up to eight thoracic segments have been found; all different from previously described *Sabellomma* species (Nogueira *et al.*, 2010). Moreover, in the original description of the genus, the inferior thoracic chaetae of members of *Sabellomma* were considered as paleate, but as the shaft runs through the hood, the chaetae should be considered as broadly hooded (Perkins, 1984; Fitzhugh, 1989; Capa *et al.*, 2015). *Sabellomma cupocolata* sp. nov. lacks the ventral sacs described for the other three nominal species in the genus (Nogueira *et al.*, 2010).

The genus *Sabellomma* was erected to accommodate the type species previously considered as a *Parasabella* and subsequently as a *Perkinsiana* Knight-Jones, 1983 (Treadwell, 1941; Knight-Jones, 1983), from Brazil, together with two new additional species from Hawaii and the Caribbean, all characterized by the presence of unpaired, simple eyespots along the outer margins of radioles and possibly also inter-ramal spots (Nogueira *et al.*, 2010). Both characters were considered as homoplastic because they have been reported in other sabellids (Nogueira *et al.*, 2010). This type and arrangement of radiolar eyes is also described in *P. microphthalma* (Perkins, 1984) and in *Pseudopotamilla cerasina* (Grube, 1870). However, their presence in *Parasabella microphthalma* may be inaccurate and pigment spots mistakenly interpreted as eyespots (according to Nogueira *et al.*, 2010), and *Ps. cerasina*, from the description (in which types were

apparently not assigned) and from further notes on some other identified specimens, may actually be a *Sabellomma* and not *Sabella*, *Potamilla*, or *Pseudopotamilla* as previously suggested (Grube, 1870; Knight-Jones, Knight-Jones & Ergen, 1991; Knight-Jones & Perkins, 1998). These two species may have the same type of companion chaetae and radiolar eyes as members of *Sabellomma*. Moreover, although *Ps. cerasina* apparently bears dorsal radiolar flanges, similar to those present in all members of *Pseudopotamilla* (Knight-Jones & Perkins, 1998), these could be in fact the basal, thickened ridges described in *Sabellomma* (Nogueira *et al.*, 2010: 4). Conspicuous differences between *Pseudopotamilla* and *Sabellomma*, apart from the types of radiolar eyes, lie in the posterior peristomial ring collar dorsal margins, fused to the faecal groove in *Pseudopotamilla* and separated by a wide gap in *Sabellomma*; and the type of interior thoracic chaetae, paleate (that is, with the shaft not reaching the tip of the hood) in *Pseudopotamilla*, and broadly hooded (with shaft along the hood), in *Sabellomma*. If this synonymy is verified then the presence of simple eyespots along the outer margins of radioles will be the synapomorphy for the genus.

***SABELLOMMA CUPOCULATA* SP. NOV.** (FIGS 4H, 5H, Y, Z, 18, 19)

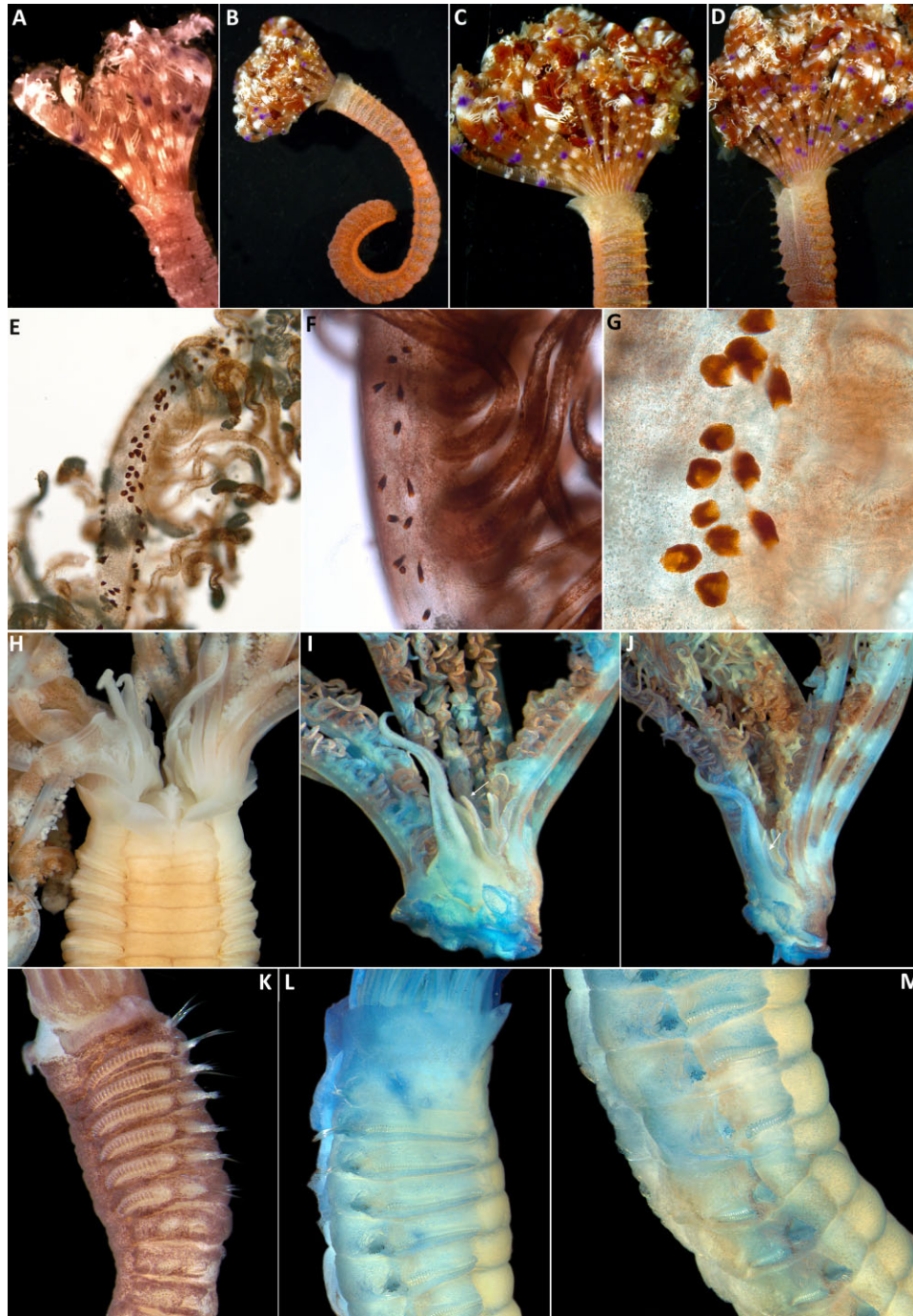
*Holotype:* AM W.47193, Queensland, Lizard Island, High Rock, 14°49'34"S, 145°33'08"E, coll. from coral rubble, 20.1 m depth, L. Avery, 11.ix.2010, CReefs Stn LI10-134, MI QLD 2233.

*Paratypes:* AM W.47192 (1), same as holotype; AM W.47191 (4), Lizard Island, MacGillivray Reef (14°39'23"S, 145°29'31"E, coll. from coral rubble, 22 m, M. Capa & P. Hutchings, 29.viii.2010, CReefs Stn LI10-028, MI QLD 2197.

*Additional material examined (see Appendix for details):* Australia. Western Australia: Lewis Island (two), Legendre Island (one); Northern Territory: Darwin Harbour (one); Queensland: Torres Strait (one); Lizard Island, (nine), Heron Island (one).

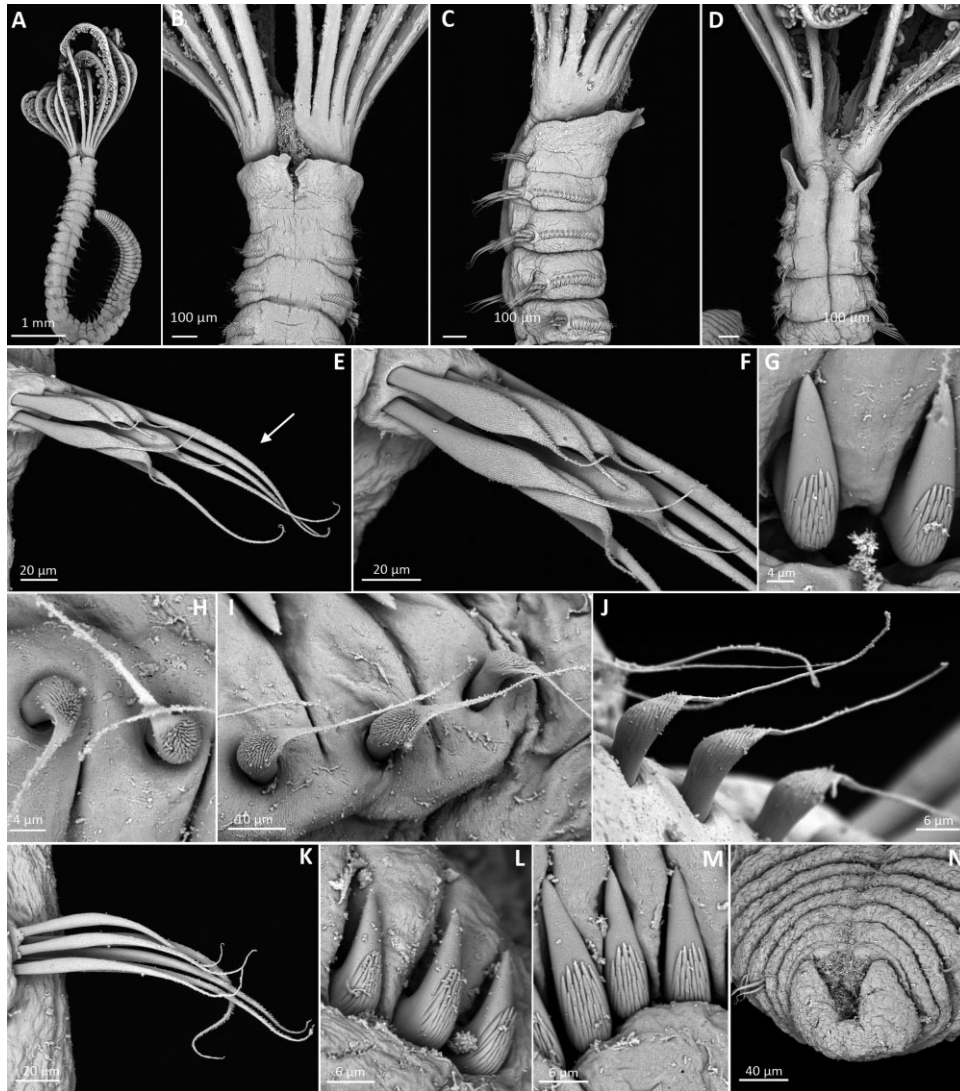
*Diagnosis:* Unpaired, simple eyespots present, randomly arranged along radiolar lateral margins. Radioles supported by six rows of vacuolated cells near base. Thoracic ventral shields in contact with neuropodial tori. Inferior thoracic notochaetae of type A, with hoods 1.5 times as wide as shaft, and as long as four to five times maximum width. Thoracic uncini with short handles, and neck slightly shorter than breast.

*Description:* Holotype 7 mm long (excluding crown), 1 mm wide, radiolar crown 5 mm long. Thorax with



**Figure 18.** *Sabellomma cupocolata* sp. nov., colour micrographs. A–D, live specimens. A, anterior end, ventral view. B, specimen missing posterior abdominal chaetigers, lateral view. C, radiolar crown and anterior thoracic chaetigers, lateral view. D, same, dorsal view. E–M, preserved specimens. E–G, detail of radiolar eyes along radiolar lateral margins. H, base of crown, ventral view, with crown opened showing ventral lips, dorsal lips with long radiolar appendages, and anterior thoracic chaetigers with ventral shields in contact with neuropodial tori and a dark pigment spot in between. I, J, half of radiolar crown showing dorsal lips with long radiolar appendages and pinnular appendages (arrow); dyed with methylene blue. K, thoracic chaetigers, holotype, lateral view, lacking inter-ramal eyes. L, thoracic chaetigers and collar. M, posterior thoracic and anterior abdominal chaetigers, lacking conspicuous inter-ramal eyes. A–D, AM W.37060; E–H, AM W.37060; I, J: AM W.37029; K, AM W.47193 (holotype); L, M, AM W.47189.





**Figure 19.** *Sabellomma cupocolata* sp. nov., scanning electron microscope photographs. A, whole specimen, ventral view. B, anterior thoracic chaetigers and base of radiolar crown, ventral view, showing collar with low ventral lappets. C, same, lateral view. D, same, dorsal view. E, midthoracic parapodium with elongate, narrowly hooded superior chaetae (arrow) and broadly hooded type A chaetae in inferior group. F, detail of inferior, broadly hooded chaetae of type B. G, thoracic uncini. H, I, companion chaetae, frontal view. J, companion chaetae, lateral view. K, midabdominal narrowly hooded neurochaetae. L, M, midabdominal uncini. N, posterior abdominal chaetigers and pygidium. A–N, AM W.39545.

seven chaetigers, abdomen with 47. Preserved holotype brown with white spots all over body (Fig. 18K). Radiolar crown with basal lobes as long as 1.5 thoracic segments, arranged in two semicircles (Figs 18C–D, H–J, 19A–D), slightly involuted dorsally. Radioles with rounded edges, flanges absent, with six rows of vacuolated cells supporting each radiole near base (Fig. 4H). Radiolar tips wide, tapering, bare for approximately length of pinnules. Cup-shaped radiolar eyes irregularly arranged along side margins of all radioles, except distally (Fig. 18E–G). Dorsal lips with radiolar appendages as long as three thoracic seg-

ments (Figs 18H–J, 19D). One pinnular appendage fused to each dorsal lip, free for one-half to one-third of length, and joined to adjacent pinnule by membrane (Fig. 18I, J). Ventral lamellae present, ventral sacs absent (Fig. 18H). Posterior peristomial ring collar slightly increasing in length from dorsal to ventral side, covering junction of crown and peristomium, with low rounded ventral lappets, shorter than one thoracic segment (Figs 18A–D, H, K, L, 19A–D); dorsal margins with rounded edges (Figs 18D, 19D). Peristomial eyes present, subdermal. Inter-ramal eyes absent. Thoracic ventral shields four times wider than long, lateral

margins in contact with neuropodial tori; first ventral shield m-shaped, twice as wide as long, with indentation along anterior margin. Collar chaetae elongate, narrowly hooded. Superior thoracic notochaetae elongate, broadly hooded (Fig. 19E); inferior thoracic notochaetae of remaining chaetigers with broadly hooded chaetae with progressively tapering distal tips (type A), with hoods 1.5 times width of shaft, and as long as 4–5 times maximum width (Figs 5H, 19E, F). Neuropodial tori similar in width along thorax, only slightly decreasing in width posteriorly. Uncini with 5–6 rows of teeth over main fang, covering just half length of main fang (Fig. 19G), well-developed breast, not reaching tip of main fang, neck longer than breast, handle short (shorter than the length of the distance between breast and main fang; Fig. 5Y). Thoracic neuropodial companion chaetae with subdistal end enlarged, conspicuous microtubercles forming hood, resulting in dentate appearance, and thin distal mucro flattened transversely, narrowing abruptly, tapering to long fine point (Fig. 19H–J). Abdominal neurochaetae narrowly hooded (Fig. 19K). Abdominal uncini with 5–6 rows of large teeth over main fang covering half length of main fang (Fig. 19L, M), uncinus proportionally higher than thoracic, with less defined breast and handle shorter than length of the distance between main fang and breast. Abdominal uncini decrease in size dorsoventrally within same torus. Pygidium a rim with ventral anus (Fig. 19N); red eyespots on both sides.

**Variation:** Specimens range in length from 3 (AM W.20495) to 37 mm (AM W.37060), including crown, with widths of 0.3–2.3 mm. Thoracic chaetigers vary from 5–8. Collar varies in height from length of one to two thoracic segments – larger specimens (AM W.47189, AM W.37060) have higher collars with subquadrate dorsal margins, and 7–8 thoracic chaetigers, as well as more pronounced involution of dorsal radioles. Number of radioles varies from 5–22 pairs. Dorsal lips vary in length between 3–5 thoracic chaetigers. Ventral shields vary from 2–4 times wider than long, depending on contraction and type of fixation. Radiolar crown of live specimens with brownish base and some brown (~five), white (~seven), and purple (three to four) transverse bands irregularly arranged across radioles and pinnules (Fig. 18A–D). Colour patterns amongst specimens from Lizard (Fig. 18A) and Heron Islands (Fig. 18B–D) show some minor differences in number and width of colour bands in radiolar crown, but all specimens with brown radiolar base with white and bright purple transverse bands and small white spots over trunk. Some preserved specimens have little or no pigment remaining (Fig. 18H), whereas others remain brown (Fig. 18K). Pigment fades first from abdomen. Some specimens with little or no pigment in thorax after preservation may have small spots of pigment

retained on ventral margin of the thoracic notopodial tori as well as ventral edges of neuropodial tori (Fig. 18H), unlikely to be eyes, and these appear to fade completely.

**Reproductive features:** None of the examined specimens were gravid females but some nontype specimens, greater than 8 mm in length, possessed sperm in anterior abdominal segments, forming creamy-white dorsolateral patches.

**Genetic data:** This species shows little genetic intraspecific variation (2.7 and 0.3%, comparing *cox1* and ITS sequences, respectively). The specimens collected from Heron and Lizard Islands show the largest divergence, suggesting some population structure along the reported distribution range. The four specimens included in the analyses are characterized by several synapomorphies or barcodes, with some nucleotides scattered along the sequences and others, such as GCGCGTCCTGCGTTCCCTCCCCTCG in the 489–513 nucleotide positions, configuring unique sequence blocks. The present phylogenetic hypothesis (Fig. 3C), after combination of the molecular and mitochondrial sequence data, suggests a sister-group relationship between *Parasabella* and *Sabellomma*, with maximum bootstrap support and genetic differences of over 25% in mitochondrial DNA fragments and over 40% in the nuclear fragment.

**Remarks:** *Sabellomma cupocolata* sp. nov. resembles the other congeners, all described from the Western Atlantic, in the presence of irregularly distributed lensed eyes on outer margins of radioles, and the presence of companion chaetae with a transversely flattened distal mucro. The main differences between *S. cupocolata* sp. nov. and previously described species are: the shape of these companion chaetae (the mucro narrows abruptly and looks almost needle-like under light microscopy in *S. cupocolata* sp. nov., whereas the other three species have broader distal ends); radioles are supported by six vacuolated cells in *S. cupocolata* sp. nov. and four in the other three species; and the radiolar lobes lack a thickened ridge on their dorsal edge, present in the other *Sabellomma* species, but are instead slightly involuted dorsally in *S. cupocolata* sp. nov. Moreover, none of the species previously reported have bright purple bands in the crown when alive, whereas these are very conspicuous in the new Australian species.

*Sabellomma cupocolata* sp. nov. resembles *P. microphthalma* in the type and arrangement of radiolar eyes in two irregular rows on outer sides of the radioles, if it can be verified that they are present in the latter species. However, these two species differ in the type of companion chaetae, which are representative of each of the two genera, and also in the

KEY TO *PARASABELLA* AND *SABELLOMMA* SPECIES IN AUSTRALIA

1. Radioles with numerous cup-shaped eyes present along outer margins; companion chaetae with distal mucro transversely flattened..... *Sabellomma cupocolata* sp. nov.
- Radioles without eyes, or a pair present only at distal tips of most radioles; companion chaetae with distal mucro laterally compressed .....*Parasabella*.....2
2. With raised fleshy swellings across anterior dorsum .....*Parasabella aberrans*.....3
- Without raised fleshy swellings across anterior dorsum.....3
3. Thoracic ventral shields separated from neuropodial tori by gap.....4
- Thoracic ventral shields in contact with or indented by neuropodial tori.....5
4. Paired eyes on distal ends of radioles..... *Parasabella bioculata* sp. nov.
- Paired eyes absent from radioles (brown pigment lines, bands, or spots may be present).....  
.....*Parasabella* sp. cf. *Parasabella japonica*
5. Inferior thoracic chaetae broadly hooded with short, abruptly tapering tips (type A); hoods generally 2–3 times the width of shaft and as long as 2–5 times its width.....*Parasabella crassichaetae* sp. nov.
- Inferior thoracic chaetae progressively tapering (type B); hoods generally up to twice the width of shaft and as long as 4–9 times its width.....6
6. Radioles form two or more rows along radiolar lobes on large specimens; each radiole with > 20 vacuolated cells supporting radioles at base. Inferior thoracic chaetae with hoods 8–9 times longer than wide.....  
.....*Parasabella* sp. cf. *Parasabella rugosus*
- Radioles in single rows along radiolar lobes; each radiole with 8–10 rows supporting vacuolated cells at base. Inferior thoracic chaetae with hoods six times longer than wide.....  
.....*Parasabella* sp. cf. *Parasabella aulaconota*

number of rows of vacuolated cells supporting the radioles, eight to 12 in *P. microphthalmia* and six in *S. cupocolata* sp. nov.

*Etymology:* The name of the species refers to the conspicuous cup-shaped radiolar eyes arranged along the outer margins of the radioles.

*Type locality:* Lizard Island, Queensland, Australia.

*Distribution:* Tropical Australia, from northern Western Australia to southern Queensland (Fig. 1B).

*Ecological notes:* Specimens collected only in tropical sites, from coral rubble, coarse sand, under boulders and live corals, between 3 and 30 m depth.

DISCUSSION

MONOPHYLY OF *PARASABELLA* AND *SABELLOMMA* AND RELATIONSHIPS WITH OTHER SABELLIDS

All species in *Parasabella* share the presence of companion chaetae with bulbous subdistal ends with a dentate appearance and a narrow tapered mucro arising from the centre and compressed laterally, which is unique in Sabellidae (Knight-Jones, 1983; Perkins, 1984; Fitzhugh, 1989; Capa *et al.*, 2015). Monophyly of the genus was indicated herein (although weakly supported) for the first time, after analyses of molecular data. The monophyly of *Sabellomma* has already been assessed by Nogueira *et al.* (2010), after analyses of morphological data and considering a comprehensive number

of sabellid terminals. It relies on the presence of unpaired eyes distributed along the radioles (Nogueira *et al.*, 2010; and see explanation as to why some of the phylogenetic hypotheses tested recovered *Sabellomma* as paraphyletic).

The phylogenetic hypothesis after combining nuclear and mitochondrial sequence data indicated a sister-group relationship between *Parasabella* and *Sabellomma*. This result differs from a previous hypothesis that recovered *Parasabella* (as *Demonax*) as sister-group to *Megalomma* (Nogueira *et al.*, 2010). These three genera, however, share several morphological features, all homoplastic. They bear broadly hooded inferior thoracic notochaetae (Fitzhugh, 1989; Capa & Murray, 2009; Tovar-Hernández & Carrera-Parra, 2011, and present study; see Nogueira *et al.*, 2010 for a different interpretation in *Sabellomma*), also shared by members of *Claviramus* Fitzhugh, 2002, *Euchoneira* Licciano, Giangrande & Gambi, 2009, *Glomerula* Nielsen, 1931 *Potamilla* Malmgren, 1866, and *Terebrasabella* Fitzhugh & Rouse, 1999, amongst others (Nogueira *et al.*, 2010; Capa *et al.*, 2015). Moreover, *Sabellomma* and most members of *Megalomma* and *Parasabella* bear pinnular appendages associated with the dorsal lips, a feature that has also been reported in other sabellids, for example, *Anamobaea* Krøyer, 1856, *Bispira* Krøyer, 1856, *Branchiomma* Kölliker, 1858, *Potamilla* Malmgren, 1866, and *Pseudopotamilla* Buch, 1905 (Nogueira *et al.*, 2010; Capa *et al.*, 2015). The presence of a short thorax with fewer than the typical eight chaetigers has been considered as a characteristic of species of *Sabellomma* and some *Parasabella* (e.g.



Knight-Jones, 1983; Perkins, 1984; Nogueira *et al.*, 2010) but has also been reported in *Megalomma* (Knight-Jones, 1983; Tovar-Hernández & Carrera-Parra, 2011) and many other sabellids (e.g. Knight-Jones & Perkins, 1998; Nogueira & Knight-Jones, 2002; Fitzhugh, 2003; Nogueira, López & Rossi, 2004; Capa, Pons & Hutchings, 2013). Members of *Parasabella* and *Megalomma* have also been reported with more than eight thoracic chaetigers (Knight-Jones, 1983; Knight-Jones & Walker, 1985; Tovar-Hernández & Carrera-Parra, 2011). But if an anomalous number of thoracic segments is indeed a consequence of imperfect regeneration after damage or reproduction by scissiparity, (Knight-Jones & Bowden, 1984; Nogueira & Knight-Jones, 2002; Fitzhugh, 2003; Nogueira *et al.*, 2004; Capa, 2008), then intact specimens with the typical number of thoracic segments may also exist (even if not yet found) and thus this feature would not be diagnostic.

At least some species of each of the three genera bear radiolar eyes, but if considered absent in *P. microphthalma* (as in Nogueira *et al.*, 2010), their number and arrangement show large differences amongst members of the three genera. *Megalomma* is characterized by the presence of subdistal, sessile, and compound radiolar eyes, at least on the internal margin of the dorsal-most pair of radioles (Fitzhugh, 1989; Capa & Murray, 2009; Tovar-Hernández & Carrera-Parra, 2011), a synapomorphy for the genus. *Sabellomma* bears numerous, unpaired, randomly arranged eyespots along the outer margin of all radioles (Nogueira *et al.*, 2010), a synapomorphy for the genus. Finally, *Parasabella* lacks eyes, except for the newly described species *P. bioculata*, which has paired simple eyespots on both sides of the distal radiolar tips of most radioles.

Morphologically, *Sabellomma* and *Megalomma* share the shape of the companion chaetae, with a distal teardrop 'membrane', albeit very narrow in the herein-described *S. cupocolata*. By contrast, the mucro is at an angle in *Parasabella*, appearing as compressed laterally instead of flattened transversely. Some members of *Sabellomma* and *Megalomma* also have ventral sacs as a continuation of the ventral lips, whereas they have not been observed in *Parasabella*. The previously described three species of *Sabellomma* were characterized by the presence of inter-ramal eyespots, more conspicuous in the abdominal region (Nogueira *et al.*, 2010), but this is a feature that has also been reported from some *Megalomma* species (Capa & Murray, 2009; Tovar-Hernández & Carrera-Parra, 2011) and is lacking (or completely faded) from *S. cupocolata* sp. nov.

*Megalomma* and *Parasabella* resemble each other in the dentition of uncini as they generally have a large number of rows (over eight) with minute teeth all similar in size (Capa & Murray, 2009; Tovar-Hernández & Carrera-Parra, 2011; Figs 7K, L, 9J, 11H, 13I, 15H,

17E, F), whereas *Sabellomma* has both thoracic and abdominal uncini with fewer than eight rows and larger teeth (Nogueira *et al.*, 2010; Fig. 19H–J). No distinct morphological features are shared between *Parasabella* and *Sabellomma*.

#### SPECIES DELINEATION AND SPECIES DIAGNOSTIC FEATURES

Species delineation by morphological means in the genera *Parasabella* and *Sabellomma* is awkward owing to the high number of homoplasies in these taxa, as in many other sabellid genera (Capa, 2008; Capa *et al.*, 2010, 2013; Tovar-Hernández & Carrera-Parra, 2011) and other polychaetes (e.g. Glasby & Alvarez, 1999; Pleijel, 1999; Eklöf, Pleijel & Sundberg, 2007; Zanol, Fauchald & Paiva, 2007; Giere, Ebbe & Erséus, 2008). The colour pattern may be a good taxonomic tool for live specimens considering that also intraspecific variation has been observed in at least some *Parasabella* species. Additionally, colour is not so useful for distinguishing species after fixation because pigment fades or can be altered. The three *Sabellomma* species reported prior to the present work were characterized by the colour patterns (although intraspecific variation has also been reported, Nogueira *et al.*, 2010) and also the presence, number, and level of fusion of the pinnular appendages to dorsal lips.

Some features that have been used to differentiate amongst and identify the currently accepted 25 *Parasabella* species (excluding the two new ones described in the present study) are based on attributes that vary with growth, damage, or regeneration of specimens (i.e. overall size, relative length of radiolar crown compared with body length, number of pairs of radioles, shape of radiolar tips, number of thoracic chaetigers). Some others, such as the degree of spiralization of the radiolar crown and the length of dorsal radiolar appendages, seem inconsistent within species but not necessarily related to growth as lobes are ventrally curled inwards in some sexually mature species and not others (Knight-Jones, 1983; Perkins, 1984; Fitzhugh, 1989). Juveniles with longer dorsal radiolar appendages than adults have also been observed during this study. A high level of variation in the size of ventral shields and shape of the anterior margin of the first shield was recorded in the present study, indicating that contraction of muscles as a result of fixation may be involved.

After examination of a large number of specimens and the review of most descriptions available in the literature, we conclude that some of the more reliable features for distinguishing species are a combination of the number of vacuolated axial cells supporting radioles near the base, absence/presence and arrangement of radiolar eyes, degree of separation of ventral

shields from thoracic tori, shapes of inferior thoracic notochaetae, lengths of handles of thoracic and abdominal uncini, and number and size of teeth over the main fang in the uncini. All of these were used in the most recent taxonomic accounts prior to the present work, but not consistently (e.g. Knight-Jones, 1983; Perkins, 1984; Knight-Jones & Walker, 1985; Giangrande, 1994). In some cases, the pigmentation pattern, or the length of dorsal collar margins, may assist in splitting two species, but should be considered with caution.

Nevertheless, some of the recognized species from Australia show little or no morphological differences from other sympatric or even geographically distant congeners. This is the case for *P. crassichaetae* sp. nov. and *Parasabella* sp. 1. They were grouped as a single morphotype after preliminary sorting of the material but clearly derive from clearly distinguished lineages (Fig. 3A–C). Within one of these lineages, *Parasabella* sp. 1, the two specimens collected from Florida and Sydney Harbour show no genetic variability (Table 4), and those grouped under *P. crassichaetae* sp. nov. complex and collected from different localities in Australia and also from Hawaii did not differ much genetically (Table 4). Additionally, Australian specimens resembling previously reported species from Japan (e.g. *P. cf. aulacnota* and *P. cf. japonica*) or the Caribbean (*P. cf. rugosa*) have been given an existing name herein. These are to be confirmed but reflect the low probability of these species possessing such a wide and disjunct distribution by natural means. The four *Parasabella* species in which reproduction has been studied show distinct strategies. *Parasabella media*, *P. microphthalmia*, and *P. pallida* are simultaneous hermaphrodites whereas *P. polarsterni* is gonochoric. The former is a brooder that incubates larvae in a jelly mass associated with the radiolar crown, and the latter three are broadcast spawners (to be confirmed in *P. polarsterni*; Kerby, 1972; Banse, 1979; McEuen, Wu & Chia, 1983; Rouse & Fitzhugh, 1994; Gambi *et al.*, 2001; Pernet, 2003; Tovar-Hernández, Méndez & Villalobos-Guerrero, 2009). Natural dispersal capacity therefore varies amongst the different species, being limited in brooding species with larvae swimming for 1 day before settling (McEuen *et al.*, 1983; Pernet, 2003). Dispersal capacity is also unknown for the spawners because there is no published information on the development of larvae and settling times in *Parasabella*. Unintentional anthropogenic translocations out of the natural distribution range can also be taken into account to explain distant and disjunct distributions of species. There are records of species of *Parasabella* as fouling fauna associated with ship hulls (Tovar-Hernández *et al.*, 2009, M. Capa, pers. observ.) and planktonic larvae could also be transported in ships together with ballast water as reported in other sabellids (e.g. Çınar,

2013; Capa, van Moorsel & Tempelman, 2014). This is suspected in the cases of *Parasabella* sp. 1 and *P. crassichaetae* sp. nov.

The large amount of intraspecific genetic variation found in some cases, even considering the low number of individuals included in the present study, may indicate that there is, in some cases, population structure and potentially even some complex of sibling species. This is the case for *P. aberrans* (Fig. 3A–C, Tables 3, 4; variation well above 10%). Similar intraspecific variation has been found in other sabellids (Capa *et al.*, 2013) but this is unusual amongst polychaetes, in which intraspecific variation is generally below 6% (e.g. Barroso *et al.*, 2010; Capa *et al.*, 2010; Nygren, Eklöf & Pleije, 2010; Nygren & Pleijel, 2010). These results contrast with our original proposition that this species had possibly been translocated from Australia to New Zealand or vice versa. The species, widespread in both countries, usually occurs as single individuals on wharf piles (G. Read, pers. comm.; M. Capa, pers. observ.) and was reported in New Zealand Port surveys from 2005–2008 (Inglis *et al.*, 2005, 2006, 2008) and in similar surveys in Australia. However, it has also been collected from more pristine coastal and offshore environments such as Lizard Island in Queensland, Kangaroo Island in South Australia, and south of Jervis Bay, New South Wales (see Appendix). This paradox amongst morphological, distributional, and genetic data would be worth studying in detail. A genetic analysis of New Zealand specimens of *P. aberrans* would also be helpful.

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## REFERENCES

- Augener H. 1914.** Polychaeta Sedentaria. In: Michaelsen W, Hartmeyer R, eds. *Fauna Südwest-Australien*. Jena, 5(1): 1–700.
- Augener H. 1922.** Litorale Polychaeten von Juan Fernandez. In: Skottsberg C, ed. *The natural history of Juan Fernandez and Easter Island*, Vol. 3. 161–218.
- Augener H. 1924.** Über litorale polychäten von Westindien. *Sitzungsberichte der Gesellschaft der naturforschende Freunde zur Berlin* **1922**: 38–53.
- Augener H. 1926.** Papers from Dr. Th. Mortensen's Pacific Expedition 1914–16. XXXIV. Polychaeta III. Polychaeten von Neuseeland. II. Sedentaria. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i København* **81**: 157–294.
- Banse K. 1979.** Sabellidae (Polychaeta) principally from the northeast Pacific Ocean. *Journal of the Fisheries Research Board of Canada* **36**: 869–882.
- Barroso R, Klautau M, Solé-Cava AM, Paiva PC. 2010.** *Eurythoe complanata* (Polychaeta: Amphinomidae), the 'cosmopolitan' fireworm, consists of at least three cryptic species. *Marine Biology* **157**: 69–80.
- Berkeley E, Berkeley C. 1952.** Canadian Pacific Fauna. 9. Annelida. *Fisheries Research Board of Canada* **9b**: 1–139.
- Bush KJ. 1905.** Tubicolous annelids of the tribes Sabellides and Serpulides from the Pacific Ocean. *Harriman Alaska Expedition* **12**: 169–346.
- Buzhinskaja GN. 1985.** [Polychaeta of the shelf off south Sakhalin and their ecology]. *Akademia nauk Zoologicheskii Institut Issledovania fauna morei* **30**: 72–224. [in Russian]
- Capa M. 2008.** Phylogenetic relationships within *Bispira* Krøyer, 1856 and *Stylomma* Knight-Jones, 1997 (Polychaeta, Sabellidae) and description of new species from Australia. *Hydrobiologia* **596**: 301–327.
- Capa M, Murray A. 2009.** Review of the genus *Megalomma* (Sabellidae: Polychaeta) in Australia with description of three new species, new records and notes on certain features with phylogenetic implications. *Records of the Australian Museum* **61**: 201–224.
- Capa M, Bybee D, Bybee S. 2010.** Integrative taxonomy reveals cryptic species within *Sabellastarte* Krøyer, 1856 (Sabellidae: Annelida) and establishes the systematics of the genus. *Organisms Diversity and Evolution* **10**: 351–371.
- Capa M, Giangrande A, Nogueira JMM, Tovar-Hernández MA. 2015.** Sabellidae Latreille, 1825. In: Westheide W, Purschke G, eds. *Handbook of zoology online*. De Gruyter. Published online [http://www.degruyter.com/view/Zoology/bp\\_029147-6-62](http://www.degruyter.com/view/Zoology/bp_029147-6-62).
- Capa M, van Moorsel G, Tempelman D. 2014.** The Australian feather-duster worm *Laonome calida* Capa, 2007 (Annelida: Sabellidae) introduced into European inland waters? *BioInvasions* **3**: 1–11.
- Capa M, Pons J, Hutchings P. 2013.** Cryptic diversity, intraspecific phenetic plasticity and recent geographical translocations in *Branchiomma* (Sabellidae, Annelida). *Zoologica Scripta* **42**: 637–655.
- Chen CA, Chen CP, Fan TY, Yu JK, Hsieh HL. 2002.** Nucleotide sequences of ribosomal internal transcribed spacers and their utility in distinguishing closely related *Perinereis* polychaetes (Annelida; Polychaeta; Nereididae). *Marine Biotechnology* **4**: 17–29.
- Claparède E. 1870.** Les Annelides Chetopodes du Golfe de Naples. Seconde Partie. *Memoires de la Societe de Physique et d'Histoire Naturelle de Geneve* **20**: 1–225.
- Costa-Paiva EM, Paiva PC, Klautau M. 2007.** Anaesthetization and fixation effects on the morphology of sabellid polychaetes (Annelida: Polychaeta: Sabellidae). *Journal of the Marine Biological Association of the United Kingdom* **87**: 1127–1132.
- Çinar ME. 2013.** Alien polychaete species worldwide: current status and their impacts. *Journal of the Marine Biological Association of the United Kingdom* **93**: 1257–1278.
- Eklöf J, Pleijel F, Sundberg P. 2007.** Phylogeny of benthic Phyllodocidae (Polychaeta) based on morphological and molecular data. *Molecular Phylogenetics and Evolution* **45**: 261–271.
- Fauchald K. 1977.** The polychaete worms. Definitions and keys to the orders, families and genera. *Natural History Museum, Los Angeles Co. Science Series* **28**: 1–91.
- Fauvel P. 1936.** Annélides Polychètes du Japon. *Memoirs of the College of Science, Kyoto Imperial University, Series B* **12**: 41–92.
- Fitzhugh K. 1989.** A systematic revision of the Sabellidae–Caobangiidae–Sabellongidae complex (Annelida: Polychaeta). *Bulletin of the American Museum of Natural History* **192**: 1–104.
- Fitzhugh K. 2002.** Fan worm polychaetes (Sabellidae: Sabellinae) collected during the Thai-Danish BIOSHELF Project. *Phuket Marine Biological Center Special Publication* **24**: 353–424.
- Fitzhugh K. 2003.** A new species of *Megalomma* Johansson, 1927 (Polychaeta: Sabellidae: Sabellinae) from Taiwan, with comments on sabellid dorsal lip classification. *Zoological Studies* **42**: 106–134.
- Fitzhugh K, Rouse GW. 1999.** A remarkable new genus and species of fan worm (Polychaeta: Sabellidae: Sabellinae) associated with marine gastropodes. *Invertebrate Biology* **118**: 357–390.
- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R. 1994.** DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* **3**: 294–299.
- Fregin S, Haase M, Olsson U, Alström P. 2012.** Pitfalls in comparisons of genetic distances: a case study of the avian family Acrocephalidae. *Molecular Phylogenetics and Evolution* **62**: 319–328.
- Gambi MC, Patti FP, Micaletto G, Giangrande A. 2001.** Diversity of reproductive features in some Antarctic polynoid and sabellid polychaetes, with a description of *Demonax polarsterni* sp. n. (Polychaeta, Sabellidae). *Polar Biology* **24**: 883–891.
- Giangrande A. 1994.** The genus *Demonax* (Polychaeta, Sabellidae) in the Mediterranean Sea, with description of *D. tommasi* n. sp. *Bollettino di Zoologia* **61**: 229–233.
- Giere O, Ebbe B, Erséus C. 2008.** Questa (Annelida, Polychaeta, Orbiniidae) from Pacific regions – new species



- and reassessment of the genus *Periquesta*. *Organisms Diversity & Evolution* **7**: 304–319.
- Glasby CJ, Read GB, Lee KE, Blakemore RJ, Fraser PM, Pinder AM, Erséus C, Moser WE, Burreson EM, Govedich FR, Davies RW, Dawson EW. 2009.** Chapter 17, Phylum Annelida – bristle worms, earthworms, and leeches. *The New Zealand inventory of biodiversity. Volume 1. Kingdom Animalia – Radiata, Lophotrochozoa, and Deuterostomia*. Canterbury: Canterbury University Press, 312–358.
- Glasby CJ, Alvarez B. 1999.** Distribution pattern and biogeographic analysis of austral Polychaeta (Annelida). *Journal of Biogeography* **26**: 507–533.
- Grube AE. 1861.** Ein Ausflug nach Triest und dem Quarnero. Beiträge zur Kenntniss der Thierwelt dieses Gebietes. Nicolaische Verlagsbuchhandlung. Berlin.
- Grube AE. 1870.** Neue Arten der Gattung *Sabella*. *Schlesischen Gesellschaft für vaterländische cultur Breslau Jahresber* **48**: 67–68.
- Grube AE. 1878.** Annulata Semperiana. Beiträge zur Kenntniss der Annelidenfauna der Philippinen. *Memoires de L'Academie Imperiale. des Sciences de St. Petersburg Ser. 7* **25**: 1–300.
- Grube AE. 1881.** Beschreibungen von neuen Anneliden des zoologischen Museums zu Berlin. In: Peters W, ed. *Sitzungsberichte der Gesellschaft der naturforschende Freunde zur Berlin*. 19(7): 109–117.
- Hartman O. 1961.** Polychaetous annelids from California. *Allan Hancock Pacific Expeditions* **25**: 1–226.
- Hartman O. 1965.** Deep-water benthic polychaetous annelids of New England to Bermuda and other North Atlantic areas. *Allan Hancock Foundation Publications Occasional Paper* **28**: 1–378.
- Hoagland RA. 1919.** Polychaetous annelids from Porto Rico, the Florida Keys and Bermuda. *Bulletin of the American Museum of Natural History* **41**: 517–591.
- Hobson KD, Banse K. 1981.** Sedentariate and archiannelid polychaetes of British Columbia and Washington. *Canadian Bulletin of Fisheries and Aquatic Sciences* **209**: 1–144.
- Imajima M, Hartman O. 1964.** The polychaetous annelids of Japan. Part II. *Allan Hancock Foundation Ocational Paper* **26**: 1–452.
- Inglis G, Gust N, Fittridge I, Floerl O, Woods C, Hayden B, Fenwick G. 2005.** Baseline survey for non-indigenous marine species (Research Project ZBS2000–04). MAF Biosecurity New Zealand Technical Papers Nos: 2008/02, 2008/05, 2008/08, 2008/03, 2005/01, 2005/02, 2005/11, 2005/12, 2005/13. Prepared for MAFBNZ Post Border Directorate.
- Inglis G, Gust N, Fittridge I, Floerl O, Woods C, Hayden B, Fenwick G. 2006.** Baseline survey for non-indigenous marine species (Research Project ZBS2000–04). MAF Biosecurity New Zealand Technical Papers Nos: 2008/02, 2008/05, 2008/08, 2008/03, 2005/01, 2005/02, 2005/11, 2005/12, 2005/13. Prepared for MAFBNZ Post Border Directorate.
- Inglis G, Gust N, Fittridge I, Floerl O, Woods C, Hayden B, Fenwick G. 2008.** Baseline survey for non-indigenous marine species (Research Project ZBS2000–04). MAF Biosecurity New Zealand Technical Papers Nos: 2008/02, 2008/05, 2008/08, 2008/03, 2005/01, 2005/02, 2005/11, 2005/12, 2005/13. Prepared for MAFBNZ Post Border Directorate. Available at: <http://www.biosecurity.govt.nz/about-us/our-publications/technical-papers>
- Johansson KE. 1922.** On some new tubicolous annelids from Japan, the Bonin Islands and the Antarctic. *Arkiv för Zoologi* **15**: 1–11.
- Johansson KE. 1925.** Bemerkungen über die Kinberg'schen Arten der Familien Hermellidae und Sabellidae. *Arkiv for Zoologi* **18A**: 1–28.
- Johansson KE. 1927.** Beiträge zur Kenntniss der Polychaeten–Familien Hermellidae, Sabellidae und Serpulidae. *Zoologiska Bidrag fran Uppsala* **11**: 1–184.
- Katoh S. 2013.** MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* **30**: 772–780.
- Kerby CJ. 1972.** The biology of *Sabella microphthalmala* (Polychaeta). PhD Thesis, George Washington University.
- Kinberg JGH. 1867.** Annulata nova. *Öfversigt af Kongliga. Vetenskapsakademien Forhandlingar, Stockholm* **23**: 337–357.
- Kinberg JGH. 1910.** Konglia Svenska Fregatten Eugenies Resa Omkring jorden under befäl af C. A. Virgin aren 1851–1853. Vetenskapliga Iakttagelser pa H. Maj:t Konung Oscar den Forstes befallning utgifna af K. Svenska Vetenskapsakademien, Zoologi VII. Annulater.–Uppsala and Stockholm, Almqvist and Wicksells. pp. 33–78.
- Knight-Jones P. 1983.** Contributions to the taxonomy of Sabellidae (Polychaeta). *Zoological Journal of the Linnean Society* **79**: 245–295.
- Knight-Jones P, Bowden N. 1984.** Incubation and scissiparity in Sabellidae (Polychaeta). *Journal of the Marine Biological Association of the United Kingdom* **64**: 809–818.
- Knight-Jones P, Perkins TH. 1998.** A revision of *Sabella*, *Bispira* and *Stylomma* (Polychaeta: Sabellidae). *Zoological Journal of the Linnean Society* **123**: 385–467.
- Knight-Jones P, Walker AJM. 1985.** Two new species of *Demonax* (Sabellidae: Polychaeta) from Liverpool Bay. *Journal of Natural History* **19**: 605–612.
- Knight-Jones P, Knight-Jones EW, Ergen Z. 1991.** Sabelliform polychaetes, mostly from Turkey's Aegean coast. *Journal of Natural History* **25**: 837–858.
- Kölliker A. 1858.** Ueber Kopfkiemer mit Augen an den Kiemen (Branchiomma dalyelli). *Zeitschrift für wissenschaftliche Zoologie* **9**: 536–541.
- Krøyer H. 1856.** Meddelelser af en Afhandling Ormeslaegten *Sabella* Linn., isaer med Hensyn til dens nordiske Arter. *Oversigt over det Kongelige Danske videnskabernes selskabs forhandlingar* **1856**: 1–36.
- Licciano M, Giangrande A, Gambi MC. 2009.** A new genus of Sabellidae (Annelida, Polychaeta) from Antarctica, with discussion of relationships among plesiomorphic genera within Sabellinae. *Zootaxa* **2226**: 28–42.
- Loi T. 1980.** Catalogue of the types of polychaete species erected by J. Percy Moore. *Proceedings of the Academy of Natural Sciences of Philadelphia* **132**: 121–149.
- Malmgren AJ. 1866.** Nordiska Hafs-Annulater. *Öfversigt af Königlich etenskapsakademiens förhandlingar, Stockholm* **22**: 355–410.

- von Marenzeller E. 1884.** Südjapanische Anneliden. II. Amphareten, Terebellacea, Sabellacea, Serpulacea. *Denkschriften der Akademie der Wissenschaften, Wien* **49**: 28.
- McEuen FS, Wu BL, Chia F. 1983.** Reproduction and development of *Sabella media*, a polychaete with extratubular brooding. *Marine Biology* **76**: 301–309.
- Monro CCA. 1933.** The Polychaeta Sedentaria collected by Dr. C. Crossland at Colon in the Panama region and the Galapagos Islands during the expedition of the S. Y. St. George. *Proceedings of the Zoological Society of London* **103**: 1039–1092.
- Monro CCA. 1938.** On a small collection of Polychaeta from Swan River, Western Australia. *Annals and Magazine of Natural History* **112**: 614–624.
- Moore JP. 1904.** New Polychaeta from California. *Proceedings of the Academy of Natural Sciences of Philadelphia* **56**: 484–503.
- Moore JP. 1909.** Polychaetous annelids from Monterey Bay and San Diego, California. *Proceedings of the Academy of Natural Sciences of Philadelphia* **61**: 235–295.
- Moore JP. 1923.** The polychaetous annelids dredged by the U.S.S. 'Albatross' off the coast of southern California in 1904. IV. Spionidae to Sabellariidae. *Proceedings of the Academy of Natural Sciences of Philadelphia* **75**: 179–259.
- Moore JP, Bush KJ. 1904.** Sabellidae and Serpulidae from Japan, with descriptions of new species of *Spirorbis*. *Proceedings of the Academy of Natural Sciences of Philadelphia* **56**: 157–179.
- Nielsen KB. 1931.** Serpulidae from the Senonian and Danian deposits of Denmark. *Meddelelser fra Dansk naturhistorisk Forening i København* **8**: 71–113.
- Nogueira JMM, Knight-Jones P. 2002.** A new species of *Pseudobranchiomma* Jones (Polychaeta: Sabellidae) found amongst Brazilian coral, with a redescription of *P. punctata* (Treadwell, 1906) from Hawaii. *Journal of Natural History* **36**: 1661–1670.
- Nogueira JMM, Fitzhugh K, Silva-Rossi MCS. 2010.** A new genus and new species of fan worms (Polychaeta: Sabellidae) from Atlantic and Pacific Oceans – the formal treatment of taxon names as explanatory hypotheses. *Zootaxa* **2603**: 1–52.
- Nogueira JMM, López E, Rossi MCS. 2004.** *Kirkia heterobranchiata*, a new genus and species of extratubular brooding sabellid (Polychaeta: Sabellidae) from São Paulo, Brazil. *Journal of the Marine Biological Association of the United Kingdom* **84**: 701–710.
- Nygren A, Pleijel F. 2010.** From one to ten in a single stroke – resolving the European *Eumida sanguinea* (Phyllodocidae, Annelida) species complex. *Molecular Phylogenetics and Evolution* **58**: 132–141.
- Nygren A, Eklöf J, Pleije F. 2010.** Cryptic species of *Notophyllum* (Polychaeta: Phyllodocidae) in Scandinavian waters. *Organisms Diversity & Evolution* **10**: 193–204.
- Nylander JJA. 2004.** *MrAIC.pl*. Program distributed by the author. Uppsala: Evolutionary Biology Centre, Uppsala University.
- Okuda S. 1939.** Annelida Polychaeta in Onagawa Bay and its vicinity II. Polychaeta errantia with some addenda of Polychaeta sedentaria. *Reports, Tohoku Imperial University* **14**: 219–244.
- Perkins TH. 1984.** Revision of *Demonax* Kinberg, *Hypsicomus* Grube, and *Notaulax* Tauber, with a review of *Megalomma* Johansson from Florida (Polychaeta: Sabellidae). *Proceedings of the Biological Society of Washington* **97**: 285–368.
- Pernet B. 2003.** Persistent ancestral feeding structures in nonfeeding annelid larvae. *Biological Bulletin* **205**: 295–307.
- Pillai TG. 1961.** Annelida Polychaeta of Tambalagam Lake, Ceylon. *Ceylon Journal of Science (Biological Sciences)* **4**: 1–40.
- Pillai TG. 1965.** Annelida Polychaeta from the Philippines and Indonesia. *Ceylon Journal of Science (Biological Sciences)* **5**: 110–177.
- Pleijel F. 1999.** Phylogenetic taxonomy, a farewell to species, and a revision of *Heteropodarke* (Hesionidae, Polychaete, Annelida). *Systematic Biology* **48**: 755–789.
- de Quatrefages A. 1866.** Histoire naturelle des Annelés marins et d'eau douce. Annelides et Géphyriens, Vol. 2. Première partie. 1–336. Deuxième Partie. 337–794.
- Read G. 2010.** *Parasabella* Bush, 1905. In: Read G, Fauchald K, eds. *World Polychaeta database*. Available through World Register of Marine Species at: <http://www.marinespecies.org/aphia.php?p=taxdetails&id=325958>
- Rouse GW, Fitzhugh K. 1994.** Broadcasting fables: is external fertilization really primitive? Sex, size, and larvae in sabellid polychaetes. *Zoologica Scripta* **23**: 271–312.
- Sarkar IN, Planet PJ, DeSalle R. 2008.** CAOS software for use in character-based DNA barcoding. *Molecular Ecology Resources* **8**: 1256–1259.
- Stamatakis A. 2006.** RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics (Oxford, England)* **22**: 2688–2690.
- Tamura K, Stecher G, Peterson D, Filipowski A, Kumar S. 2013.** MEGA6: molecular evolutionary genetics analysis version 6.0. *Molecular Biology and Evolution* **30**: 2725–2729.
- Thomson J. 1860.** *Essai d'une classification de la famille des cérambycides et matériaux pour servir à une monographie de cette famille*. Paris.
- Tovar-Hernández MA, Carrera-Parra LF. 2011.** *Megalomma* Johansson, 1925 (Polychaeta: Sabellidae) from America and other world-wide localities, and phylogenetic relationships within the genus. *Zootaxa* **2861**: 1–71.
- Tovar-Hernández MA, Harris LH. 2010.** *Parasabella* Bush, 1905, replacement name for the polychaete genus *Demonax* Kinberg, 1867 (Annelida: Polychaeta: Sabellidae). *ZooKeys* **60**: 13–19.
- Tovar-Hernández MA, Salazar-Vallejo SI. 2006.** Sabellids (Polychaeta: Sabellidae) from the Grand Caribbean. *Zoological Studies* **45**: 24–66.
- Tovar-Hernández MA, Méndez N, Villalobos-Guerrero TF. 2009.** Fouling polychaete worms from the southern Gulf of California: Sabellidae and Serpulidae. *Systematics and Biodiversity* **7**: 319–336.
- Treadwell AL. 1941.** Polychaetous annelids from the New England region, Porto Rico and Brazil. *American Museum Novitates* **1138**: 1–4.
- Uchida H. 1968.** Polychaetous annelids from Shakoten (Hokkaido). *Journal of Faculty of Science Hokkaido University Series VI. Zoology* **16**: 595–612.

**Verrill AE. 1873.** Report upon the invertebrate animals of Vineyard Sound and the adjacent waters, with an account of the physical characters of the region. Report of the United States Commission for Fisheries, 1871–1872: 295–778.

**Zanol J, Fauchald K, Paiva PC. 2007.** A phylogenetic analysis of the genus *Eunice* (Eunicidae, polychaete, Annelida). *Zoological Journal of the Linnean Society* **150**: 413–434.

## APPENDIX

### MATERIAL EXAMINED

Notes: Throughout the Appendix, where collection depth is known for specimens, it is indicated in metres (m); CSIRO–CRIMP is Commonwealth Scientific and Industrial Research Organisation–Centre for Research on Introduced Marine Pests.

#### PARASABELLA ABERRANS SPP. COMPLEX

Western Australia. NTM W02419 (one), Bunbury, Stn BY–2, coll. 2.ii.1983; AM W.37031–37032 (two in 95% ethanol = DX 07–08), CReefs Ningaloo Expedition 2010, Ningaloo Reef, 22°37'S, 113°38'30"E, 15.v.2010, 6.4 m, coarse coral rubble; AM W.47000 (one), CReefs Ningaloo Expedition 2009, MI WA 1038, 22°37'25"S, 113°38'28"E, 20.v.2009, 7 m, coarse coral rubble. Northern Territory. AM W.46996 (one), Darwin Harbour, North Shell Island, 12°29'48"S, 130°53'12"E, coral rubble, 5–8 m, vii.1993, NT 346. Queensland. AM W.197045 (one), Lizard Island, 14°40'S, 145°27'E, St C06–15–2, iv.1977, identified by P. Knight-Jones as “*Sabella*” aberrans?; NTM W023122 (two), Lizard Island patch reef near lagoon entrance, 14°41'20"S, 145°28'12"E, Stn CGLI–018, 2 m, 1.iv.2008. New South Wales. AM W.32586 (one, in 95% ethanol = PS26), east of Coffs Harbour, Park Beach Bommie, 30°17'42"S, 153°12'E, grey sponge, 12.7 m, 3.v.2005, NSW 2825; AM W.36950 (seven), southern headland of Fingal Bay, Port Stephens, 32°45'01"S, 152°10'25"E, red encrusting algae from rock platform, intertidal, 27.v.1998, NSW 1391; AM W.36957 (one), north-west side of Little Island, east of Port Stephens entrance, 32°42'07"S, 152°14'16"E, brown massive sponge, 21.6 m, 30.v.1998, NSW 1441; AM W.36937 (one), Queens Wharf, Newcastle, 32°55'48"S, 151°46'48"E, pylon scraping, 3 m, 28.viii.1997, CSIRO–CRIMP collection from New South Wales (NSW) Port Surveys, as ‘*Sabella* spNTLC’, Stn AUNTLQWP3–3; AM W.36953 (one), West Basin Berth 3, Newcastle, 32°55'12"S, 151°46'12"E, scraping from wharf piles at 7 m, 25.viii.1997, CSIRO–CRIMP collections from NSW Port Surveys as ‘*Sabellidae* spNTLF’; AM W.36954 (one), West Basin Berth 3, Newcastle, 32°55'12"S, 151°46'12"E, scraping from wharf piles at 7 m, 25.viii.1997, CSIRO–CRIMP collections from NSW Port Surveys as ‘*Sabellidae* spNTLAC’; AM W.36939 (one), east of Malabar, 1 km south of ocean outfall, 33°59'00"S,

151°17'33"E, 79.4 m, 20.vi.1996, Environmental Protection Authority – Malabar Deep Ocean Outfall Study (DOO); AM W.36940 (one), outer end of Kurnell Pier, Botany Bay, 34°00'12"S, 151°12'30"E, pylon scraping, 3 m, 21.x.1998, NSW Fisheries for CSIRO–CRIMP, St BB P1–3; AM W.36955 (one), outer end of Kurnell Pier, Botany Bay, 34°00'12"S, 151°12'30"E, pylon scraping, 3 m, 21.x.1998, NSW Fisheries for CSIRO–CRIMP NSW Ports Survey, as ‘*Sabellidae* spBTB’; AM W.32018 (one on SEM pin), Brotherson Dock Berth 1/1A, Botany Bay, 33°58'18"S, 151°12'24"E, pylon/piling scraping, 3 m, 19.x.1998, NSW Fisheries for CSIRO–CRIMP Ports Survey; AM W.46707 (one in 95% ethanol), Botany Bay, east of Inscription Point, 34°11'01"S, 151°13'23"E, 12 m, from tube of *Sabella* sp., 6.iii.2012; AM W.37050–37052 (eight, including PS29–31), north-east of Kurnell, ‘Anchor Reef’, 34°00'33"S, 151°13'5"E, 17.8 m, rock epifauna, 16.iii.2009 MI NSW 3423; AM W.36854 (one), Port Kembla outer harbour, 34°28'15"S, 150°54'06"E, 16.v.2000, NSW Fisheries; AM W.36956 (one), north end of No. 4 Jetty, Port Kembla Outer Harbour, 34°28'15"S, 150°54'06"E, scraping from pylon, 0.5 m, NSW Fisheries for CSIRO–CRIMP collection from NSW Port Surveys, as ‘*Sabellidae* spPKL’; AM W.47003 (one), north-east end of Martin Island, off Port Kembla, 34°29'43"S, 150°56'28"E, from rock surface, 21 m, 12.v.2012, MI NSW 4142; AM W.23058 (one), east of Bass Point, 34°36'S, 150°54'E, 25–50 m, 01.ii.1990, The Ecology Lab; AM W.36941 (one), 400 m south of southern entrance to Jervis Bay, 35°07'S, 150°46'E, 23 m, 22.vii.1972; AM W.36951 (one), Murrays Beach, Jervis Bay, 35°07'30"S, 150°45'30"E, 23.i.1973; AM W.46675 (two), north of Ulladulla, east of Bendalong and Red Point, 35°15'00"S, 150°32'46"E, *Ecklonia* holdfasts, 17 m, 11.v.2013, MI NSW 4195a; AM W.46703 (one), east of Ulladulla, south-east of Sullivans Reef, Home Bommie, 35°21'39"S, 150°29'36"E, red algae (*Curdiea* sp.), 22.5 m, 14.v.2013, MI NSW 4222; AM W.46704 (one), east of Bannister Head, Ulladulla, 35°19'29"S, 150°29'15"E, from red hydroids and black gorgonia under rock ledge, 17 m, 10.v.2013, MI NSW 4171; AM W.36935 (three, including one on two SEM stubs), 500 m south of Tathra Head, 36°43'44"S, 149°49'46"E, *Ecklonia* holdfast, 17 m, 16.v.1995; AM W.36936 (one), north side of Burrawarra Point, south of Batemans Bay, 35°49'48"S, 150°14'01"E, 17 m, from hydroid (*Gymnangium* sp.) and red algae, 23.iii.2004, NSW 2491; AM W.36855 (two), south-west side of Grasshopper Island, north-east of Point Upright, 35°38'01"S, 150°19'51"E, from alga *Peyssonnelia novaehollandiae*, 13 m, coll. 10.ii.2003; AM W.36933 (one), Eden, 37°04'S, 149°55'E, scraping, CSIRO–CRIMP collection from NSW Port Surveys, as ‘*Sabellastarte* sp. D’, Stn NSWELBQ1; AM W.36934 (one), Eden, Snug Cove, Wharf A, 37°04'S, 149°55'E, 6.xi.1996, scraping from pylon, 7 m, CSIRO–CRIMP collection from NSW Port Surveys, as ‘*Sabellastarte*



sp. D', Stn NSWEWHA P1–7; AM W.36942 (one), Eden, Snug Cove, Wharf A, 37°04'S, 149°55'E, 6.xi.1996, scraping from pylon, 3 m, CSIRO–CRIMP collection from NSW Port Surveys, as 'Sabellastarte sp. D', Stn NSWEWHA P2–3; AM W.36943 (one), Eden, Harris–Daishowa woodchip berth, 37°06'S, 149°55'48"E, 4.xi.1996, scraping from pylon, 3 m, CSIRO–CRIMP collection from NSW Port Surveys, as 'Sabellastarte sp. C', Stn NSWEWB P1–3; AM W.36944 (two), Eden, Snug Cove, 37°04'12"S, 149°54'E, 5.xi.1996, scraping from pylon, 0 m, CSIRO–CRIMP collection from NSW Port Surveys, as 'Sabellastarte sp. C', Stn NSWESCC P1–0; AM W.32017 (one), Eden, Harris–Daishowa woodchip berth, 37°06'S, 149°55'48"E, scraping from pylon, 4.xi.1996, CSIRO–CRIMP collection from NSW Port Surveys, as 'Sabellastarte sp. D', Stn AUQDNWBP1–7; AM W.36430 (one photographed, and put on SEM stub), Eden, Snug Cove, 37°04'12"S, 149°54'E, 5.xi.1996, scraping from wharf piles, 3 m, CSIRO–CRIMP collection from NSW Port Surveys, as 'Sabellastarte sp. C', Stn AUQDNSCCP1–3; AM W.36947 (two), Munganno Point, Twofold Bay, 37°06'12"S, 149°55'42"E, 9 m, brown sponges and ascidians on subtidal wharf pile, 19.xii.1985, Site M8; AM W.36948 (two), Munganno Point, Twofold Bay, 37°06'12"S, 149°55'42"E, 9 m, kelp holdfasts on subtidal rock platform, 19.xii.1985, Site M11; AM W.36945 (one), Munganno Point, Twofold Bay 37°06'12"S, 149°55'42"E, from sponges and bryozoan colonies on wharf pile, 12 m, 27.vi.1985, Site M9; AM W.36946 (two, including one on SEM stub), Murrumbulga Point, Twofold Bay, 37°04'42"S, 149°53'06"E, 25.vi.1985, 0.7 m, subtidal cryptic fauna, under rocks and *Diopatra* tubes, Site Q6; AM W.36949 (one), Munganno Point, Twofold Bay, 37°06'12"S, 149°55'42"E, 12 m, tunicate and sponges, 27.vi.1985, Site M10. South Australia. AM W.36952 (nine), Old Wharf, Muston Point, American River, Kangaroo Island, 35°47'12"S, 137°46'24"E, 5 m, clumps of sponges, 2.iii.1979; SAM TE 14513 (two), Port Hughes jetty, Yorke Peninsula, 34°04'30.5"S, 137°32'36.4"E, 5–8 m, sand and *Posidonia* seagrass, 18.iii.1994.

*PARASABELLA* SP. CF *PARASABELLA AULACONOTA*

Western Australia. Outer Bunbury Harbour, 33°18'50"S, 115°38'14"E, 3 m, iii.1993, AM W.22017 (four, one on SEM). Northern Territory. AM W.37026–37027 (two), AM W.46999 (three), Darwin Harbour, Tipperary Waters, 12°27'S, 130°51'E, 30.viii.2010. Queensland. AM W.41879–41880 (> 100), Townsville, Ross Creek Harbour, from fouling panels at jetty, 19°15'30.48"S, 146°49'32.32"E, coll. R. Smith, 1983–1985; AM W.37058 (one in 95% ethanol = PS 38), Heron Island, First Point, 23°25'57"S, 151°56'02"E, 20 m, coral rubble, 12.xi.2009, CReefs Heron Island Expedition 2009, MI QLD 2094. New South Wales. AM W.47182 (one), north-west side

of Little Island, east of Port Stephens entrance, 32°42'07"S, 152°14'16"E, brown massive sponge, 21.6 m, 30.v.1998, NSW 1441; AM W.32009 (one), Queens Wharf, Newcastle, 32°56'S, 151°47'E, scraping from wharf pile at surface, 28.viii.1997, CSIRO–CRIMP collections from NSW Port Surveys; AM W.32015 (one), West Basin Berth 3, Newcastle, 32°55'12"S, 151°46'12"E, scraping from wharf piles at 7 m, 25.viii.1997, CSIRO–CRIMP collections from NSW Port Surveys as 'Sabellidae spNTLF'; AM W.36938 (two), Newcastle, Queens Wharf, 32°56'S, 151°47'E, pylon/piling scraping, 3 m, 28.viii.1997, CSIRO–CRIMP collections from NSW Port Surveys; AM W.47005 (one) and AM W.47007 (one), Newcastle, Dyke Berth 4, 32°55'12"S, 151°46'12"E, amongst barnacles, 0 m, 27.viii.1997, CSIRO–CRIMP collections from NSW Port Surveys; AM W.47006 (three), Newcastle, Stockton Bridge, 32°53'S, 151°47'E, scraping, 7 m, 31.viii.1997, CSIRO–CRIMP collections from NSW Port Surveys; AM W.47009 (two), Newcastle, 32°56'S, 151°46'E, pylon scraping, 0.5 m, 31.viii.1997, CSIRO–CRIMP collections from NSW Port Surveys; AM W.47010 (two), Newcastle, West Basin Berth 2, 32°55'S, 151°46'E, pylon scraping, 3 m, 25.viii.1997, CSIRO–CRIMP collections from NSW Port Surveys; AM W.27826 (one), Port Jackson, Balls Head Bay north, 33°50'34"S, 151°11'31"E, scrapings from wooden piles, 3 m, 24.iv.2001, Sydney Ports Survey; AM W.27827 (five), Port Jackson, Blackwattle Bay, 33°52'31"S, 151°11'14"E, scrapings from wooden piles, 3 m, 18.iv.2001, Sydney Ports Survey; AM W.27828 (13), Port Jackson, Blackwattle Bay, 33°52'31"S, 151°11'14"E, scrapings from wooden piles, 6 m, 18.iv.2001, Sydney Ports Survey; AM W.27833 (three), Port Jackson, Glebe Island east, 33°51'59"S, 151°11'11"E, scrapings from cement facing, 3 m, 18.iv.2001, Sydney Ports Survey; AM W.27834 (one), Port Jackson, Glebe Island west, 33°52'04"S, 151°10'44"E, scrapings from wooden piles, 0.5 m, 17.iv.2001, Sydney Ports Survey; AM W.27836 (four), Port Jackson, White Bay east, 33°51'40"S, 151°11'25"E, scrapings from cement facing, 0.5 m, 18.iv.2001, Sydney Ports Survey; AM W.47143 (seven), Berrys Bay slipway, Port Jackson, 33°51'48"S, 151°11'48"E, scraped from hull of tugboat 'Ben Shortridge', 29.ii.1972, coll. P. Hutchings; AM W.22480 (eight, one on SEM stub), Rozelle Bay, Port Jackson, 33°52'24"S, 151°10'30"E, iii.1986, 6 m, fine mud; AM W.28866 (one), Pymont, Port Jackson, 33°51'51"S, 151°11'42"E, iv.2003, inside air-conditioning cooling pipe (saltwater intake); AM W.47008 (one), Botany Bay, 33°58'12"S, 151°12'42"E, pylon/piling scraping, 0.5 m, 20.x.1998, NSW Fisheries collections from Port Surveys; AM W.37043 (two, in 95% ethanol = PS01), Jolong Reef, approximately 700 m north-east of Cape Banks, 33°59'48"S, 151°15'14"E, coll. 21.vii.2009, 20.5 m, sediment on rock, MI NSW 3642; AM W.35612 (one in 95% ethanol, photographed live), same locality and date, from sponges,

22.5 m, MI NSW 3645; AM W.37045 (one in 95% ethanol = PS22), north-east of Kurnell, 'Anchor Reef', 34°00'33"S, 151°13'51"E, encrusting coralline algae with epibionts, 17.8 m, 16.iii.2009, MI NSW 3423; AM W.47004 (one), Port Kembla, north-west of Bass Island, 34°27'57"S, 150°56'22"E, brown algae, 20.5 m, 22.v.2014, MI NSW4298; AM W.32011 (one), No. 2 (Old) Coal Berth, Port Kembla Inner Harbour, 34°27'36"S, 150°53'42"E, pylon/piling scraping, 0.5 m, 9.v.2000, NSW Fisheries collections from Port Surveys; AM W.32013 (one) north end of No. 4 Jetty, Port Kembla Outer Harbour, 34°28'15"S, 150°54'06"E, pylon/piling scraping, 0.5 m, 16.v.2000, NSW Fisheries collections from Port Surveys; AM W.32014 (17), north end of No. 4 Jetty, Port Kembla Outer Harbour, 34°28'15"S, 150°54'06"E, pylon/piling scraping, 7 m, 16.v.2000, NSW Fisheries collections from Port Surveys; AM W.32016 (11), Grain Berth, Port Kembla Inner Harbour, 34°27'15"S, 150°53'36"E, pylon/piling scraping, 0.5 m, 8.v.2000, NSW Fisheries collections from Port Surveys; AM W.46676 (one in 95% ethanol), Port Kembla, north-east of Martin Island, 34°29'47"S, 150°56'11"E, algae *Ecklonia radiata* holdfasts, 14 m, MI NSW 4115.

**PARASABELLA BIOCULATA SP. NOV.**

*Additional material examined:* Australia. Western Australia: AM W.46997 (one), Ningaloo Reef, north of Tantabiddi, lagoon off Jurabi Point, patch reef, 21°51'41"S, 113°59'46"E, reef rock with brown algae, 3.5 m, vi.2008. New South Wales: AM W.46840 (one), Port Stephens, Nelson Bay, 32°42'56"S, 152°08'58"E, soft coral, 11.3 m, ii.2011. Timor-Leste. AM W.46835 (one), east of Atauro Island, Inner Reef, reef slope, 8°14'30"S, 125°36'49"E, dead coral rubble and algae, 14 m, ix.2012.

**PARASABELLA CRASSICHAETAE SP. NOV. COMPLEX**

*Additional material examined:* Australia. Western Australia. NMV F.108905 (one), north-east end of Vancouver Peninsula, off Albany, 35°03'24"S, 117°56'12"E, red algae, 10 m, 8.iv.1984; NMV F.108906 (three), western end of Lucky Bay, near Esperance, 33°59'S, 122°14'E, sponges, red and coralline algae, 12.iv.1984; NMV F.108908 (three), north end of Little Beach, Two Peoples Bay, 34°58'24"S, 118°11'42"E, tufted algae, 5–12 m, 5.iv.1984; AM W.47148 (five), Ningaloo Reef, 22°37'25"S, 113°38'28"E, coarse coral rubble, 7 m, 20.v.2009, CReefs Ningaloo 2009 Expedition, WA 1038; AM W.47150 (many), AM W.36447 (two on SEM pins), Ningaloo Reef, 22°45'19"S, 113°42'40"E, sponge and bryozoan, 17 m, 19.v.2009, CReefs Ningaloo 2009 Expedition, WA 1035; AM W.47144 (three), Dampier Archipelago, west of Angel Island, 20°29'03"S, 116°47'50"E, dead coral, 6 m, 25.vii.2000, WA 619; AM W.47149 (six),

Dampier Archipelago, Enderby Island, 2 km west of Rocky Head, 20°37'06"S, 116°26'43"E, dead coral, 14 m, 3.viii.2000, WA 637; AM W.21996 (two), outer Bunbury Harbour, 33°18'25"S, 115°38'35"E, 10.1 m, 27.iii.1993. Northern Territory. AM W.32579 (one = PS16), Darwin, East Point Reef, 12°27'S, 130°50'E, intertidal, 17.ix.2005; AM W.36298 (one on SEM stub), Darwin Harbour, West Point, 12°26'14"S, 130°46'E, coral rubble, sponges, and algae, 6–8 m, 17.vii.1993, NT 324; AM W.47147 (one), Darwin Harbour, Weed Reef, 12°30'S, 130°48'E, coral rubble, 4 m, 6.vii.1993, NT 348. Queensland. AM W.47151 (one), Weipa, Evans Landing Wharf, 12°40'S, 141°57'E, x.1999, scraping from wharf piles, 'P1014', CRIMP QLD Ports Survey; AM W.47177 (one), Weipa, Evans Landing Wharf, 12°40'S, 141°57'E, x.1999, benthic grab, 'P973', CRIMP QLD Ports Survey; AM W.36448 (one, plus one on SEM pin), Weipa, Humbug Point Wharf, 12°40'S, 141°57'E, x.1999, 'P862', CRIMP QLD Ports Survey; AM W.47152 (one), Weipa, Lorim Point Wharf, 12°40'S, 141°57'E, x.1999, scraping from wharf piles, 'P962', CRIMP QLD Ports Survey; AM W.47178 (one), Weipa, Evans Landing Wharf, 12°40'S, 141°57'E, x.1999, 'P1020', CRIMP QLD Ports Survey; AM W.47179 (five), Cairns, Wharf 12, 16°52'S, 145°49'E, 20.xi.2001, 'P3207', CRIMP QLD Ports Survey; AM W.47180 (one), Cairns, Wharf 1, 16°52'S, 145°49'E, 18.xi.2001, shrimp trap, 'P3024', CRIMP QLD Ports Survey. New South Wales. W25992 (one), South Ledge, Cook Island, 28°11'39"S, 153°34'38"E, colonial ascidian, 9.vi.1993; W25993 (three), South Ledge, Cook Island, 28°11'39"S, 153°34'38"E, frilly bryozoan, 9.vi.1993; W25984 (one), Byron Bay, 100 m north-west of Julian Rocks, 28°36'48"S, 153°37'48"E, rock with finger sponge, 03.iii.1992; W25985 (one), Byron Bay, 100 m north-west of Julian Rocks, 28°36'48"S, 153°37'48"E, shelly sand amongst turf on top of rocks, 4.iii.1992; W25986 (one), 100 m north-west of Split Solitary Island, 30°14'S, 153°10'48"E, encrusting algae and ascidians, 7.iii.1992; W25987 (one), 100 m north-west of Split Solitary Island, 30°14'S, 153 10'48"E, brown algae, 7.iii.1992; W25990 (one), Solitary Islands, 200 m north of Korffs Islet, 30°18'54"S, 153°09'18"E, mixed sponges, 22.vi.1992; W25991 (one), Solitary Islands, 100 m north of Korffs (Pig) Islet, 30°19'S, 153°09'18"E, *Ecklonia* holdfasts, 26.vi.1992; W25988 (one), Coff's Harbour, Coff's Harbour Jetty, 30°18'24"S, 153°08'30"E, orange sponge on jetty pilings, 9.iii.1992; W25989 (one), Coff's Harbour, Coff's Harbour Jetty, 30°18'24"S, 153°08'30"E, finger sponge on jetty pilings, 9.iii.1992; AM W.32572 (one) Port Stephens, Nelson Bay marina, 32°42'58"S, 152°09'00"E, 14.iii.2006, brown algae, 0.1 m, NSW 3058; AM W.47181 (ten), south of Point Stephens Lighthouse, 32°45'02"S, 152°11'35"E, from small brown cup sponge, 16 m, 31.v.1998, NSW 1492; AM W.27830–32 (nine), Port Jackson, Garden Island, 33°51'48"S, 151°13'44"E, scrapings from jetty piles, 0.5–5 m, 21.v.2001, Sydney

Ports Survey; AM W.37037 (one = PS13), Port Jackson, White Bay Berth 3, 33°51'47"S, 151°11'00"E, scrapings from wharf piles, 11.8 m, 5.iii.2009, MI NSW 3399; AM W.27835 (one) Port Jackson, White Bay, 33°51'40"S, 151°11'25"E, scrapings from wooden piles, 7 m, 18.iv.2001, Sydney Ports Survey; AM W.47184 (one), Port Jackson, Glebe Island east, 33°51'59"S, 151°11'11"E, scrapings from cement facing, 3 m, 18.iv.2001, Sydney Ports Survey; AM W.37044 (four in 95% ethanol, one of which = PS21), north-east of Kurnell, 'Anchor Reef', 34°00'33"S, 151°13'51"E, rock scrapings, 17.8 m, 16.iii.2009, MI NSW 3423; AM W.37049 (one in 95% ethanol = PS28), Jolong Reef, approximately 700 m north-east of Cape Banks, 33°59'48"S, 151°15'14"E, from sediment on rock, 20.5 m, 21.vii.2009, MI NSW 3642; AM W.37046 (one in 95% ethanol = PS23), same locality and date, sponges, 22.5 m, MI NSW 3645; AM W.37047 (one in 95% ethanol = PS24), from same sample, MI NSW 3645; AM W.46708 (two in 95% ethanol), Botany Bay, east of Inscription Point, 34°11'01"S, 151°13'23"E, tube of *Sabella spallanzanii* on rock, 12 m, 6.iii.2012, MI NSW 4093; AM W.43270 (> five in 95% ethanol), Botany Bay, off Inscription Point, 34°00'08"S, 151°13'30"E, scraping from rock, 11 m, 28.v.2013, MI NSW 4152; AM W.37028 (one = PS03), Shellharbour, north-east of Bass Point, 'The Humps', 34°35'35"S, 150°54'22"E, from orange sponge, 22.4 m, 4.v.2010, MI NSW 3956; W25994 (one), east side of Plantation Point, Jervis Bay, 35°04'30"S, 150°41'36"E, foliose coralline algae on rock platform, high intertidal, 27.vi.1981, NSW 41; AM W.47185 (one), north of Batemans Bay, north-west side of Brush Island, 35°31'39"S, 150°24'58"E, from *Caulerpa* algae, 12–14 m, 9.ii.2003, NSW 2031; AM W.31103 (two, one on SEM stub), west side of Wasp Island, north of Batemans Bay, 35°40'02"S, 150°18'29"E, from alga *Peyssonelia novae-hollandiae*, 16 m, 10.ii.2003, NSW 2047; AM W.31102 (three), south of Batemans Bay, north of Burrewarra Point, east wall, 35°50'01"S, 150°14'10"E, from alga *Peyssonelia novae-hollandiae*, 25 m, 25.x.2002, NSW 1985.

USA. Hawaii. AM W.37034 (one = PS10), AM W.37035 (one = PS11), AM W.37036 (one = PS12), AM W.47183 (five), Oahu, Coconut Island, 21°25'48"N, 157°57'43"W, 0.5 m, intertidal epifauna, 4.xi.2008.

*PARASABELLA* SP. CF. *PARASABELLA* *JAPONICA*

Western Australia, AM W.46994 (three), Kimberley region, sandy cay on Port George IV, 15°22'26"S, 124°39'50"E, dredged, coral rubble, 1–10 m, vii.1988; AM W.36451 (one), Ningaloo Reef, 22°40'16"S, 113°38'33"E, coarse coral rubble and tubes in sediment, 4.6 m, 19.v.2009, CReefs Ningaloo 2009 Expedition, MI WA 1031. Northern Territory. AM W.36450 (one on SEM stub), Darwin Harbour, West Point, 12°26'14"S,

130°46'E, coral rubble, sponges and algal washings, 6–8 m, vii.1993; AM W.46998 (one), Darwin Harbour, off Nightcliff, Old Man's Rock, 12°28'30"S, 130°54'12"E, coral rubble, sponges and hydroids, 5–7 m, vii.1993. Queensland. AM W.46993 (one), Heron Island, channel, 23°27'15"S, 151°55'E, coral rubble, 30 m, xi.2009; AM W.37063 (one), Heron Island, First Point, 23°25'56"S, 151°56'02"E, coral rubble, 13 m, xi.2009; AM W.37039 (one), Heron Island, canyons, 23°27'21"S, 151°55'02"E, coral rubble, 10 m, xi.2009; AM W.37038 (one), Heron Island, Harrys canyons, 23°28'23"S, 151°57'02"E, coral rubble, 15 m, xi.2009; AM W.37062 (one), Heron Island, Sykes Reef, 23°25'56"S, 152°02'02"E, coral rubble, 15 m, xi.2009; AM W.46995 (one), Lizard Island, lagoon, 14°41'14"S, 145°27'18"E, coral rubble, 1 m, viii.2010. New South Wales. AM W.37042 (one), Jolong Reef, north-east of Cape Banks, 33°59'48"S, 151°15'14"E, sediment on rock, 21 m, vii.2009; AM W.31101 (one photographed, then on SEM), north of Burrewarra Point, eastern wall, 35°50'01"S, 150°14'10"E, from algae, 25 m, 25.x.2002, NSW 1985; AM W.46989 (two), north of Burrewarra Point, in gutters, 35°50'01"S, 150°14'10"E, from algae, 24 m, 27.x.2002, NSW 1992; AM W.46988 (one), AM W.46991 (one), off Burrewarra Point, in gutters, somewhat inshore, 35°49'52"S, 150°14'17"E, from algae, 23 m, 27.x.2002, NSW 1992. Tasmania. SAM TE 14511 (one), Port Davey, Bathurst Channel off Joan Point, 43°20'30"S, 146°05'E, steep rock slope, 5–21 m (WEB Stn 5), 5.iv.1993, coll. W. Zeidler, K. L. Gowlett–Holmes, F. A. Bauerdam. South Australia. AM W.14042 (one), Kangaroo Island, 35°47'08"S, 137°46'31"E, 1976.

*PARASABELLA* SP. CF. *PARASABELLA* *RUGOSA*

*Material examined:* Victoria. NMV F.108884 (one), Port Phillip Bay, 38°16'18"S, 144°41'30"E, fine sand with shell, 6 m, 3.iv.1963, identified by T. H. Perkins in 1992 as *Demonax* sp.; AM W.36431 (two, one on SEM stub), Port Phillip Bay, 38°16'18"S, 144°41'30"E, fine sand with shell, 6 m, 3.iv.1963, identified by T. H. Perkins as *Demonax* sp. in 1992.

*SABELLOMMA* *CUPOCULATA* SP. NOV.

*Additional material examined:* Australia. Western Australia: AM W.47189 (two), south-west tip of West Lewis Island, 20°36'15"S, 116°35'43"E, gravel, 10 m, 27.vii.2000, WA 623; AM W.47190 (one), Dampier Archipelago, Legendre Island, 1 km north-east of Cape Legendre, 20°21'16"S, 116°50'34"E, under small boulders, 27 m, 6.viii.2000, WA 644. Northern Territory: AM W.47188 (one), Darwin Harbour, North Shell Island, 12°29'48"S, 130°53'12"E, sponges and algae in coral rubble, 5–8 m, 16.vii.1993, NT 346. Queensland: AM W.30495 (one), Torres Strait, Prince of Wales Island, bommies north-west of Bamfield Point, 10°41'08"S, 142°06'02"E, live



coral, 3 m, 3.x.2006, QLD 1927; MAGNT W23104 (five, one on SEM pin = AM W.39545.001), Lizard Island, off North Head, 14°38'44"S, 145°27'12"E, 12 m, 14.iv.2008, CReefs Stn CGLI-025; AM W.37061 (one = PS 41), Lizard Island, MacGillivray Reef, 14°39'23"S, 145°29'31"E, coral rubble, 22 m, 29.viii.2010, MI QLD 2197, CReefs Stn LI10-028; AM W.37029-37030 (two, one = PS 06), Lizard Island, High Rock, 14°49'34"S,

145°33'08"E, coral rubble, 20.1 m, 11.ix.2010, MI QLD 2233, CReefs Stn LI10-134; AM W.37057 (one = PS 37), MacGillivray Reef, deep reef slope, 14°39'25"S, 145°28'22"E, coral rubble, 30 m, 4.ix.2010, CReefs Stn LI10-073; AM W.37060 (one = PS 40), Heron Island, Sykes reef, 23°25'57"S, 151°02'02"E, coarse coral rubble, 30 m, 14.xi.2009, MI QLD 2073, CReefs.